RESEARCH ARTICLE

Measuring competitive impact: Joint-species modelling of invaded plant communities

Andrew O'Reilly-Nugent[1] [iD] | Elizabeth M. Wandrag[1,2] [iD] | Jane A. Catford[3,4,5] [iD] |
Bernd Gruber[1] [iD] | Don Driscoll[6] [iD] | Richard P. Duncan[1] [iD]

[1]Institute for Applied Ecology, University of Canberra, Canberra, Australia; [2]School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia; [3]Department of Geography, King's College London, London, UK; [4]School of BioSciences, The University of Melbourne, Melbourne, VIC, Australia; [5]Fenner School of Environment & Society, Australian National University, Canberra, ACT, Australia and [6]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University Geelong, Burwood, VIC, Australia

Correspondence
Andrew O'Reilly-Nugent
Email: andrew.oreilly-nugent@canberra.edu.au

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 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 simultaneously modelling how species respond to environmental variation and to changes in community composition. We describe a JSDM to model variation in plant cover and show how this can be applied to compositional data to detect dominant competitors that cause other species to decline in abundance.

3. We applied the model to an experiment in an invaded grassy-woodland community in Australia where we manipulated biomass removal (through slashing and fencing to prevent grazing by kangaroos) along a fertility gradient. Non-native species dominated plant cover at high fertility sites in the absence of biomass removal. Results from the JSDM identified three of the 72 non-native plant species (*Bromus diandrus*, *Acetosella vulgaris* and especially *Avena fatua*) as 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 non-native grasses *Bromus diandrus* and *Avena fatua* were among the tallest species in the community and had the greatest impact on shorter-statured species, most likely through competition for light under conditions of high fertility and low grazing.

4. *Synthesis*. We demonstrate a method to measure competitive impact using a joint-species distribution model, which allowed us to identify the species driving compositional change through competitive displacement, and where on the landscape

wileyonlinelibrary.com/journal/jec
449

competitive impacts were 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.

KEYWORDS

grasslands, grazing, impact, invasive species, joint-species distribution model (JSDM), light competition, nutrient addition, tobit regression

1 | 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). 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).

Joint-species distribution models (JSDM) are extensions of standard species distribution models that have the potential to measure both competitive impact and species responses to environmental conditions using community composition data from sites along known environmental gradients (Kissling et al., 2012; Nieto-Lugilde, Maguire, Blois, Williams, & Fitzpatrick, 2018). JSDMs use data on species composition across multiple sites to jointly model individual species responses to environmental variation, interpreting residual among-species covariation as potentially resulting from interactions such as competition (Latimer, Banerjee, Sang, Mosher, & Silander, 2009; Ovaskainen, Hottola, & Shtonen, 2010; Pollock et al., 2014; Warton et al., 2015). To date, JSDMs have mostly been used to model presence–absence data, where large negative residual covariance between two species could be interpreted as the competitive displacement of one species from sites that both could occupy. However, presence–absence data can only detect competitive impacts that result in complete exclusion

from a site, yet dominance without exclusion is an important component of species impact (Levine et al., 2003; Seabloom et al., 2013). Here, we use a method proposed by Clark, Nemergut, Seyednasrollah, Turner, and Zhang (2017) to model cover data in a JSDM that overcomes the problem of zero inflation that is typically inherent in these data (see: Joint-species tobit modelling in Materials and Methods; Figure 1). With this approach, we can detect declines in species abundance associated with the presence of competitors, which should provide greater resolution in quantifying competitive impacts.

Even with these improvements to JSDMs, separating environmental responses from competitive impacts is challenging (Adler
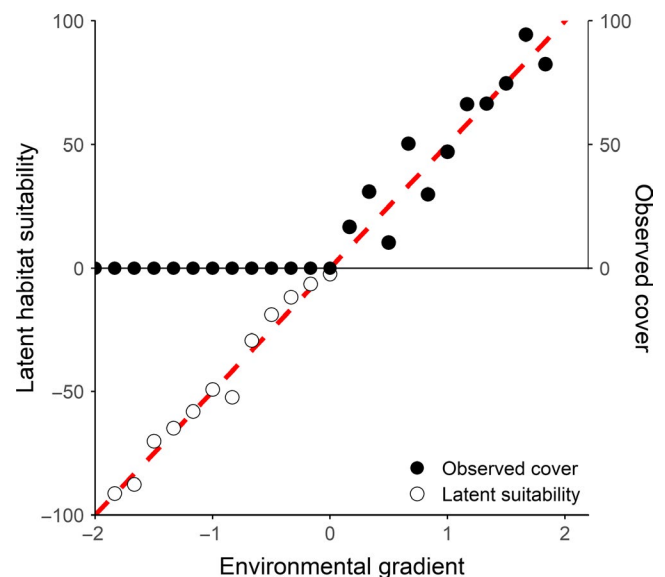

FIGURE 1 A simulated example of tobit regression. Black circles show observed cover for a species measured at points along an environmental gradient. Cover declines as environmental suitability decreases, eventually reaching a point where the environment is unsuitable for the species and cover is zero. 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

et al., 2018), suggesting we should apply JSDMs to systems where the primary environmental drivers of species abundances are well understood (Giannini, Chapman, Saraiva, Alves-dos-Santos, & Biesmeijer, 2013; Wisz et al., 2013; Zurell, Pollock, & Thuiller, 2018). In grasslands around the world, non-native plant species often increase in dominance at higher fertility sites and when grazing is excluded (Seabloom et al., 2015). This shift in dominance has been attributed to the competitive displacement of native species by non-native species that are competitively superior under conditions of high resource availability and low grazing. This competitive superiority arises because, relative to native species, many non-native grassland species have traits associated with rapid growth and high biomass (Ordonez, Wright, & Olff, 2010; Van Kleunen, Weber, & Fischer, 2010), traits that are likely beneficial when there is little aboveground disturbance and competition for light is intense (Borer et al., 2014; Hautier, Niklaus, & Hector, 2009). These trait differences between native and non-native species should be less important under herbivory where biomass removal may reduce any competitive advantage of fast growth (Lind et al., 2013).

We aim to test these ideas using data from a 7-year experiment that tracked changes in plant cover over time following herbivore exclusion (Driscoll, 2017). Sites were arrayed along a fertility gradient and we predicted that non-native species would dominate under high fertility and would increase in dominance following herbivore exclusion. We used JSDMs 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 (a) 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 (b) 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.

2 | MATERIALS AND METHODS

2.1 | 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/h[1]; 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 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 (Bureau of Meteorology, 2017). Soils are typically of relatively low fertility, shallow and rocky, although some deeper soils occur on slopes and in depressions.

2.2 | Data collection

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

Vegetation surveys were conducted every year from 2010 to 2016, except for 2014. In late spring (October) of each year, the per cent cover of all vascular plant species was visually estimated in four 1 m × 1 m quadrats placed in the corners of each plot (only three quadrats per plot were surveyed in 2013 due to time constraints). We use plant cover as a proxy for abundance. Our dataset thus comprised 6 years of vegetation cover data from 160 quadrats across 40 plots. In total, we had 920 quadrat level vegetation measurements, comprising 10,780 cover estimates for 142 species (70 native and 72 non-natives; see Appendix S1, Figure S2 for more detail). In 2015 and 2016, we measured the traits of abundant species, defined as those comprising the first 80% of total 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). These traits included canopy height (m), maximum height (m), canopy width (m), leaf length and width (cm) and specific leaf area (mm[2]/mg; SLA). To avoid the influence of outliers, we used 90th 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 2,420 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 S1), 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; Figure S3). We obtained data on total rainfall for the 4 months prior to each survey (August–November) from the Australian Bureau of Meteorology (BOM, Appendix S1) as a proxy for water availability. Total rainfall during these 4 months ranged from 185 to 414 mm over the 7 years of the study. Both total nitrogen and spring rainfall were centred and scaled prior to model fitting.

2.3 | Analyses

2.3.1 | Relative dominance of non-native species

We examined how the dominance of non-native species changed over time, in relation to soil fertility and rainfall, 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 by 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 S2.

2.3.2 | Joint-species tobit modelling

To test whether dominance by non-native species was a consequence of environmental responses or competitive displacement, we specified a JSDM that modelled the cover of each species in response to variation in soil fertility, rainfall and experimental treatment (JSDM1). This model included a single covariance matrix to capture unexplained residual variation, with negative residual covariances potentially indicating competitive impacts. We fitted a second model (JSDM2) to test whether competitive impacts varied with grazing and slashing treatments. JSDM2 had the same structure as JSDM1, but we fitted separate residual covariance matrices for each experimental treatment, which allowed us to test whether the magnitude of negative residual covariances was greater in the absence of biomass removal where light competition should be most intense. We analysed data for the years 2013–2016, which were the years during which the experimental treatments showed clear effects (see: Figure 2 and Figure 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; Figure 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 (Figure 1). Quadrats where
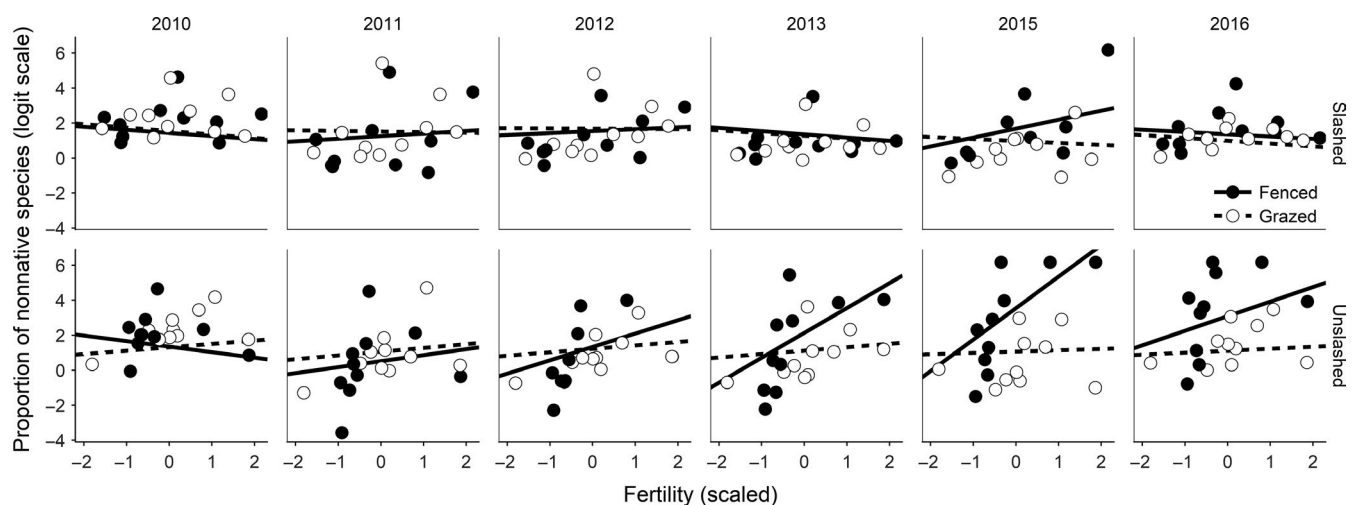

FIGURE 2 Proportional cover of non-native species (logit-transformed) as a function of soil fertility at 10 sites measured over 7 years (2010–2016 with no measurement in 2014). There were four treatments at each site, which are plotted separately. Slashed plots are shown on the top line and unslashed 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 S1

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 is as follows:

JSDM 1

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

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

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

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

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

where $\boldsymbol{y}^*_{[ijkl]}$ 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 ($s = 1 \ldots N$) 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. $\boldsymbol{\Sigma}$ is an $N \times N$ covariance matrix with the diagonal containing the residual variances in suitability for each species, σ^2, and the off-diagonals containing the residual covariances between each species pair, conditional on the value of $\boldsymbol{\mu}_{[ijkl]}$. 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 caused 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.

2.3.3 | Change in species covariances by treatment

Specifying a single covariance matrix in JSDM1 meant the covariances were estimated from the data in all treatments. In JSDM2, we specified a separate covariance matrix for each of the four treatments:

JSDM2

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

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

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 JSDM2 allowed us to evaluate whether competitive interactions were stronger in plots without slashing or grazing.

2.3.4 | 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 JSDM2 against the absolute difference in measured trait values for each species pair. Trait values were normalized 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.
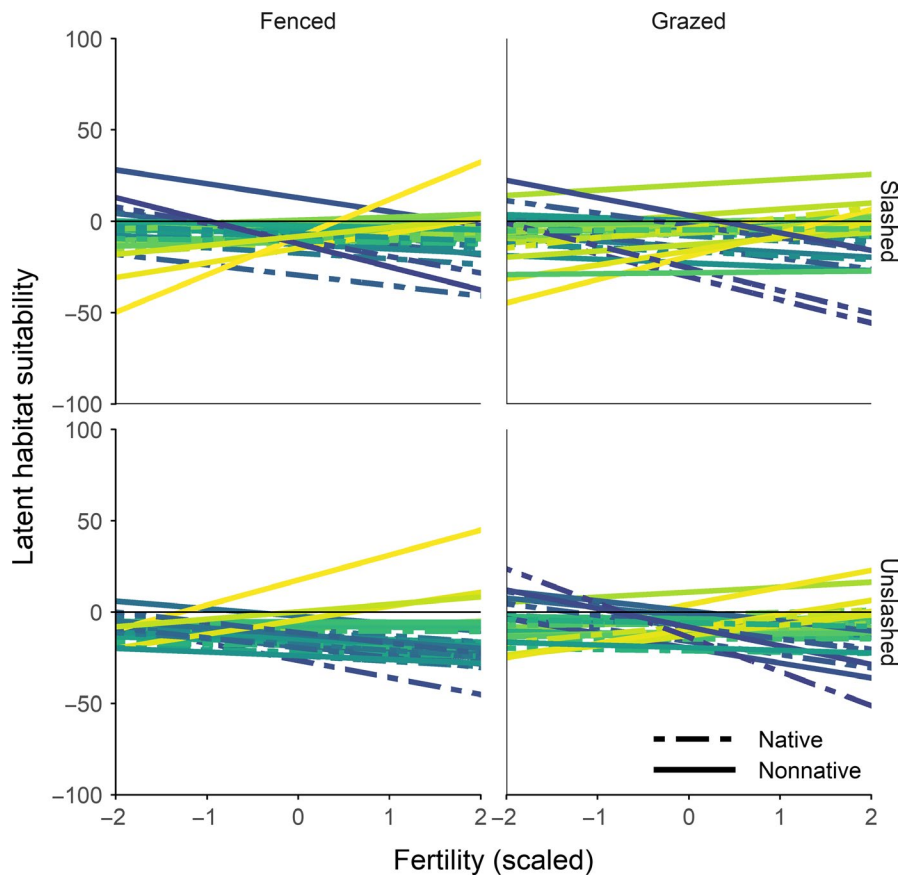
FIGURE 3 Latent suitability with respect to soil fertility for 30 species estimated using a joint-species distribution model and tobit regression (see text). Separate relationships were fitted for each species in each of four treatments, shown as different panels. Native species are drawn with dashed 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

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 S2 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 S2), meaning that strong residual covariances required strong support from the data.

3 | RESULTS

3.1 | Relative dominance of non-native species

Overall, the proportion of total cover that comprised non-native species increased with increasing soil fertility (Figure 2, Figure S4a). Prior to and immediately after fencing (2010 and 2011), the relationship between fertility and proportion of non-native cover was similar in the fenced and grazed, 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 (Figure 2, Figure S4b). The proportion of

non-native cover was higher in years with higher spring rainfall (Figure S3a).

3.2 | Joint-species tobit modelling

Species responded differently to changes in soil fertility, with latent site suitability increasing strongly with higher soil fertility (i.e. total extractable nitrogen) for two native and five non-native species (95% credible intervals above zero in at least one treatment; Figure 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 (Figure S3b).

Figure 4 shows the species' residual covariances from JSDM1 as a pairwise covariance matrix (Figure 4a) along with the median covariance for each species across all pairwise interactions (Figure 4b). 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
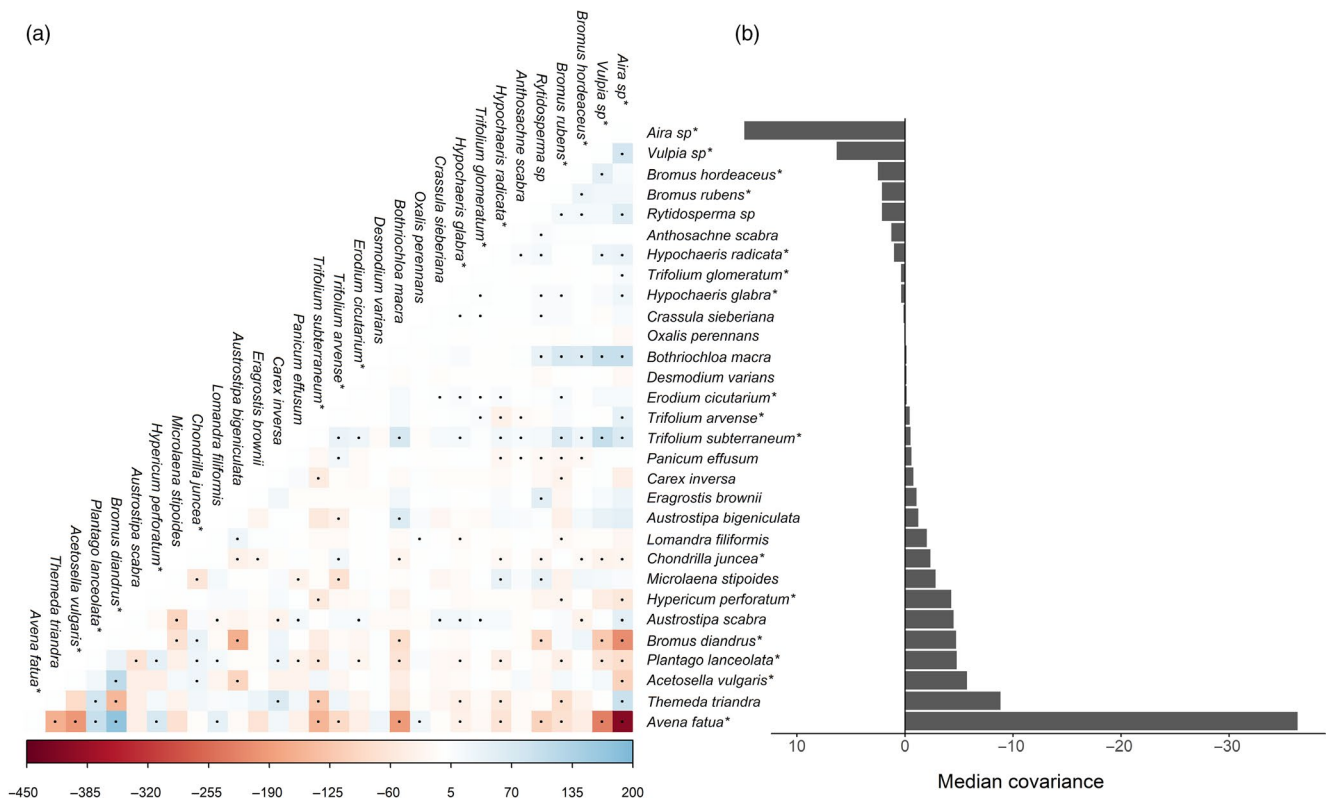
(a)

(b)

FIGURE 4 (a) The full residual covariance matrix for joint-species distribution model 1 (JSDM1) and (b) the median residual covariance from all pairwise interactions for each species, with negative covariances 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

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* (Figure 4a), such that high cover of *A. fatua* was associated with low cover *T. triandra* and vice versa. Small-statured species, such as those in the genera *Aira*, *Vulpia* and *Hypochaeris*, tended to covary positively.

3.3 | Change in species covariances by treatment

JSDM2 revealed that species' residual covariances varied by grazing and slashing treatment (Figure 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* (Figure 5). This implies these species had a greater competitive impact on other species in the absence of biomass removal.

3.4 | Predicting impact from functional traits

In the fenced, unslashed treatment, stronger negative covariances between species were associated with greater differences in plant height (Figure 6). This relationship was evident, though weaker, in the grazed, unslashed treatment but largely absent in both slashed treatments. Covariances were less negative between species that had greater differences in SLA in all treatments, but the strength of this relationship was much weaker than for height. None of the remaining trait differences (canopy width and leaf dimensions) showed strong relationships with covariances.

4 | 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 JSDM 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, along with the conditions under which 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 of native species after accounting for differences in environmental responses. This outcome is consistent with previous studies that have measured the impact of non-native species in Australian temperate grasslands (Driscoll & Strong, 2017; Prober, Thiele, Lunt, & Koen, 2005) and in grasslands globally (Chang & Smith, 2014; Flores-Moreno et al., 2016; Harpole et al., 2016).
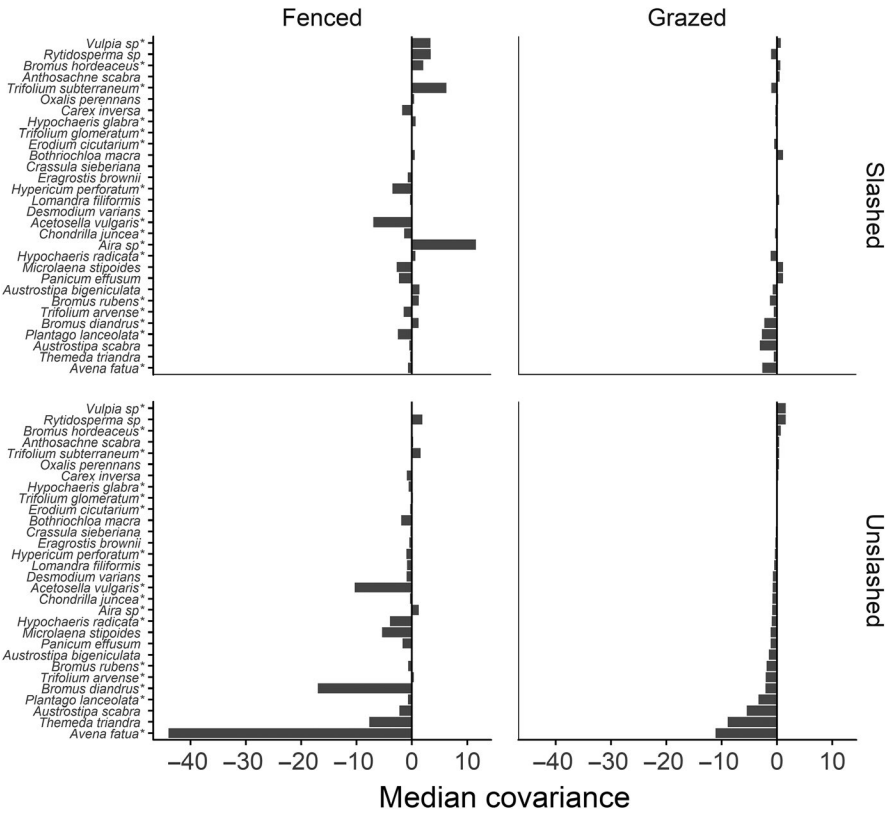

FIGURE 5 The median residual covariance from all pairwise interactions for each species from joint-species distribution model 2 (JSDM2), where a separate covariance matrix was fitted for each treatment (shown as separate panels). The median covariance summarizes the magnitude of competitive displacement 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
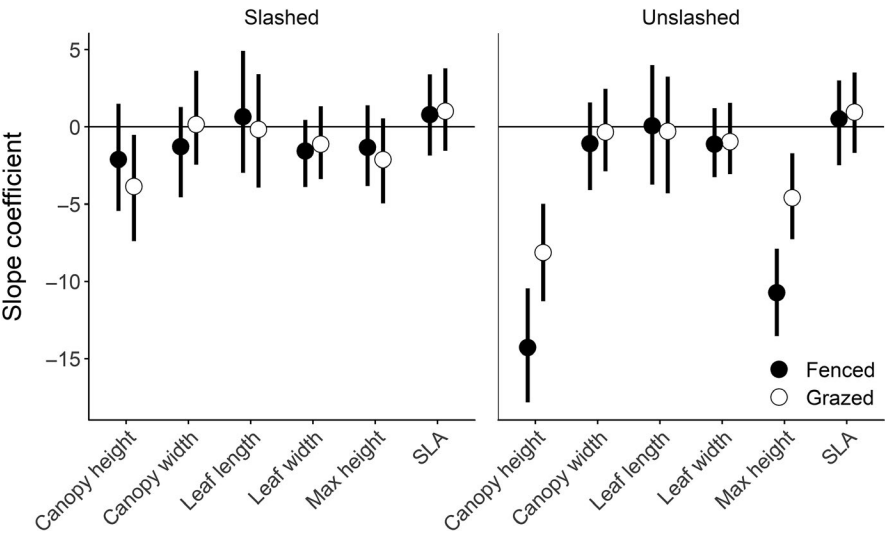

FIGURE 6 Mean (circles) and 95% credible intervals for the slope of the relationship between covariance and trait differences among species. Negative values indicate that competitive displacement is associated with greater difference in trait values between species. The relationships are plotted separately 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

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 (Figure 5). Second, under low or no biomass removal, the strength of negative covariances was 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 (Figure 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 (Figure 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 (Figure 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 (Figure 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* (Figure 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 (Figure 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 emphasize that interpreting negative residual covariation as due to species interactions relies on having measured and correctly modelled the major environmental variables, fertility and rainfall in our case, that control 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 environmental variation. Nevertheless, the model appeared successful in identifying species having impact in the unmanipulated treatment alone (grazed, unslashed; Figure 5), suggesting JSDMs can detect interactions in systems without experimental manipulation where the environmental drivers are well understood.

5 | CONCLUSIONS

Quantifying the importance of competitive interactions is difficult when species abundance is confounded with environmental variation (Adler et al., 2018). We approached the problem using a JSDM to model changes in the cover of Australian temperate grassland species in response to gradients of fertility and rainfall, biomass removal treatments and variation in community composition. This identified the dominant non-native species driving compositional change through competitive displacement in this community, highlighting the utility of JSDMs in studies of plant invasion where it is often unclear which non-native species, if any, are directly impacting invaded communities (HilleRisLambers et al., 2010; Lai et al., 2015; MacDougall & Turkington, 2005). By experimentally altering grazing, we were able to show that the competitive impact of the dominant non-native species increased in the absence of grazing and that species responses were mediated by trait differences in height, consistent with the outcome we would expect due to competition for light (Borer et al., 2014). Hence, the modelling approach provided insights into the mechanisms underlying impact, paving the way for general tests of the drivers of community structure in other communities (Mortensen et al., 2018). We have provided the data and code in an R package (https://github.com/aornugent/impact2) to reproduce our analyses and encourage further application of the approach.

AUTHORS' CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

ORCID

Andrew O'Reilly-Nugent https://orcid.org/0000-0003-2071-6279

Elizabeth M. Wandrag https://orcid.org/0000-0001-8140-539X

Jane A. Catford https://orcid.org/0000-0003-0582-5960

Bernd Gruber https://orcid.org/0000-0003-0078-8179

Don Driscoll https://orcid.org/0000-0002-1560-5235

Richard P. Duncan https://orcid.org/0000-0003-2295-449X

REFERENCES

Adler, P. B., Kleinhesselink, A., Hooker, G., Taylor, J. B., Teller, B., & Ellner, S. P. (2018). Weak interspecific interactions in a sagebrush steppe? Conflicting evidence from observations and experiments. *Ecology*, *99*(7), 1621–1632. https://doi.org/10.1002/ecy.2363

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., ... Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*(7497), 517–520. https://doi.org/10.1038/nature13144

Bureau of Meteorology (2017). Daily rainfall. Retrieved from http://www.bom.gov.au/climate/data/

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., ... Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*(1), https://doi.org/10.18637/jss.v076.i01

Chang, C. C., & Smith, M. D. (2014). Resource availability modulates above- and below-ground competitive interactions between genotypes of a dominant C4 grass. *Functional Ecology*, *28*(4), 1041–1051. https://doi.org/10.1111/1365-2435.12227

Clark, J. S., Nemergut, D., Seyednasrollah, B., Turner, P. J., & Zhang, S. (2017). Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. *Ecological Monographs*, *87*(1), 34–56. https://doi.org/10.1002/ecm.1241

Driscoll, D. A. (2017). Disturbance maintains native and exotic plant species richness in invaded grassy woodlands. *Journal of Vegetation Science*, *28*(3), 573–584. https://doi.org/10.1111/jvs.12513

Driscoll, D. A., & Strong, C. (2017). Covariation of soil nutrients drives occurrence of exotic and native plant species. *Journal of Applied Ecology*, *55*(2), 777–785. https://doi.org/10.1111/1365-2664.12984

Evju, M., Austrheim, G., Halvorsen, R., & Mysterud, A. (2009). Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. *Oecologia*, *161*(1), 77–85. https://doi.org/10.1007/s00442-009-1358-1

Fan, J., & Harris, W. (1996). Effects of soil fertility level and cutting frequency on interference among *Hieracium pilosella*, *H. praealtum*, *Rumex acetosella*, and Festuca novae-zelandiae. *New Zealand Journal of Agricultural Research*, *39*(1), 1–32. https://doi.org/10.1080/00288233.1996.9513159

Flores-Moreno, H., Reich, P. B., Lind, E. M., Sullivan, L. L., Seabloom, E. W., Yahdjian, L., ... Borer, E. T. (2016). Climate modifies response of non-native and native species richness to nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1694), 20150273. https://doi.org/10.1098/rstb.2015.0273

Gallien, L., Münkemüller, T., Albert, C. H., Boulangeat, I., & Thuiller, W. (2010). Predicting potential distributions of invasive species: Where to go from here? *Diversity and Distributions*, *16*(3), 331–342. https://doi.org/10.1111/j.1472-4642.2010.00652.x

Giannini, T. C., Chapman, D. S., Saraiva, A. M., Alves-dos-Santos, I., & Biesmeijer, J. C. (2013). Improving species distribution models using biotic interactions: A case study of parasites, pollinators and plants. *Ecography*, *36*(6), 649–656. https://doi.org/10.1111/j.1600-0587.2012.07191.x

Godsoe, W., Franklin, J., & Blanchet, F. G. (2017). Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. *Ecology and Evolution*, *7*(2), 654–664. https://doi.org/10.1002/ece3.2657

Gross, N., Börger, L., Duncan, R. P., & Hulme, P. E. (2013). Functional differences between alien and native species: Do biotic interactions determine the functional structure of highly invaded grasslands? *Functional Ecology*, *27*(5), 1262–1272. https://doi.org/10.1111/1365-2435.12120

Guo, J., Lee, D., Sakrejda, K., Gabry, J., Goodrich, B., De Guzman, J., ...Fletcher, J. (2016). rstan: R Interface to Stan. *R Package Version*, *2*, 0–3.

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., ... Wragg, P. D. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, *537*(7618), 93–96. https://doi.org/10.1038/nature19324

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*(5927), 636–638. https://doi.org/10.1126/science.1169640

HilleRisLambers, J., Yelenik, S. G., Colman, B. P., & Levine, J. M. (2010). California annual grass invaders: The drivers or passengers of change? *Journal of Ecology*, *98*(5), 1147–1156. https://doi.org/10.1111/j.1365-2745.2010.01706.x

Hui, F. K. C., Taskinen, S., Pledger, S., Foster, S. D., & Warton, D. I. (2015). Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution*, *6*(4), 399–411. https://doi.org/10.1111/2041-210X.12236

Kissling, W. D., Dormann, C. F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G. J., ... O'Hara, R. B. (2012). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, *39*(12), 2163–2178. https://doi.org/10.1111/j.1365-2699.2011.02663.x

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*(4), 336–346. https://doi.org/10.1111/ele.12414

Latimer, A. M., Banerjee, S., Sang, H., Mosher, E. S., & Silander, J. A. (2009). Hierarchical models facilitate spatial analysis of large data sets: A case study on invasive plant species in the northeastern United States. *Ecology Letters*, *12*(2), 144–154. https://doi.org/10.1111/j.1461-0248.2008.01270.x

Leishman, M. R., & Thomson, V. P. (2005). Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney. *Australia. Journal of Ecology*, *93*(1), 38–49. https://doi.org/10.1111/j.1365-2745.2004.00938.x

Levine, J. M., Vilà, M., Antonio, C. M. D., Dukes, J. S., Grigulis, K., & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London. Series B:*

Biological Sciences, *270*(1517), 775–781. https://doi.org/10.1098/rspb.2003.2327

Lind, E. M., Borer, E., Seabloom, E., Adler, P., Bakker, J. D., Blumenthal, D. M., … Wragg, P. D. (2013). Life-history constraints in grassland plant species: A growth-defence trade-off is the norm. *Ecology Letters*, *16*(4), 513–521. https://doi.org/10.1111/ele.12078

MacDougall, A. S., Gilbert, B., & Levine, J. M. (2009). Plant invasions and the niche. *Journal of Ecology*, *97*(4), 609–615. https://doi.org/10.1111/j.1365-2745.2009.01514.x

MacDougall, A. S., & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, *86*(1), 42–55. https://doi.org/10.1890/04-0669

Morgan, J. W., Dwyer, J. M., Price, J. N., Prober, S. M., Power, S. A., Firn, J., … Camac, J. S. (2016). Species origin affects the rate of response to inter-annual growing season precipitation and nutrient addition in four Australian native grasslands. *Journal of Vegetation Science*, *27*(6), 1164–1176. https://doi.org/10.1111/jvs.12450

Mortensen, B., Danielson, B., Harpole, W. S., Alberti, J., Arnillas, C. A., Biederman, L., … Seabloom, E. W. (2018). Herbivores safeguard plant diversity by reducing variability in dominance. *Journal of Ecology*, *106*(1), 101–112. https://doi.org/10.1111/1365-2745.12821

Nieto-Lugilde, D., Maguire, K. C., Blois, J. L., Williams, J. W., & Fitzpatrick, M. C. (2018). Multiresponse algorithms for community-level modelling: Review of theory, applications, and comparison to species distribution models. *Methods in Ecology and Evolution*, *9*(4), 834–848. https://doi.org/10.1111/2041-210X.12936

Ordonez, A., Wright, I. J., & Olff, H. (2010). Functional differences between native and alien species: A global-scale comparison. *Functional Ecology*, *24*(6), 1353–1361. https://doi.org/10.1111/j.1365-2435.2010.01739.x

Ovaskainen, O., Hottola, J., & Shtonen, J. (2010). Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology*, *91*(9), 2514–2521. https://doi.org/10.1890/10-0173.1

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167. https://doi.org/10.1071/BT12225

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., … McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*(5), 397–406. https://doi.org/10.1111/2041-210X.12180

Prober, S. M., & Lunt, I. D. (2009). Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. *Biological Invasions*, *11*(2), 171–181. https://doi.org/10.1007/s10530-008-9222-5

Prober, S. M., Thiele, K. R., Lunt, I. D., & Koen, T. B. (2005). Restoring ecological function in temperate grassy woodlands: Manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. *Journal of Applied Ecology*, *42*(6), 1073–1085. https://doi.org/10.1111/j.1365-2664.2005.01095.x

Prober, S. M., Thiele, K. R., & Speijers, J. (2013). Management legacies shape decadal-scale responses of plant diversity to experimental disturbance regimes in fragmented grassy woodlands. *Journal of Applied Ecology*, *50*(2), 376–386. https://doi.org/10.1111/1365-2664.12036

Prober, S. M., Thiele, K. R., & Speijers, J. (2016). Competing drivers lead to non-linear native–exotic relationships in endangered temperate grassy woodlands. *Biological Invasions*, *18*(10), 3001–3014. https://doi.org/10.1007/s10530-016-1194-2

Pysek, P., Jarosik, V., Hulme, P. E., Kuhn, I., Wild, J., Arianoutsou, M., … Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(27), 12157–12162. https://doi.org/10.1073/pnas.1002314107

R Core Team. (2016). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, *83*(3), 263–282. https://doi.org/10.1890/13-0183.1

Seabloom, E. W., Borer, E. T., Buckley, Y., Cleland, E. E., Davies, K., Firn, J., … Yang, L. (2013). Predicting invasion in grassland ecosystems: Is exotic dominance the real embarrassment of richness? *Global Change Biology*, *19*(12), 3677–3687. https://doi.org/10.1111/gcb.12370

Seabloom, E. W., Borer, E. T., Buckley, Y. M., Cleland, E. E., Davies, K. F., Firn, J., … Yang, L. (2015). Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nature Communications*, *6*, 7710. https://doi.org/10.1038/ncomms8710

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, *17*(4), 170–176. https://doi.org/10.1016/s0169-5347(02)02495-3

Soberón, J. M. (2010). Niche and area of distribution modeling: A population ecology perspective. *Ecography*, *33*(1), 159–167. https://doi.org/10.1111/j.1600-0587.2009.06074.x

Tobin, J. (1958). Estimation of relationships for limited dependent variables. *Econometrica*, *26*(1), 24. https://doi.org/10.2307/1907382

Van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta analysis of trait differences between invasive and non invasive plant species. *Ecology Letters*, *13*(2), 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J. L., Messier, J., … Sax, D. F. (2017). Plant biodiversity change across scales during the Anthropocene. *Annual Review of Plant Biology*, *68*(1), 563–586. https://doi.org/10.1146/annurev-arplant-042916-040949

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., … Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*(7), 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modelling in community ecology. *Trends in Ecology & Evolution*, *30*(12), 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Williamson, M., & Fitter, A. (1996). The varying success of invaders. *Ecology*, *77*(6), 1661–1666. https://doi.org/10.2307/2265769

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., … Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, *88*(1), 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

Zurell, D., Pollock, L. J., & Thuiller, W. (2018). Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments? *Ecography*, *125*(3), 336–342. https://doi.org/10.1111/ecog.03315

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.