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Effects of exotic annual grass litter and local environmental gradients on annual plant community structure

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Abstract Exotic annual grasses have been introduced into many semi-arid ecosystems worldwide, often to the detriment of native plant communities. The accumulation of litter from these grasses (i.e. residual dry biomass) has been demonstrated to negatively impact native plant communities and promote positive feedbacks to exotic grass persistence. More targeted experiments are needed, however, to determine the relative impact of exotic grass litter on plant community structure across local environmental gradients. We experimentally added exotic grass litter to annual forb-dominated open woodland communities positioned along natural canopy cover gradients in southwest Western Australia. These communities are an important component of this region's plant biodiversity hotspot and are documented to be under threat from exotic annual grasses. After a one-year treatment period, we measured the effects of exotic grass litter, soil properties, and canopy cover on native and exotic species richness and abundance, as well as common species' biomass and abundances. Plant community structure was more strongly influenced by soil properties and canopy cover than by grass litter. Total plant abundances per plot, however, were significantly lower in litter addition plots than control plots, a trend driven by native species. Exotic grass litter was also associated with lower abundances of one very common native species: *Waitzia acuminata*. Our results suggest that exotic grass litter limits the establishment of some native species in this system. Over multiple years, these subtle impacts may contribute substantially to the successful advancement of exotic species into this system, particularly in certain microenvironments.

Keywords Annual plants · Community structure · Exotic grass · Invasion · Litter · Semi-arid ecosystem

Introduction

Understanding the mechanisms that promote the persistence of exotic plant species in invaded systems is complementary to understanding the factors that enhance invasion resistance. The introduction of exotic propagules in conjunction with various forms of exogenous disturbance may trigger invasions by

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creating opportunities for exotic species to establish aided by altered resource levels or reduced competition from native species (Hobbs and Huenneke 1992; MacDougall and Turkington 2005). It is less clear, however, which abiotic and biotic processes permit exotic species to persist once these disturbances have ended (D'Antonio and Chambers 2006). Identifying these processes and their contingencies may reveal the barriers to recovery of invaded plant communities while also providing insights into general abiotic and biotic conditions for species coexistence (Hobbs and Norton 1996; Palmer et al. 1997; D'Antonio and Chambers 2006).

In many plant communities in Mediterranean-type ecosystems, introduced annual grasses and forbs persist after disturbance has ceased by inhibiting the establishment of native competitors (D'Antonio and Vitousek 1992; Seabloom et al. 2003; Grman and Suding 2010). One mechanism of this inhibition is the suppression of native species by accumulation of residual exotic annual grass biomass, or litter. Annual grass litter may inhibit other species by imposing direct and indirect barriers to growth and activity at various life stages. This inhibition can begin as early as the dispersal phase by physically preventing native seed from reaching the soil surface (Fowler 1986). Annual grass litter may also benefit distinct trait values in resident species, such as species with larger seeds (Dwyer et al. 2015) and alter native species germination patterns and their productivity through modifications to the microenvironment, such as changes in nutrient levels, water availability, altering soil temperature, facilitating pathogen attack, and decreasing light penetration to the soil surface (reviewed in Facelli and Pickett 1991). Once native germination has occurred, annual litter can act as a physical barrier to further prevent or suppress seedling growth (Lenz et al. 2003). Neutral or facilitative interactions between exotic grass litter and conspecific seedlings have also been found to promote a positive feedback to their abundance that may compound over time and facilitate exotic grass dominance in some systems (D'Antonio and Vitousek 1992; Lenz et al. 2003; Coleman and Levine 2007).

Natural environmental features of recipient plant communities may modify the impacts of exotic species over small spatial scales. In particular, overstory vegetation may contribute substantially to variation in understory floristic composition in savannah grasslands (Belsky 1994; Scholes and Archer 1997), as well as eucalypt woodlands in southeastern (Prober et al. 2002a) and Western Australia (Prober and Wiehl 2011; Dwyer et al. 2015). The effects of trees on understory vegetation are twofold, encompassing both aboveground and belowground processes. Tree canopies reduce direct solar radiation, which may alleviate water stress in understory plant assemblages (Weltzin and Coughenour 1990; Dwyer et al. 2015). Prober and Wiehl (2011) found that both tree species and tree proximity were significant sources of variation in soil properties such as bulk density, total nitrogen, and pH in semi-arid eucalypt woodlands. Topsoils beneath trees are often more fertile than soils found in open patches as a result of nutrient deposition and physical disturbance from faunal congregation, as well as nutrient concentration near tree root systems, runoff zones, and areas of litter accumulation (Belsky 1994; Facelli and Brock 2000; Prober et al. 2002a). However, inhibitory effects of trees on understory vegetation have also been documented in semi-arid eucalypt woodlands (Lamont 1985) and may be due to allelopathic effects of tree leaf litter (May and Ash 1990) or resource drawdown by tree roots (Lamont 1985; Belsky 1994).

In semi-arid plant communities where canopy cover is historically a major source of microenvironmental variation, the addition of grass litter may significantly impact local patterns of diversity and invasion resistance. The extent to which exotic annual grass litter interacts with tree proximity to impact resident annual plant community structure and invasion dynamics remains unclear. To explore these processes simultaneously, we conducted a field study in a semi-arid eucalypt woodland in southwest Western Australia in which we experimentally added exotic annual grass litter from an adjacent invaded area at varying distances from established native trees. We measured the relative influences of exotic grass litter and several naturally-occurring abiotic gradients on resident plant community structure over a full growing season. In particular, we isolated the aboveground effects of litter deposition from belowground effects of exotic annual grass presence. In this study we asked the following questions:

1. How does tree proximity affect microenvironmental conditions important for annual plant performance and community structure?

2. What are the effects of litter addition on microenvironmental conditions?
3. How does the presence of exotic annual grass litter, in combination with underlying environmental gradients, affect annual plant community structure?

Methods

Study system

Our study was undertaken in the Kunjin Reserve woodland remnant (32°21′19, 31″S 117°45′42.32″) in the south-central region of Western Australia (Fig. 1a). Kunjin Reserve experiences a typical Mediterranean-type climate, with mild wet winters and prolonged summer drought. Long-term average annual rainfall is 371.8 mm, and mean maximum daily temperatures range from a mean of 16.5 °C in July to 30.5 °C in December (Bureau of Meteorology Station ID: 10536, http://www.bom.gov.au/climate/data/). Soils in this region are generally nutrient-poor gravelly loams resulting from erosion of the underlying granitic block (Anand and Paine 2002; Hopper and Gioia 2004). The woodland at Kunjin is considered York gum-jam woodland, which is a formerly common woodland type that contributes to the regions globally recognised plant biodiversity hotspot (Myers et al. 2000). York gum-jam woodlands have a sparse canopy composed of two tree species: York gum (*Eucalyptus loxophleba* Beth. subsp. *loxophleba*) and jam (*Acacia acuminata* Benth.). The understory, however, is unusual for the region in that it is dominated by dense native and exotic annual forbs (e.g. *Arctotheca calendula* (L.) Levyns, *Waitzia* spp. J.C. Wendl., *Rhodanthe* spp. Lindl., *Podotheca* spp. Cass., *Trachymene* spp. Rudge) interspersed with occasional perennial tussock grasses (e.g., *Austrostipa* spp. S.W.L. Jacobs & J. Everett) (Dwyer et al. 2015). The annual component of the understory is active during late winter and spring (June to October). Annual grasses are not native to York gum-jam woodlands, and as such their litter is not a natural feature in the absence of invasion. Litter from the native annuals in this system is sparse and short-lived, though more persistent leaf litter from the York gum and jam trees does form in areas with greater canopy cover.

Experimental design

To test effects of exotic annual grass litter on annual plant community structure, we added litter to native-

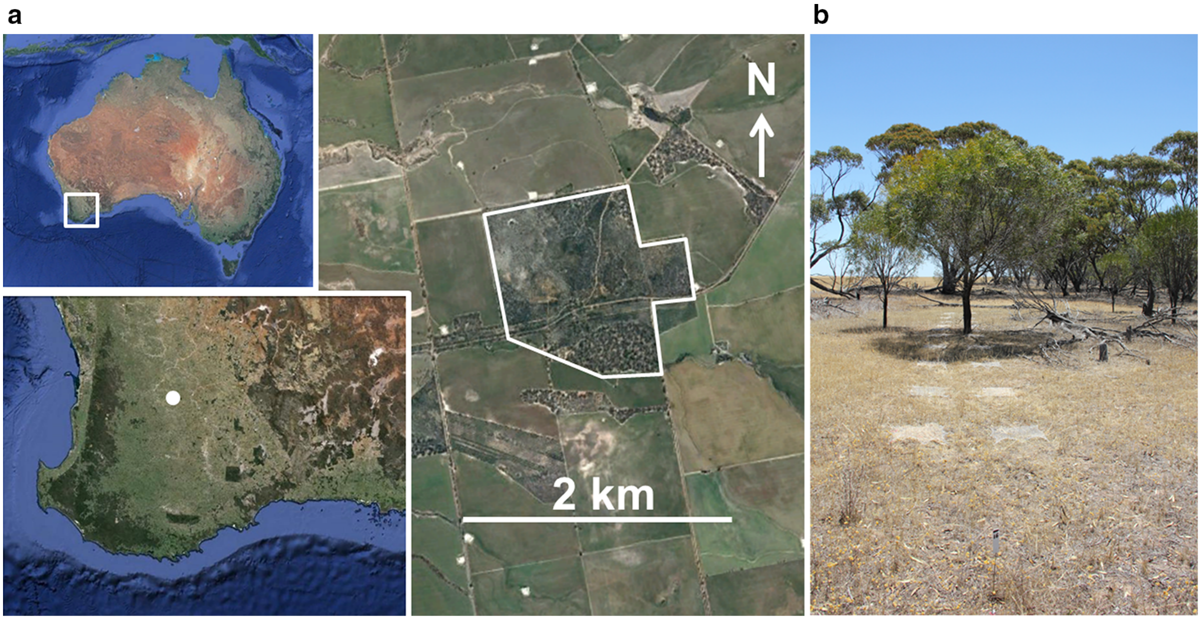

Fig. 1 **a** Location of Kunjin Reserve within southwest Western Australia and **b** an example of a transect of experimental plot pairs (control and treatment) centred about an *A. acuminata* tree running along a north–south axis (Map imagery: Landsat, CNES/Astrium, Google)

dominated understory areas within Kunjin Reserve at the end of the 2012 growing season. We did this systematically along natural canopy cover and soil gradients (related to distance from *E. loxophleba* and *A. acuminata* trees) within the reserve. At peak biomass 2013, we then assessed plant community dynamics within our control and manipulated study plots.

A total of six pairs of transects were established within Kunjin Reserve in November 2012, four radiating out from *E. loxophleba* trees and two from *A. acuminata* trees. Each pair of transects consisted of one transect running north away from a single tree and the second transect running south away from the same tree (Fig. 1b). *A. acuminata* trees are less abundant at Kunjin Reserve; thus, fewer of these trees were used in this study. Along each transect, five pairs of 0.5 × 0.5 m plots were placed every 1–3 m, avoiding the scattered perennial bunchgrasses in this reserve. Native bunch grasses, though sparsely distributed, are much larger than the native annuals and were excluded to ensure that all plots were dominated by annual species only. The same plot spacing was used for north and south transects in each pair. The litter treatment was applied to one plot per pair along transects (Fig. 1b). Litter plots were alternated with each consecutive plot pair to avoid any east–west biases. Plot pairs were separated by 0.5 m to minimise variation in underlying abiotic conditions and plant community composition while avoiding edge effects of the litter on control plots. Plot sizes and spacing are appropriate for these herbaceous communities as they capture compositional variation at the scale of the local metacommunity and the “interaction neighbourhood” of individual plants in this system (Dwyer et al. 2015; Lai et al. 2015). All selected trees were surrounded by relatively homogenous annual plant communities and were far enough from other trees to avoid overlapping shadows.

All litter treatment plots received 65 g of stem and leaf litter of *Avena barbata* Link, an exotic annual grass that has become common in this region, particularly in degraded York gum-jam woodlands (Prober et al. 2011; Dwyer et al. 2015). The litter was collected from a nearby roadside, cleaned of seeds, and oven-dried at 60 °C for one week before application. The litter was applied to each treatment plot and loosely held in place with a thin layer of bird netting, which was left in place for the entire experiment. Control plots also received a layer of bird netting to minimize differences between treatment and control plots not due to the presence of grass litter. The bird netting was unlikely to affect plant emergence, as we chose a 2 cm mesh aperture, large enough for all annual seedlings in this system to grow through. The *A. barbata* litter was added in November 2012 after community senescence and natural seed release in the experimental plots. We chose to add 65 g of litter to each 0.5 × 0.5 m treatment plot based on a survey of the mean mass of litter sampled in adjacent areas in Kunjin Reserve that had already been invaded by *A. barbata*. *A. barbata* was present in only three of our 120 plots (distributed among two transects) prior to experimental litter application, and each of the three plots contained only one individual of *A. barbata*. Existing litter (exotic annual, native annual or native sclerophyll) did not differ between control and treatment plots and was not removed or redistributed from plots prior to the experiment, but was quantified and included in analyses (Supplementary Material).

Data collection

Plant community data from nine of our 120 plots were discarded due to animal damage, but this damage was distributed among treatments and transects. In August 2013, plant community structure was evaluated by recording the identity and abundance of all plant species using a 30 × 30 cm quadrat centred within each 0.5 m × 0.5 m plot to eliminate edge effects. In early October 2013, plots were harvested at peak biomass and samples were dried in drying ovens and weighed to assess treatment effects on productivity. Previous studies have found grass litter in this system to be correlated with a community-level increase in mean seed mass (Dwyer et al. 2015). Thus, we compiled seed mass data for each species observed in our experimental plots (Dwyer, unpublished data) to assess whether grass litter affected the seed size distribution of our experimental plots.

In addition to measures of plant performance across experimental treatments, several abiotic variables were measured for each plot both prior to and post-litter application. Soil samples (0–10 cm depth and excluding litter and debris) were collected from the centre of each plot before litter application and again during biomass harvests, and analysed for nutrient content [nitrate, Colwell phosphorus (P), and Colwell

Potassium (K)] according to methods described in Prober and Wiehl (2011). To measure whether N-cycling rates were different between litter addition and control plots, we deployed three anion-exchange membrane strips in each plot for seven weeks for estimating net nitrate immobilization, which was determined according to methods described in Jasrotia and McSwiney (2008) and Vogt (2013). Soil moisture was measured in each plot using a soil moisture probe (0–10 cm, TDR method) partway through the growing season in September 2013 and values were used to quantify relative soil moisture differences in control versus litter plots. Canopy cover of *E. loxophleba* and *A. acuminata* was measured as an average of cover facing north, east, and west of each plot using a spherical crown densiometer (Forestry Suppliers Inc., Jackson MS, USA). Cover to the south was not included in analyses because it does not contribute to shading during the winter growing season in these communities.

Data analysis

All analyses and graphs were produced in R (v 3.1.2, R Development Core Team 2014). To account for spatial dependence of responses, we included spherical correlation structures (Diggle et al. 2002) in all models except those of focal species abundances and verification of pre-treatment litter cover.

To verify that pre-treatment litter amounts (herbaceous, *E. loxophleba*, and *A. acuminata*) did not inherently differ between control and litter plots, we used linear mixed-effects models (package ‘nlme’ (Pinheiro et al. 2014)) to model cover of each litter type in each plot by treatment assigned to the plot, with random effect specified as plot pair nested with transect to account for spatial dependence of observations. Cover values were square-root transformed (herbaceous litter) or ln-transformed (*E. loxophleba* and *A. acuminata*) prior to analyses to meet model assumptions of normality. Then we examined natural (pre-treatment) variation in important abiotic variables along transects by fitting generalized additive mixed models (package ‘gamm4’ (Wood 2012)) of canopy cover, soil nitrate, soil P, and soil K by distance to tree, with a random effect of plot pair nested within transect. Because the number of *E. loxophleba* and *A. acuminata* transects were unequal, differences in relationships of abiotic variables to tree proximity according to tree species could not be statistically estimated in one model. Thus, separate models were fit for transects of either tree species. A number of these variables were log normally distributed and were therefore ln-transformed or logit-transformed. To visually estimate the non-linear trends of these abiotic variables by tree proximity, smoothed splines of model-predicted values were plotted with one SE interval around each spline. To investigate natural directional differences in soil moisture and nitrate cycling around trees, we used mixed effects models of ln-transformed soil moisture and nitrate adsorption values from control plots only by aspect (north or south), with plot nested within transect specified as a random effect. In addition, we modelled the relationship between pre-treatment native sclerophyllous litter and overhead canopy cover using mixed effects models of plot-level ln-transformed *E. loxophleba* and *A. acuminata* litter percent cover by overhead canopy cover, with random effects of plot nested within transect to account for spatial dependence and over-dispersion (Elston et al. 2001).

This was followed by investigation of how litter addition impacted these variables, using mixed effects ANOVAs with fixed effects of treatment (litter addition or control) and tree species and random effect of transect.

Then, we analysed how litter addition and pre-treatment abiotic variation explained aspects of community structure and plant performance using mixed effects models, using fixed effects of treatment (categorical: litter addition or control) and continuous measures of pre-treatment abiotic variables, and a random effect of transect. First we related treatment and abiotic variables to community-level measures of total species richness, exotic and native plant abundance, and total plant abundance (exotic and native species pooled). Then, we chose four common focal annual species and assessed the impact of treatment and abiotic variables on their abundance and mean biomass per individual: *Waitizia acuminata* Steetz (native, Asteraceae), *Rhodanthe polycephala* (A. Gray) P. Wilson (native, Asteraceae), *A. calendula* (exotic, Asteraceae), and *Vulpia myuros* (L.) C.C. Gmel. (exotic, Poaceae). Lastly, we analysed whether mean seed mass (weighted by species abundances) of annuals was different in litter versus control plots to determine whether litter may be excluding relatively small-seeded species (Dwyer et al. 2015).

We rarefied species richness values to investigate the effect of litter on richness while accounting for differences in plant abundances among plots (Supplementary Material). Aggregate measures of plant abundance (total, native, and exotic) were square-root transformed to meet assumptions of normality. Focal annual species abundances were analysed using generalized linear mixed effects models with Poisson errors and a log link function (package lme4; Bates et al. 2014) and plot-level random effect nested within transect to account for spatial dependence and overdispersion. Biomass responses of focal species and annual community seed mass responses were ln-transformed to improve normality of residuals before linear mixed effects models were fitted.

Results

Pre- and post-treatment natural variation

Environmental variables varied along transects depending on the distance from tree, aspect, and tree species (Fig. 2). *A. acuminata* canopies were smaller than *E. loxophleba* canopies, reflected in percent canopy cover values (Fig. 2a). Nitrate increased with distance to *A. acuminata* trees, but only to the north (Fig. 2b). By contrast, there were no strong trends in nitrate values around *E. loxophleba* trees (Fig. 2b). There was no relationship between net nitrate immobilization and aspect (south estimate: 0.36, SE: 0.76, $p = 0.64$). Phosphorus values declined with distance to *E. loxophleba* trees only (Fig. 2c). No discernible trends were found for potassium around either tree species (Fig. 2d). Soil moisture measured in control plots was significantly greater to the south of trees than to the north (south estimate: 0.17, SE: 0.04, $p = 0.0001$). Percent cover of native sclerophyllous litter was significantly positively correlated with overhead tree canopy cover (*E. loxophleba* estimate (SE): 0.02 (0.003), $p < 0.0001$; *A. acuminata* estimate (SE): 0.03 (0.004), $p < 0.0001$).

Litter addition did not affect the measured abiotic variables with the exception of soil moisture (Fig. 3a), which significantly increased with litter addition (estimate: 0.07, SE: 0.02, $p = 0.0001$).

Species richness and plant abundances

Rarefied species richness was unaffected by the litter treatment (Table 1; Fig. 4a; Supplementary Material). However, total plant abundance declined with litter addition ($p = 0.02$), as well as canopy cover ($p = 0.004$). This trend was driven by native species, which declined in abundance with litter addition ($p = 0.04$, Fig. 4b) and canopy cover ($p = 0.02$), while exotic abundance was unrelated to any explanatory variable in this study. Mean seed mass was larger in litter addition plots on average, though this difference was not significant (control: 0.38 ± 0.01 mg, litter: 0.40 ± 0.01 mg; $p = 0.15$).

Abundance and biomass of focal native and exotic species

W. acuminata (native Asteraceae) abundance declined with litter addition and canopy cover ($p = 0.03$ and $p < 0.0001$ respectively, Table 2; Supplementary Materia), and phosphorus ($p = 0.01$). *R. polycephala* (native Asteraceae) abundance was positively associated with phosphorus ($p = 0.05$, Table 2; Supplementary Material). *A. calendula* and *V. myruos* (exotic Asteraceae and Poaceae) abundances both decreased with canopy cover ($p = 0.04$ and $p = 0.003$, respectively; Table 2; Supplementary Material). Mean individual biomass was not significantly influenced by any of the abiotic variables, with the exception of *R. polycephala*, which were smaller in areas of higher potassium ($p = 0.01$, Table 2; Supplementary Material).

Discussion

In general, plant community structure and the productivity of focal species were more strongly influenced by soil and canopy cover gradients than the presence of exotic grass litter. However, native species were significantly less abundant where litter was added across all natural gradients. Combined with evidence from regional-scale studies, these results suggest that one of the strongest effects of exotic annual grass litter in this system may be the inhibition of native annual plant establishment, though the mechanism underlying this inhibition was not examined in this study. If negative impacts of exotic grass litter compound over time (multiple years), the fairly subtle impacts observed in our short study could easily lead to significant changes in plant community structure.

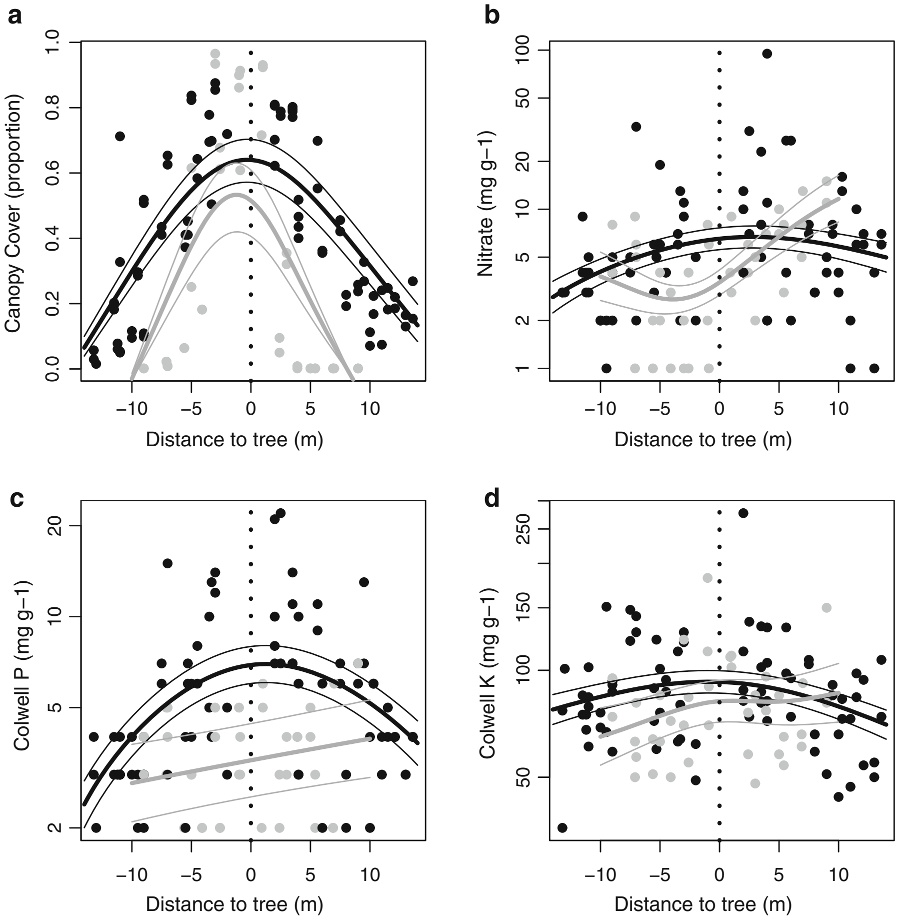

Fig. 2 Smoothed splines (±1 SE) of transformed environmental variables with proximity to tree (*grey A. acuminata*, *black E. loxophleba*) measured in experimental plots in 2012 prior to litter addition. Position along the *x*-axis denotes position along the south (negative)–north (positive) transect relative to the tree at the origin

Natural microenvironmental gradients

Higher soil moisture to the south of trees likely reflected greater shading by trees during the winter and spring in this system. Native sclerophyll litter was concentrated at the bases of trees, confirming that the effects of tree litter on understory communities may not be as strong in open areas relative to shaded areas. Nitrate was higher to the north of trees, especially in open patches adjacent to *A. acuminata*, which was surprising given previous findings in this system of greatest total N near trees (Prober and Wiehl 2011). As nitrate adsorption rates were unrelated to aspect, this may have been due to inherent soil differences leading to lower N long-term leaching rates to the north of jam trees (Austin et al. 2004; Prober et al. 2005). Though somewhat intriguing, this consistent microenvironmental difference between north and south transects did not seem to relate to or impact litter-based results.

Litter effects on microenvironmental conditions

The most pronounced effect of *A. barbata* litter on measured abiotic variables was to elevate soil moisture, consistent with findings in other systems (reviewed in Facelli and Pickett 1991). Higher soil moisture in litter addition plots was likely due to reduced evaporation from the soil surface (Fowler 1986; Facelli et al. 1999). There is increasing evidence from other studies within this system that soil moisture at local scales has a strong organising effect on these annual communities (Dwyer et al. 2015). The elevated soil moisture associated with exotic grass litter did not

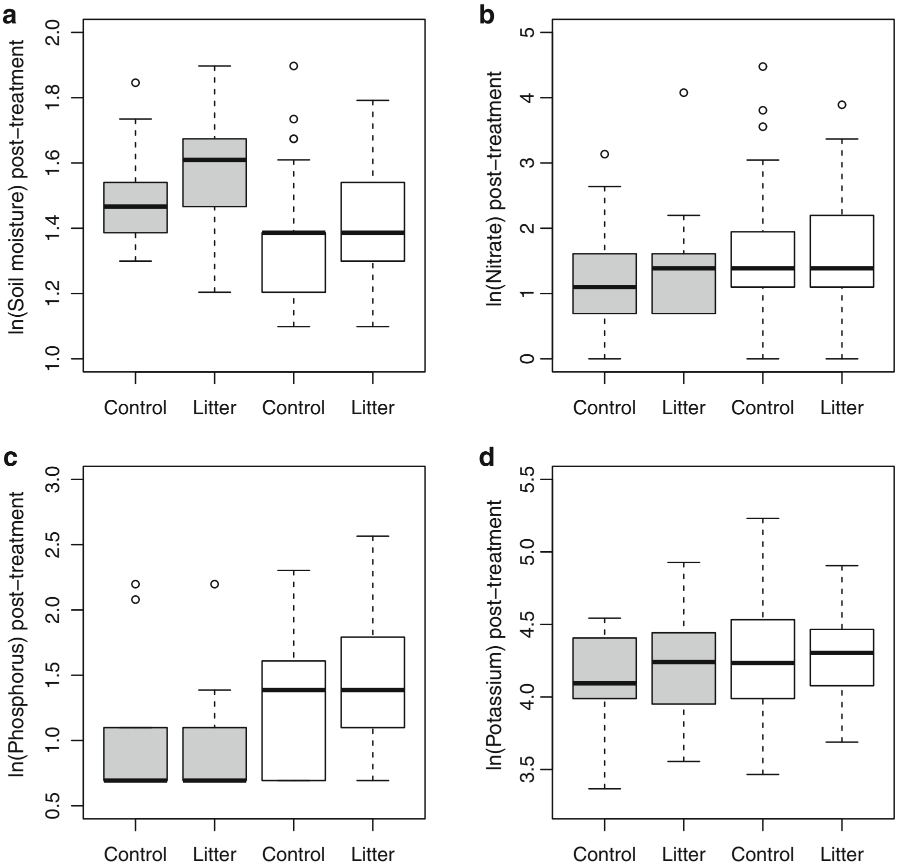

Fig. 3 Post-treatment abiotic variables measured in control and litter addition plots in the spring of 2013 (*grey A. acuminata*, *white E. loxophleba*). *Boxes* represent abiotic variable quantiles in control and litter plots (points are outliers)

impact individual productivity of focal native or exotic species in this study, at least over a single growing season. Further study of invasion in this system should involve long-term investigation of how microenvironmental changes associated with exotic invasion impact the performance and local distribution and abundance of native species. In temperate eucalypt woodlands, these long-term effects may include increased levels of soil organic carbon (Dwyer et al. 2015) and increases in internal soil nitrogen cycling rates (Prober et al. 2002b; Prober and Smith 2009).

Microenvironmental and litter effects on community structure

Overall, canopy cover and soil nutrient gradients were more informative predictors of plant community structure than the presence of exotic grass litter. Canopy cover in particular proved to be among the strongest drivers of understory annual community responses. Total and native annual plant abundance declined in shadier areas closest to trees, confirming previous observations of negative relationships between annual plants and York gum-jam overstories (Prober and Wiehl 2011). While we did not isolate the specific mechanisms driving canopy cover effects on understory communities, there are factors correlated with overhead canopy cover that may have contributed to this pattern. For example, our results suggest that the canopy effect was not driven by an increase in nutrient content closer to trees. However, sclerophyllous leaf litter, which was significantly more abundant closer to trees, may have been a driver of the negative canopy effect, especially given evidence of allelopathic potential in other low-rainfall systems (May and Ash 1990). Testing for allelopathic compounds in the soil and leachates would help confirm this hypothesized mechanism.

Table 1 Coefficients and standard errors (SEs) from mixed effects models of plant community responses to litter addition and pre-treatment environmental variables, with transect specified as a random effect

	Estimate	SE
Rarefied species richness		
(Intercept)	2.25*	0.95
Litter addition	0.04	0.12
Canopy cover (%)	−0.003	0.003
Ln(nitrate)	0.09	0.10
Ln(P)	−0.34	0.18
Ln(K)	0.27	0.24
Random effects (variance estimates)	Among: <0.0001	
	Within: 0.37	
Total plant abundance		
(Intercept)	8.33**	2.45
Litter addition	−0.64*	0.28
Canopy cover (%)	−0.02**	0.01
Ln(nitrate)	−0.12	0.26
Ln(P)	−0.20	0.47
Ln(K)	−0.356	0.61
Random effects (variance estimates)	Among: 0.66	
	Within: 2.76	
Sqrt (Exotic plant abundance)		
(Intercept)	4.91*	2.05
Litter addition	−0.25	0.22
Canopy cover (%)	−0.01	0.01
Ln(nitrate)	0.14	0.21
Ln(P)	−0.63	0.40
Ln(K)	−0.18	0.50
Random effects (variance estimates)	Among: 0.72	
	Within: 3.10	
Sqrt (Native plant abundance)		
(Intercept)	5.94*	2.53
Litter addition	−0.63*	0.30
Canopy cover (%)	−0.02*	0.01
Ln(nitrate)	−0.37	0.27
Ln(P)	0.17	0.48
Ln(K)	−0.17	0.64
Random effects (variance estimates)	Among: 0.42	
	Within: 2.56	

Asterisks denote level of significance (* $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Of the soil nutrients measured, only P had a significant negative relationship with focal species abundances. Consistent with previous findings in York gum-jam woodlands (Dwyer et al. 2015), native *W. acuminata* declined in abundance as P increased. While phosphorus can be toxic to perennial species in this historically P-limited region (Lambers et al. 2008), it is unknown how it affects herbaceous annuals other than through competitive exclusion by exploitative annuals that thrive on P-enriched soils (Dwyer et al. 2014; Lai et al. 2015), which was not the case in this study. Given that *R. polycephala* (the other native forb examined in this study) was positively associated with P, our study provides no evidence of consistent toxicity of P. While the dynamics underlying modifications to this system by exotic grasses and other invaders are complex, differential P-avoidance by certain common native species may be sufficient to

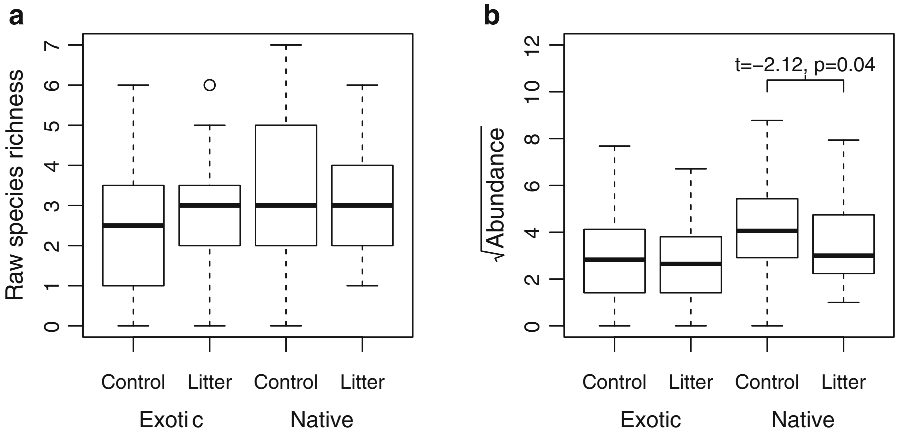

Fig. 4 **a** Raw species richness and **b** square-root transformed abundances of native and exotic annuals in control and litter addition treatment plots. *Boxes* represent quantiles of richness and abundance values of native and exotic species in control and litter treatment plots

drive locally substantial changes in community composition in addition to direct impacts of exotic species.

Unlike previous studies (Lenz et al. 2003), there was no detectable effect of *A. barbata* litter on species richness. There was, however, a significant negative effect of litter on plant density, driven by declines in the abundance of native species where litter was present. While this study examined the effects of litter deposition over one year, significant population declines of native species may, over time, lead to localised extinction. Even though the litter was added after the completion of natural seed dispersal in this system, it may have prevented or delayed small, wind-dispersed native seeds from subsequently reaching the soil surface (Fowler 1986). This seed barrier effect of accumulated litter has been implicated in a previous observational study in several invaded York gum-jam woodland remnants (Dwyer et al. 2015). Dwyer et al. (2015) found that exotic grass litter in this system was associated with an increase in community-level mean seed mass and a narrowed community seed mass distribution, which they suggested may reflect the exclusion of relatively small-seeded native species. This was not the case in this study, however, suggesting reductions in abundance of native species may have been driven more strongly by litter effects on germination and emergence than seed dispersal. Even if seed did germinate under the litter in our study, the litter may also have acted as a mechanical barrier to emergence of native germinants (Facelli and Pickett 1991), or promoted seedling herbivory (Facelli 1994) or granivory (Brown et al. 1979).

Altered soil microclimate conditions beneath grass litter may have further reduced the abundance of native annuals by rendering the soil microenvironment unfavourable for germination or seedling success. Temperature, light availability, and soil humidity cycles play key roles in regulating the germination of annuals in this system (Erickson et al. unpublished data) and in other semi-arid plant communities in Australia (Bell et al. 1999) and worldwide (Baskin et al. 1993; Levine et al. 2008). In addition, an increase in moisture may have corresponded to elevated rates of infection of seedlings by fungal pathogens (Goldberg and Werner 1983; Facelli et al. 1999).

The fact that the abundance of exotic annuals was not affected by *A. barbata* litter likely reflects inherent physiological differences between common native and exotic annuals in this system. To begin with, many common exotic annuals in York gum-jam annual plant communities exhibit more consistent and greater rates of germination than native annuals (Pérez-Fernández et al. 2000; Wainwright and Cleland 2013; Mayfield et al. unpublished data). Exotic species in York gum-jam annual communities typically have larger seeds that may assist germination and penetration through dense layers of litter compared to smaller-seeded natives (Carson and Peterson 1990; Facelli and Pickett 1991; Dwyer et al. 2015). In other locations, exotic annual grass litter has had positive effects on conspecifics by direct feedback mechanisms promoting their abundance or through reductions in interspecific competition (Evans and Young 1970; Lenz et al. 2003; Coleman and Levine 2007). The combination of

Table 2 Coefficients and standard errors (SEs) from mixed effects models of focal species responses to litter addition and pre-treatment abiotic variables

Fixed effects	Abundance		ln(Biomass) (g)	
	Estimate	SE	Estimate	SE
A. calendula				
(Intercept)	−4.99	4.04	2.55	4.32
Litter addition	0.50	0.48	0.21	0.45
Canopy cover (%)	−0.02*	0.01	0.02	0.01
Ln(nitrate)	0.77	0.41	0.54	0.39
Ln(P)	−0.95	0.77	0.19	0.80
Ln(K)	0.90	1.0	−1.09	1.09
Random effects (variance estimates)	Transect: 0.32		Among: 4e−8	
	Plot: 1.43		Within: 1.99	
R. polycephala				
(Intercept)	−1.09	4.95	1.95	2.25
Litter addition	−0.04	0.55	0.23	0.26
Canopy cover (%)	0.02	0.01	0.002	0.01
Ln(nitrate)	−0.57	0.46	0.22	0.24
Ln(P)	1.74*	0.90	0.51	0.45
Ln(K)	−0.72	1.18	−1.54*	0.57
Random effects (variance estimates)	Transect: 6.32		Among: 0.29	
	Plot: 2.40		Within: 0.48	
V. myuros				
(Intercept)	−1.71	6.38	−4.88*	2.13
Litter addition	0.30	0.79	0.02	0.27
Canopy cover (%)	−0.05**	0.02	<0.0001	0.01
Ln(nitrate)	0.64	0.68	0.25	0.24
Ln(P)	−0.10	1.17	0.35	0.43
Ln(K)	−0.14	1.59	0.23	0.52
Random effects (variance estimates)	Transect: 1.01		Among: 0.22	
	Plot: 7.46		Within: 0.81	
W. acuminata				
(Intercept)	0.68	1.89	−4.95*	2.39
Litter addition	−0.47*	0.22	<0.0001	0.25
Canopy cover (%)	−0.02***	0.01	−0.01	0.01
Ln(nitrate)	0.06	0.17	0.18	0.23
Ln(P)	−0.84*	0.33	0.39	0.43
Ln(K)	0.29	0.46	0.59	0.59
Random effects (variance estimates)	Transect: 0.32		Among: 0.53	
	Plot: 0.23		Within: 1.32	

Models of abundance used Poisson errors with log link, and plot within transect specified as a random effect. Biomass models were linear models of ln-transformed individual plant biomass values with transect specified as a random effect. Asterisks denote level of significance (* $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$)

insensitivity or even positive responses to exotic grass litter may thus also be a factor promoting exotic annual grass persistence in invaded communities (Lenz et al. 2003) including York gum-jam woodlands. More studies are clearly needed to determine which of these possibilities contribute to the reduction of native species abundances under exotic grass litter.

Conclusion

Here, we have documented the simultaneous contributions of underlying abiotic gradients and experimental exotic annual grass litter addition to the structure of an annual plant community. Notably, we have isolated the short-term effects of dead exotic grass individuals on the native community from the effects of concurrent competition with live exotic grass individuals. We have shown that canopy cover and soil nutrients are important drivers of community structure in this system regardless of whether exotic annual grass litter is present. In addition, we have demonstrated that aboveground exotic grass litter has the potential to reduce native species abundances even over short timeframes, implying that litter presence alone could eventually lead to localized extinction of native species and dramatically altered community structures.

Of course, the presence of a naturally-occurring layer of exotic annual grass litter in this system is inherently tied to altered ecological processes that promoted the establishment of a dense exotic grass canopy. Our results thus represent effects on the microenvironment and community composition driven solely by litter, without the effects of live grass presence or the environmental conditions that may have promoted live grass presence and thus litter deposition in the first place. In reality, the proximate effects of robust exotic annual grasses (especially *A. barbata*) on native annuals are much more extensive. Live *A. barbata* individuals are known to be highly competitive for light and may also rapidly deplete soil moisture (Dyer and Rice 1999; Lenz and Facelli 2005; Coleman and Levine 2007; Standish et al. 2008). Further, annual grass invasion is often reinforced by eutrophication or ungulate grazing, which may be selectively detrimental to native species (HilleRisLambers et al. 2010; Prober et al. 2011). An increasing volume of litter may accumulate over time in given microsites (Facelli and Pickett 1991; Facelli and Carson 1991), and so our study almost certainly underestimates the potential long-term effects of exotic grass invasions on the structure of these native communities. Still, over one year, the presence of litter significantly impacted the native annual plant community in this study. Thus, our results demonstrate that litter may degrade native semi-arid plant communities in the absence of ongoing disturbance. Combined, the direct effects of grass competition and disturbance may interact with litter deposition to dramatically change community composition in favour of exotic annual grass persistence.

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