



Understory species richness and light intensity regulate emergence, establishment and trait responses of two invasive grasses

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Abstract The role of native species richness in mediating ecosystem resistance to exotic plant invasion is thought to arise from niche filling and resource limitation that influence the competitive ability of an invader. However, there is a lack of empirical evidence examining the role of species richness and light availability during an invasion event. Here, a mesocosm experiment with constructed grassy woodland understory communities were used to examine the effects of native richness and light availability on the invasion success, growth and leaf traits of two invasive grasses, *Paspalum dilatatum* Poir. and *Eragrostis curvula* (Shrad.) Nees. Native species richness significantly reduced the emergence, survival and above-ground biomass of both invasive grasses. However, interspecific variation in the relative and specific leaf area and intraspecific variation induced by different light

and richness treatments was observed in both species. Strong negative relationships were identified between the above-ground biomass of both invasive and native grasses, which may indicate competitive interactions. Conversely, a positive relationship was observed between *E. curvula* and the biomass of native shrubs indicative of a facilitation effect. Distance-based linear modelling revealed community resistance to both invasive species manifested most strongly with the inclusion of multiple native species from differing functional groups, suggesting that complementarity mediated by functional trait diversity is a principal component of biotic resistance to invasion in this system. These results provide evidence that species richness confers invasion resistance beyond interspecific, competitive mechanisms and may limit establishment success and trait expression.

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resistance

Introduction

Studies on the relationship between native diversity and ecosystem functioning have repeatedly concluded that native diversity is a key determinant of ecological resistance to invasion (Elton 1958; Naeem et al. 2000; Fargione and Tilman 2005; Liao et al. 2015; Smith and Cote 2019). Invasion resistance, that is, the

ability of native communities to prevent the establishment of invaders, has been shown to manifest from both species richness (Levine and D'Antonio 1999) and evenness (Hillebrand et al. 2008). However, functional trait diversity, has emerged as the most consequential mechanistic, biotic component in mitigating biological invasion (Byun et al. 2012; Wang et al. 2019).

The diversity-resistance hypothesis (Elton 1958) – the propensity for rich native communities to exhibit greater ecological resistance to invasion—has been attributed to priority effects. Priority effects (or niche pre-emption) resulting from the early use of resources by remnant or revegetated flora can reduce the performance of later-arriving invasive species, thereby increasing ecosystem resistance (Fukami 2015; Byun et al. 2023). This effect can arise from at least two mechanisms. Firstly, species-rich communities have a greater chance of containing a species which may be highly effective at excluding an invader—the ‘sampling effect’ (Wardle 2001; Fargione and Tilman 2005). This may result from a species’ wielding competitive dominance associated with resource competition over a subordinate invader (Tilman 1997; Harpole and Tilman 2007) or a species which possesses traits capable of hindering an invader’s establishment (interference competition, e.g. allelopathic exudates) (Adomako et al. 2019). Secondly, species-rich communities may have less unoccupied niche space and more exhaustive resource utilisation via ‘resource use complementarity’ (MacDougall et al. 2009; Zhu et al. 2015). The larger the pool of resident species, the larger the likelihood of niche overlap between a resident and an invader, resulting in their competitive exclusion via limiting similarity (Byun et al. 2017). Recent empirical studies have demonstrated that the germination, establishment, and dominance of invasive plants is contingent on the early and effective utilisation of resources (Yannelli et al. 2020; Byun et al. 2023) which is inhibited in established, diverse, native assemblages (Hess et al. 2019).

Adaptive variability in phenotypical expression (i.e. plasticity), augmenting resource acquisition strategies, is a key driver of invasive plant success (Funk 2008; Yang et al. 2025). Invaders with high plasticity in physiological or morphological traits are able to persist in a broader array of environmental and competitive environments (Baker 1965; Rejmanek and Richardson 1996; Callaway et al. 2004), and

may retain higher levels of fitness than less plastic native competitors, in response to resource fluctuations (Poorter and Lambers 1986; Davis et al. 2000). For example, many invasive species exhibit plastic responses to low-light availability such as increases in leaf area or the ratio of dry leaf mass and leaf area (specific leaf area), which enhances shade tolerance and are considered adaptive (Valladares and Niinemets 2008; Fynn et al. 2011; Gruntman et al. 2019). However, the adaptive benefits conferred by phenotypic plasticity are contingent upon the functional diversity of the recipient environment; where there are fewer or smaller vacant niches to move into, fitness benefits are less likely to be realised (Drenovsky et al. 2012).

Despite the importance of interspecific competitive interactions, abiotic drivers may also be strong determinants of invasion success. In Australian grassy woodlands threatened by exotic grass invasion, Prober et al. (2016) concluded that competitive interactions between native and exotic richness were moderated by rainfall, whereby native and exotic richness positively covary as a consequence of universal abiotic drivers. Similarly, in the Avon Wheatbelt Bioregion of south-western Australia, Towers and Dwyer (2018) attributed a positive native-exotic richness relationship to low-productivity soils which permit greater resource partitioning between native and exotic communities via high within-neighbourhood niche dimensionality (Harpole and Tilman 2007; Harpole and Suding 2011; Harpole et al. 2016), increasing the incidence of facilitative relationships between species. However, the incorporation of these exogenous, environmental factors in observational studies confounds the measurement of the subtler intraspecific mechanisms in operation (Nunez-Mir et al. 2017).

To allow mechanisms of biotic resistance (or facilitation) to manifest, an experimental study which controls the significant environmental covariates (i.e. resource availability, disturbance, predation) is required (Mungi et al. 2021). There is a paucity of literature on how native species richness interacts with invasive propagules in most woodland ecosystems (but see Gooden and French 2015; Mason et al. 2018). Most studies have focused on the effects of native richness on the growth and fecundity of invasive plants once they have overcome an ecosystem’s resistance rather than the germination dynamics preceding their establishment (but see Adomako et al. 2019). Where these processes

are strong mediators of invasion success, they may be manipulated to achieve desirable conservation and restoration outcomes.

In this study, we compare the invasion success, growth and phenotypic response of two exotic grass species, *Paspalum dilatatum* Poir. and *Eragrostis curvula* (Shrad.) Nees, to high and low native understory species richness across full sun and shaded environments as experienced under an open canopy. Both invasive grass species are agriculturally important ‘trade-off’ grasses (sensu Godfree et al. 2017) and possess traits such as high biomass production and resources acquisition ability conferring a competitive advantage over subordinate native species in open woodlands and grasslands where light is not a limiting resource (Adler et al. 2018; Bates et al. 2021). As such, both species have been identified as amongst the most significant invaders of south-east Australian grassy woodlands (Rayment et al. 2022) and invasion of native communities by exotic perennial grasses is listed as a Key Threatening Process under the NSW *Biodiversity Conservation Act 2017* (NSWDPE 2021).

We predicted that, the number of individuals, growth rate and biomass (used as proxies for invasion success) of both invasive species would be lower in high richness mesocosms compared to low richness mesocosms owing to competitive, niche-based processes (i.e. sampling or niche-filling effects). Secondly, we expected that the number of individuals, growth rate and biomass of both invasive species would be lower in shaded environments owing to variation in the responses of species to light. Lastly, we predicted that both invasive species would express phenotypic plasticity in leaf traits between assemblage richness and light-intensity treatments, and specifically, SLA will reduce as a result of environmental shifts limiting resource availability and/or competitive effects.

Methods

The study system

Here we constructed experimental floristic communities of CPW, which is a highly fragmented grassy woodland community now reduced to 8% of its pre-colonial distribution and listed as critically endangered under NSW and Australian Federal legislation

(DECCW 2011). This plant community type has a characteristic woodland structure with a eucalypt-dominated canopy reaching 25 m height, a mid-storey of sparse shrubs and a species-rich understorey dominated by grasses and herbs. Notably, the majority of the native floristic diversity in CPW is held within the understorey layer (Benson and Howell 2002) making this ecosystem particularly susceptible to diversity loss via exotic grass invasion.

Experimental design

Forty-eight mesocosms were subjected to one of eight treatment combinations, comprising two-levels of sun exposure (i.e. full sun and shaded) crossed with two levels of species richness (i.e. high; 12 species or low; 3 species) and either of two invasion challenges (i.e. *P. dilatatum* and *E. curvula*). Each treatment combination was replicated across six pots.

This experiment was conducted in the Austral spring–summer between September 2023 and February 2024 within an enclosed, open-air mesocosm facility located at the University of Wollongong’s Ecological Research Centre on the south coast of New South Wales, Australia (34° 24′ 16.56″ S, 150° 52′ 18.05″ E). Each mesocosm consisted of a white, rectangular plastic tub (420×320×3215 mm) with eight 1 cm drainage holes drilled into the base. These dimensions were selected to facilitate the natural root architecture of constituent species whilst encouraging maximum below- and above-ground competition for the duration of the experiment. Mesocosms were placed on elevated metal nursery benches in a concentric circular pattern to allow for even overhead watering via a centrally-position dome sprinkler (Metal Dome Sprinkler; Holman Industries). Rainwater collected at the experimental location was used as a water source. To maintain their statistical independence, mesocosms were separated by at least 30 cm and their positioning and orientation within their circle was randomly rearranged every two weeks.

The light treatments were established to alter the available light, while maintaining similar temperature and water availability throughout the experiment. Sun-exposed pots were positioned in full-sun, whilst shaded pots were positioned under 25% shade cloth (mesh). While PAR was not measured directly in this experiment, the 25% shade cloth has been shown in Bernich et al. (2024) to reduce light availability to

levels comparable to 50–60% canopy cover. High species richness mesocosms had 12 species from 5 different functional groups while low species richness had 3 species from 3 different functional groups.

The study site has a warm, temperate climate with mean annual rainfall of 1323 mm and mean annual maximum temperature of 21.8 °C (Bureau of Meteorology 2023). Supplemental watering was provided to maintain adequate water availability throughout the experiment. To simulate naturally occurring levels of CPW soil volumetric water content in the pots (Fitzgerald 2009; $5 \pm 3\%$) between treatments, 750 mL and 1250 mL of water was added at 10 pm for shaded and sun-exposed pots, respectively. Watering was increased by 500 mL for all mesocosms during two days of above average temperatures on 30 September–1 October 2023.

Each tub was filled with 20 L of a 50:50 mix of coarse river sand and commercially available native potting mix (NPK: 9:1:8), followed by a native inoculum of 5 L of CPW soil. Soil was collected in August 2023 from a pasture in Orchard Hills, New South Wales, Australia (33° 48' 27.47'' S, 150° 42' 35.22'' E) where CPW has been cleared. Soil was collected from a depth of 0–25 cm and included A and B-horizon soils which were replicated in the mesocosms. A horizon soil had a sandy clay loam texture, an average pH of 5.01 and an average C/N content of 99.2 mg/kg and 34.3 mg/kg, respectively. B horizon soil had a clay texture, an average pH of 5.16 and an average

C/N content of 84.5 mg/kg and 26.6 mg/kg, respectively (Raupp 2024, unpubl. data). The soil was sifted using 5 mm mesh to remove all large pieces of remnant, living biomass and thoroughly homogenised before its addition to the mesocosms (Fig. 1). Mesocosms were left fallow for three weeks to allow soil chemistry to re-equilibrate following the initial set-up disturbance and to enable the colonisation of the mesocosms by soil microbiota.

Assembly of mesocosm plant communities

Mesocosm plant communities were assembled from a suite of native species commonly found across the geographic range of CPW where the invasive perennial grasses *P. dilatatum* and *E. curvula* are also common. The experimental communities consisted of 12 plants drawn from a total pool of 34 species further divided into five functional groups each with at least 6 species; 6 graminoid (i.e. sedges and rushes) species, 7 herbaceous species, 8 grasses, 7 leguminous species and 6 shrubs (see Appendix 1). This plant density was based on a general appraisal of remnant CPW communities. All native species were sourced from the Cumberland region and plants grown in local, commercial nurseries. While every attempt was made to keep the age of species constant, difficulties in procuring obscure species resulted in variation in the age (3 months to 1 year old) and pot size (93 cm³ Hiko tubes to 300 cm³ forestry tubes) between

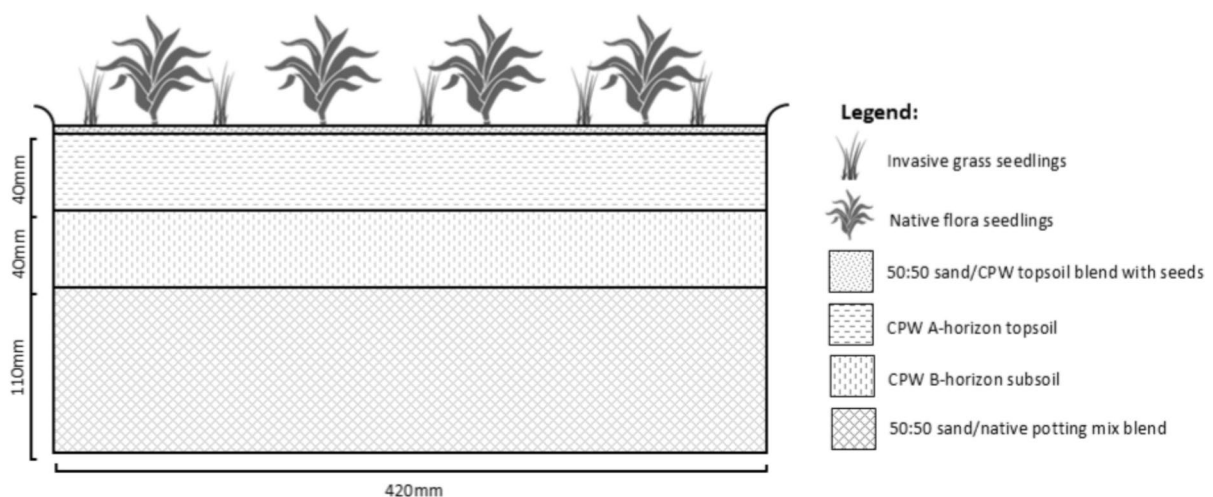


Fig. 1 Schematic diagram of constructed mesocosms. Native seedlings were planted in an evenly spaced 3 × 4 grid whilst invasive grass seeds were scattered at random on the soil surface

individual species. Species were randomly selected from the total pool to reduce the confounding effects of different ages. All plants were introduced as seedlings to replicate the priority effects of niche pre-emption in 'natural' invasion events (Mwangi et al. 2006) and restoration plantings (Weidlich et al. 2020).

The composition of each mesocosm assemblage was designed to replicate the dominance of grasses, graminoids and herbaceous species and the relative paucity of woody shrubs in the understory of remnant stands of CPW (Benson et al. 1996). Trees were not included as we aimed to strictly model the interspecific interactions between these understory species. All mesocosms were planted with 12 individual plants arranged in a 3×4 grid approximately 8 cm apart in August 2023. The upper limit of the species richness (n=12) treatment was bound by the estimated maximum planting density for unimpeded assemblage growth over the duration of the experiment (Stachova et al. 2012) whilst the lower richness treatment (n=3) was based on evidence from prior invasion challenges in experimental grass-dominated assemblages which suggest that reductions in invasive grass fitness begin to manifest at this richness (Naeem et al. 2000; Symstad 2000; Crawley et al. 2001; Oakley and Knox 2012).

In high species richness mesocosms, plantings incorporated single plants from each of 3 herbaceous species, 3 graminoid species, 3 grass species, 1 leguminous species and 1 random shrub or leguminous species. In low species richness mesocosms, 3 species were planted; 4 plants from 2 randomly selected herbaceous, graminoid or grass species and 4 plants from either a shrub or legume species. The establishment of individual plants was monitored, and any senescing or dead plants were replaced as required to ensure constant species richness and density prior to the simulated *P. dilatatum* and *E. curvula* invasion. Following the addition of invasive propagules to the mesocosms in September 2023, dead native plants were not replaced. Other alien species which arrived in the mesocosms voluntarily or germinated from the native topsoil were hand removed fortnightly over the duration of the experiment. A single application of an organic, low-phosphorous liquid fertiliser (10mLs of BushTucker; Neutrog Australia Pty diluted in 2.5L of water/mesocosm as per recommended application rates; NPK 10.0:0.7:8.0%w/v) was administered across all replicates on 1st December 2023 to

maintain nutrient availability and growth as the plants established. We knowledge the potential for confounding effects on richness-biomass relationships, and the competitive relationships should be interpreted within a non-resource limited environment.

Procurement of invasive species

Mature seeds of *P. dilatatum* and *E. curvula* were collected between March–April 2023 from multiple stands of CPW. Collections were taken from spatially isolated remnants across a wide geographic distribution to capture the high diversity found in both *P. dilatatum* (Glison et al. 2014) and *E. curvula* (Roberts et al. 2021).

For both species, mature, dry seed heads were collected in the field, then post-processed to isolate the propagules. For *P. dilatatum*, where seeds ripen sequentially on their raceme, care was taken to remove only mature caryopses and those unaffected by the common ergot fungus *Claviceps paspali*, which reduces germination success (Tischler and Burson 1999). For *E. curvula*, seed heads were hand-sieved and winnowed in a laboratory to separate the seeds from the chaff. Once isolated, seeds from each species were homogenised and stored in paper bags under ambient conditions until their introduction into mesocosms.

As propagule pressure is one of the main determinants of invasion success (Lockwood et al. 2009; Simberloff 2009), seed germination trials were conducted to ensure analogous rates of invasion between species treatments. In a pilot study, for each species, five replicates of 20 seeds were placed between two moist sheets of filter paper in petri dishes for 7 days. Seeds were declared viable if a radicle was visible following this period. Germination success was low in both species with only $7.0 \pm 2.0\%$ viability in *P. dilatatum* and $14.0 \pm 2.9\%$ in *E. curvula* which is consistent with previous assessments (i.e. Schrauf et al. 1995; Roberts et al. 2021). It was therefore estimated that for equivalent invasion treatments, *E. curvula* required half the number of seeds compared to *P. dilatatum*.

A simulated invasion by *P. dilatatum* and *E. curvula* was induced in the mesocosms on 1st September 2023, one month after the initial establishment of the native mesocosm assemblages. At this stage, most of

the native species were well-established and displaying active above-ground growth. At this time, 100 *P. dilatatum* and 50 *E. curvula* seeds were added to their respective mesocosms by mixing the seed with 100 g of coarse river sand and 100 g of finely sieved CPW topsoil and hand-broadcasting the mix onto the soil surface. Exotic grasses were introduced as seeds to simulate the natural dynamics of their arrival into native communities (van Klinken and Friedel 2017). The experiment ran for a duration of 6 months; commencing with the addition of invasive grass seed in September 2023 and culminating with the destructive sampling of each mesocosm's constituent plants in February 2024.

Data collection

The total number of invasive plants in each mesocosm was determined by counting the number of emerging seedlings for each species at the beginning of every month, commencing October 2023, once they could be robustly identified from other monocotyledonous alien species. Individuals were counted following the emergence of an epicotyl and only living seedlings were counted.

A measure of relative total leaf area of invasive grass per mesocosm was calculated during the monthly sampling period as a proxy for invasive plant growth. Using three of the largest invasive grasses per pot on the sampling days, the mean area of invasive grass foliage in each individual mesocosm was measured using a modified equation from Kemp (1960) as follows:

$$A_i = \sum_{n=1}^3 0.905 \times (L_n \times B_n)$$

where, A_i =average leaf area of the i^{th} mesocosm, 0.905=an allometric constant for grass leaf area derived by Kemp (1960), L =absolute length of the leaf from apex to ligule, and, B =absolute breadth of the leaf midway along the blade.

Every leaf on the three largest plants were measured by a sole observer using a ruler and 10×hand lens. Measurements were only made when leaves were fully turgid and only living biomass was included.

At the culmination of the experiment in February 2024, the specific leaf area of the invasive grass in

each mesocosm was calculated using three randomly selected leaves from individuals in each mesocosm. All leaves were mature, entire and unblemished. The area of each leaf from leaf apex to ligule was measured using a portable leaf area meter (LI-COR LI-3000A; LI-COR Inc.) before being immediately dried at 75 °C to a constant weight (± 0.001 g). Specific leaf area was calculated sensu Evans (1972) as follows:

$$SLA = \frac{\text{Total leaf area (mm}^2\text{)}}{\text{Dry leaf weight (mg)}}$$

The biomass of the invasive grass and native species in each mesocosm was measured at the culmination of the experiment by harvesting all the individuals at ground-level, bagging and drying the biomass at 75 °C to a constant weight (± 0.001 g). In some low richness mesocosms, some rhizomatous or stoloniferous native plants (i.e. *Dichondra repens*, *Goodenia paniculata*, *Viola hederacea*) were unable to be separated into discrete individuals, thus biomass was pooled and divided by 4 to attain the average weight of each individual planted into the mesocosm.

Statistical analyses

To test our prediction that the number of individuals, growth rate, and biomass of both invasive species would be lower in high- than low-richness mesocosms and vary between light intensity treatments, we used 3-way repeated-measures ANOVAs to evaluate temporal trajectories of emergence and survival. Light intensity and species richness were included as between-subject main effects and time (factor with five levels, i.e. the sampling dates) as the within-subject main effect. We incorporated time as a repeated factor to capture early emergence and establishment dynamics, which are central components of invasion success and may differ from final biomass outcomes. Where the analyses identified a significant interaction between time and a main effect, the effects of each treatment were compared for each time period separately. Within each time period, differences between each main effect were determined via a Tukey's *post-hoc* test.

To evaluate the prediction that phenotypic plasticity in leaf traits would vary across richness and light treatments, we analysed changes in relative leaf area

over time using repeated-measures ANOVA. The data was log transformed to fulfil assumptions of normality and curtail large outliers. For each model, assumptions of normality were confirmed using a Shapiro–Wilk test (accepted when $p > 0.05$) and homogeneity of variance was tested using Mauchly’s Test for Sphericity. As this test was repeatedly violated by all repeated measures ANOVA models ($p < 0.05$), Greenhouse–Geisser corrections were applied. These statistics and corrections were performed using the ‘afex’ package within R v.4.3.2 (R Core Team 2025; Singmann et al. 2015). Similarly, we analysed the effect of richness and light treatments on specific leaf area of both invasive grasses using a two-factor ANOVA, with light intensity and richness as fixed effects plus an interaction term.

Moreover, to isolate the impacts of native species richness associated with biomass from other impacts, we performed a three-way ANCOVAs testing the effect of light intensity, richness and native biomass on invasive grass biomass. Subsequently, as invasive biomass showed a significant, non-linear relationship with native biomass for both species, overall invasive biomass was modelled with a power analysis and collective invasive biomass categories (< 50 g/mesocosm and > 50 g/mesocosm) were modelled with linear regression analyses to model the direction and strength of the relationships.

To investigate the presence of sampling effects in the pool of native species, we undertook analyses to identify strong influential species. Distance-based linear models (DISTLMs) were run for each invasive grass separately. DISTLM partitioned the variance in invasive biomass according to a multiple-regression analysis and is an ideal distance-based model for elucidating the interactions between factors in a multivariate dataset where non-Euclidean distances are to be expected (i.e. species biomass) (Legendre and Anderson 1999). Moreover, as it uses non-parametric permutation methods, it is suitable for unbalanced datasets which do not meet assumptions of multivariate normality, such as the data collected by this study, where each mesocosm had a unique assemblage of native species drawn at random from a larger pool.

Initially, DISTLM was used to investigate which functional groups explained variation in invasive biomass. Subsequently, we used DISTLM on the critical functional groups identified in the previous model to determine whether there were important species

within that functional group that were invoking resistance (i.e. sampling effects). Akaike’s information criterion (AIC) selection metrics with 999 randomized permutations were used to select the best DISTLM models. A distance-based redundancy analysis was then undertaken to visualise the best model relationships and marginal tests were used to understand the strength of the chosen species in influencing biomass. All DISTLM procedures were performed using the PERMANOVA+ package in Primer v.7 (Anderson et al. 2008).

Results

Differences in native assemblage richness and light intensity had significant effects on the invasion success of both exotic grasses in mesocosms. The mean number of *P. dilatatum* individuals per mesocosm varied significantly in a three-way interaction between richness, light intensity and time ($F_{1,6, 31,9} = 9.84$, $p = 0.001$). Emergence of *P. dilatatum* individuals was highest in the full sun, low richness treatment, visible as a unimodal spike in November ($F_{1, 20} = 4.49$, $p = 0.047$) (Fig. 2a). The mean number of *E. curvula* individuals per mesocosm varied significantly in response to richness ($F_{1, 20} = 4.44$, $p = 0.048$) and light main effects ($F_{1, 20} = 5.31$, $p = 0.032$) however, an interaction between light and time was also identified ($F_{1,4, 29,8} = 5.87$, $p = 0.012$). Emergence of *E. curvula* individuals was lowest in the shaded, high richness treatment ($F_{1, 20} = 4.88$, $p = 0.038$; Tukey test: $P = 0.05$; Shade/High $<$ all other treatments), and stayed low, with richness displaying a significant effect on *E. curvula* establishment in the shaded treatment, but not full sun at the culmination of the experiment ($F_{1, 20} = 7.82$, $p = 0.011$; Tukey test: $p = 0.05$; Shade/High $<$ Shade/Low $<$ Sun/High = Sun/Low; Fig. 2b). Notably, the rank order of treatment combinations was the same for both exotic species at the experiment’s conclusion (Shade/High $<$ Shade/Low $<$ Sun/High $<$ Sun/Low). Interactions between light and time manifested in both exotic species as greater germination success in full sun treatments followed by a greater decline in seedling survival in shaded treatments as the experiment progressed. The effect of richness on seedling establishment over time appeared to manifest differently between both grasses, with the strongest negative influence on *P.*

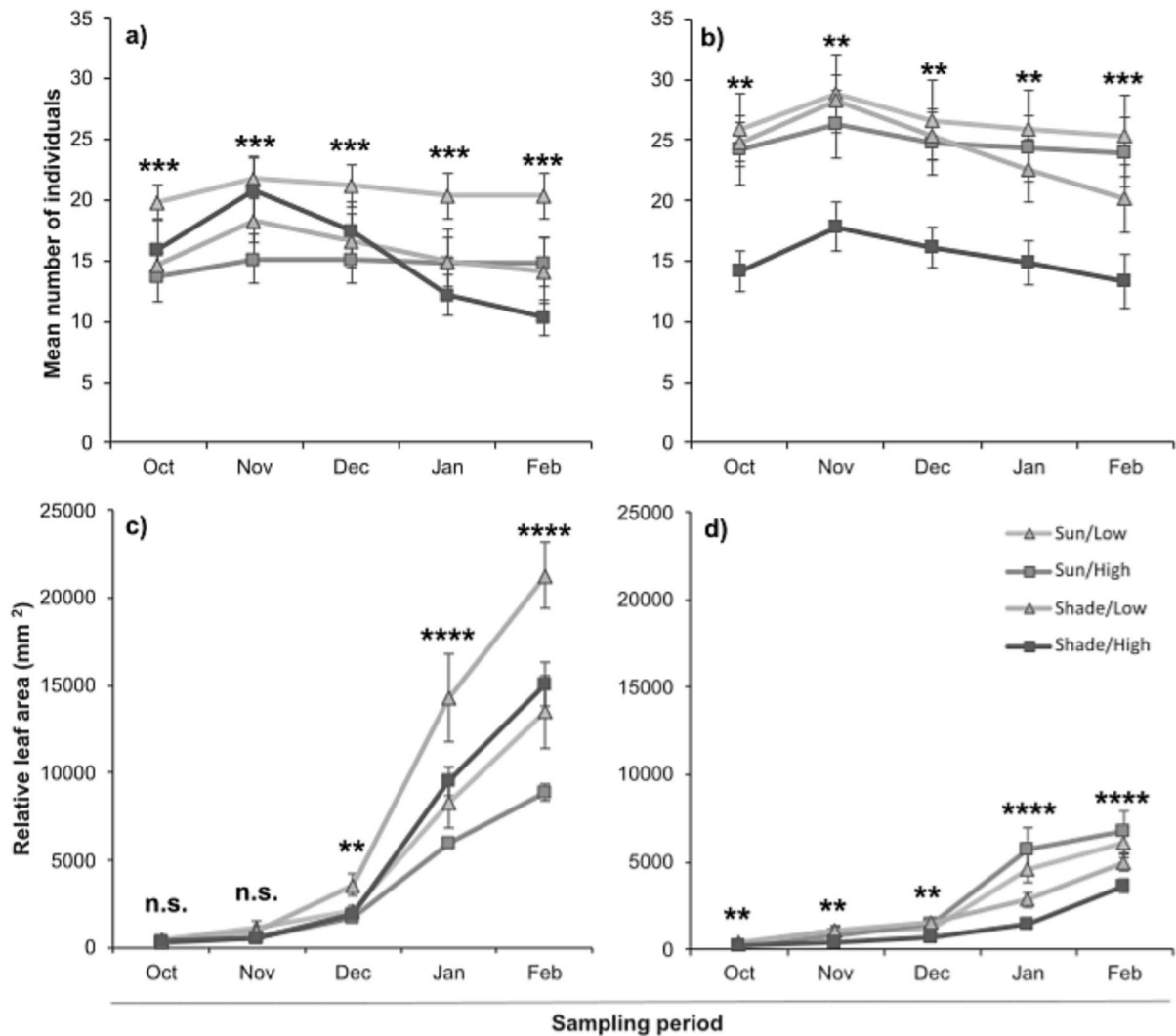


Fig. 2 Mean number of **a** *P. dilatatum* and **b** *E. curvula* individuals in mesocosms of each treatment combination over the sampling period. Germination of invasive grass occurred between October–November and seedling mortality between November–February. Mean relative leaf area of **c** *P. dilatatum* and **d** *E. curvula* individuals in mesocosms of each treat-

ment combination. Data presented are the pooled leaf area of the three largest individuals per mesocosm. Error bars denote standard error ($n = 6$) and asterisks denote the number of significantly different means as per Tukey HSD post-hoc tests. Asterisks between means denote significance at $p = 0.05$ (*), 0.010 (**) and <0.001 (***)

dilatatum visible at the culmination of the experiment across both light treatments. While for *E. curvula*, the high richness treatment displayed a more consistent negative effect on seedling establishment as the experiment progressed and was much greater in shaded treatments.

The mean relative leaf area of both exotic grasses displayed significant three-way interactions between richness, light intensity and time. Month by month

analysis indicated that this interaction in *P. dilatatum* was driven by the i) increasing strength of both light and richness' effects across the study period, which was not evident in the first two months (October and November), ii) significantly greater relative leaf area in shaded mesocosms in January ($F_{1, 20} = 12.01$, $p = 0.002$) and iii) significantly greater relative leaf area in shaded ($F_{1, 20} = 24.46$, $p = >0.001$) and low richness mesocosms ($F_{1, 20} = 12.00$, $p = 0.002$) in

February (Fig. 2c). Month by month analysis suggested this interaction had arisen from a shift from richness-dominated effects to light-dominated effects across the study period. Mean relative leaf area for *E. curvula* was lower in high richness mesocosms in October ($F_{1, 20}=7.52$, $p=0.012$) and November ($F_{1, 20}=11.15$, $p=0.003$), whilst a significant interaction between light and richness in December ($F_{1, 20}=10.02$, $p=0.004$) marks a shift to solely light-mediated effects in January ($F_{1, 20}=21.35$, $p=>0.001$) and February ($F_{1, 20}=8.61$, $p=0.008$) (Fig. 2d). Whilst *E. curvula* displayed greater relative leaf area in full sun treatments, the temporal variation in the effects of richness and light intensity observed for both species suggest differences in interspecific competitive trait strategies.

Both invasive grasses displayed significant differences in trait morphology in response to light intensity and native species richness treatments, indicative of abiotic and biotic stress during invasion. The specific leaf area of *P. dilatatum* was significantly higher in shaded mesocosms ($F_{1, 68}=358.0$, $p=>0.001$) and in mesocosms with high native richness ($F_{1, 68}=5.055$, $p=0.027$). A congruous response was observed in *E. curvula*, which also displayed higher SLA in shaded mesocosms ($F_{1, 68}=202.1$, $p=>0.001$) and those with high native richness ($F_{1, 68}=8.815$, $p=0.004$). Notably, the mean SLA of *E. curvula* was approximately one-quarter of *P. dilatatum*'s mean SLA across all treatment groups (Fig. 3a, b). Similarly, the final above-ground biomass of both *P. dilatatum* and *E. curvula* was significantly lower in high richness and shaded mesocosms (Fig. 3c, d; Table 1a). The biomass of the native assemblages was not significantly different between richness or light intensity treatments seeded with either exotic species, indicating that assemblage biomass was not confounding any significant 'richness' effects identified in the analyses (Table 1b).

A strong negative relationship between invasive biomass and above-ground native biomass was observed in the power analyses models for both *P. dilatatum* ($F_{1, 16}=10.05$, $p=0.005$) (Fig. 4a) and *E. curvula* ($F_{1, 16}=12.07$, $p=0.003$) (Fig. 4b). Sharp declines in the biomass of both invasive species were observed with increasing native biomass until pooled native biomass reached 50 g, after which a relatively neutral relationship emerges which may

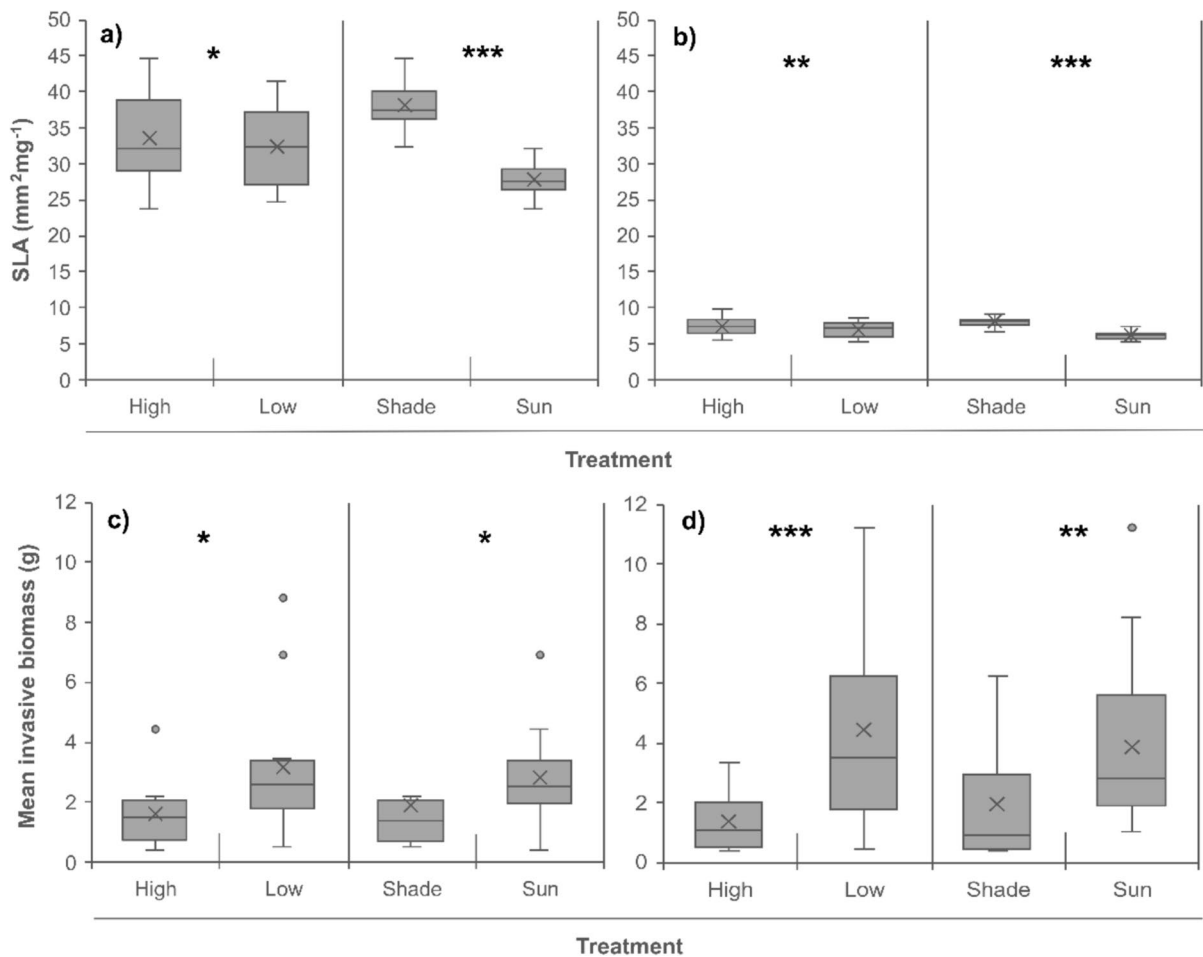
reflect community-level complementarity in invasion resistance.

Moreover, species-level and functional group effects identified by DISTLM analyses suggest sampling effects may also underlie invasion resistance in this system. For *P. dilatatum*, only two functional groups were incorporated into the best DISTLM model to explain 34% of the variation in biomass; shrubs and grasses (Fig. 5a). As a group, shrubs had a positive relationship with *P. dilatatum* biomass. Within the shrubs, *Bursaria spinosa* and *Goodenia paniculata* were the most influential in this relationship but each only accounted for about 11% of the variation. For grasses, four species contributed to the best model. *Cymbopogon refractus* and *Microlaena stipoides* did not significantly influence invasive biomass only accounting for about 10% of variation in the models, however *Poa labillardierei* and *Themeda triandra* were significantly negatively related to invasive biomass, accounting for 25 and 14% of the variation, respectively. While *T. triandra* remained small, growing slowly over the duration of the experiment, *P. labillardierei* accumulated more biomass than all other grasses.

For *E. curvula*, all functional groups, except shrubs, were incorporated into the best model to explain 56% of the variation in biomass (Fig. 5b). In marginal tests (where each functional group is tested alone), shrubs were highly significant, explaining 22% of variation and were positively related to *E. curvula* biomass. Within each functional group the best models included only one species; for herbs, *Germanium solanderi*, for graminoids, *Lomandra longifolia*, for grasses, *Poa labillardierei*, and for legumes, *Acacia linifolia*. However, only *Poa labillardierei* and *Lomandra longifolia* had a significant negative effect on *E. curvula* biomass, accounting for 26% and 21% of the variation, respectively.

Discussion

The study provided evidence indicating that native species richness confers resistance to invasion extending across the breadth of an invasion event, reducing invasive propagule success and altering the leaf morphology of an invader once established. The species richness of a floristic community is considered to be one of the principal factors contributing to



treatments ($n = 36$). Boxplots represent mean (cross), median (horizontal line), 25th and 75th quartiles and whiskers represent 1.5x the interquartile range. Outlying values are displayed as circles. Asterisks between means denote significance at $p = 0.05$ (*), 0.010 (**) and <0.001 (***)

community resistance to exotic plant invasion (Elton 1958; Levine and D'Antonio 1999; Bjarnason et al. 2017) although the mechanisms involved in resistance can vary. Here, the biotic interactions between common understory plant species associated with CPW and two highly invasive grasses, *P. dilatatum* and *E. curvula*, are empirically quantified for the first time. Increased species richness reduced the invasion of both grasses, at the emergence stage and later at the seedling stage, particularly in high light environments. This included a reduction in the number of individuals and their overall biomass of both invasive grasses. This is despite evidence that both grasses

showed phenotypic variation in the SLA induced by different light and species richness treatments, suggesting phenotypic plasticity is a contributor to their invasion success (Hiatt and Flory 2019). Furthermore, we were able to identify species that were more influential in this resistance, as well as some evidence of niche-based mechanisms facilitating resistance.

Seedling emergence and survival through time

The emergence of both grasses was mediated by the richness of sympatric native assemblages; however, species-specific responses were observed. The

Table 1 Native + invasive biomass vs richness and light a. Results of a three-way ANCOVA for effects of light, richness and native biomass on invasive grass biomass. b. Results of atwo-way ANOVA for effects of light and richness treatments on native biomass across *P. dilatatum* and *E. curvula* invasion challenges

Response variable								
Source of variation	<i>P. dilatatum</i>				<i>E. curvula</i>			
	<i>df</i>	MS	F	<i>p</i>	<i>df</i>	MS	F	<i>p</i>
a) <i>Invasive biomass</i>								
Light	1	1.860	5.183	0.037*	1	4.859	12.07	0.003**
Richness	1	2.118	5.901	0.027*	1	7.239	17.98	<0.001***
Native biomass	1	3.609	10.05	0.006**	1	1.911	4.746	0.045*
Light × Richness	1	0.078	0.217	0.648	1	0.708	1.758	0.203
Light × Native biomass	1	0.064	0.179	0.677	1	0.648	1.608	0.223
Richness × Native biomass	1	0.462	1.286	0.274	1	0.321	0.797	0.385
Light × Richness × Native biomass	1	0.096	0.267	0.612	1	0.359	0.891	0.359
Residuals	16	0.359			16	0.403		
b) <i>Native biomass</i>								
Light	1	340.0	0.253	0.620	1	778.7	1.948	0.178
Richness	1	2947	2.195	0.154	1	1492	3.733	0.068
Light × Richness	1	3805	2.834	0.108	1	16.70	0.042	0.840
Residuals	20	1343			20	399.7		

Statistically significant results are in bold and asterisks denote significance at $p=0.05$ (*), $p=0.010$ (**) and $p<0.001$ (***)

emergence of *P. dilatatum* was lowest in the full sun, high richness mesocosms and highest in sunny, low richness mesocosms, with shady environments experiencing a delayed germination (peaking in November). Given the differential response in shade and sunlight towards species richness, these results suggest that light intensity, rather than richness, is a strong mediator of emergence in this species. However, while post-emergence establishment remained the same in sunny mesocosms, survival through time declined in shady environments, particularly in high richness mesocosms. This concurs with our predictions, and other studies purporting a compounding negative effect of shading and native species richness on invasive plant success (Milbau et al. 2005; Naeem et al. 2000).

The emergence of *E. curvula* was consistently higher in low richness mesocosms irrespective of light treatment, supporting the notion that richness provides invasion resistance. Similarly to *P. dilatatum*, survival through time in shady environments declined over the experiment's duration, indicating that resistance is stronger in shadier environments.

Many invasive grasses exhibit high germination rates under a broad range of light conditions conferring broader colonisation optima in novel environments (i.e. Chejara et al. 2008; Tinoco-Ojanguren et al. 2016; Pham and Wu 2023). Germination plasticity resulting in the breaking of seed dormancy when conditions are unfavourable for seedling persistence may constitute a maladaptive response in these species (Hauvermale and Sanad 2019). However, as *P. dilatatum* and *E. curvula* are highly fecund, perennial flora (Schrauf et al. 1995; Roberts et al. 2021), this is unlikely to contribute significant reductions in the fitness of a novel population during the invasion process. Conversely, it is more likely that the germination plasticity in both these species is adaptive, and shade-induced mortality is due to high post-emergence competitive pressures in the mesocosms, despite the moderate shade tolerance of both grasses (Gomes and Asaeda 2009; Barro et al. 2012). Where shaded environments displayed unfavourable but reasonable abiotic conditions, a highly adverse biotic environment with strong niche pre-emption by native flora excluded these individuals.

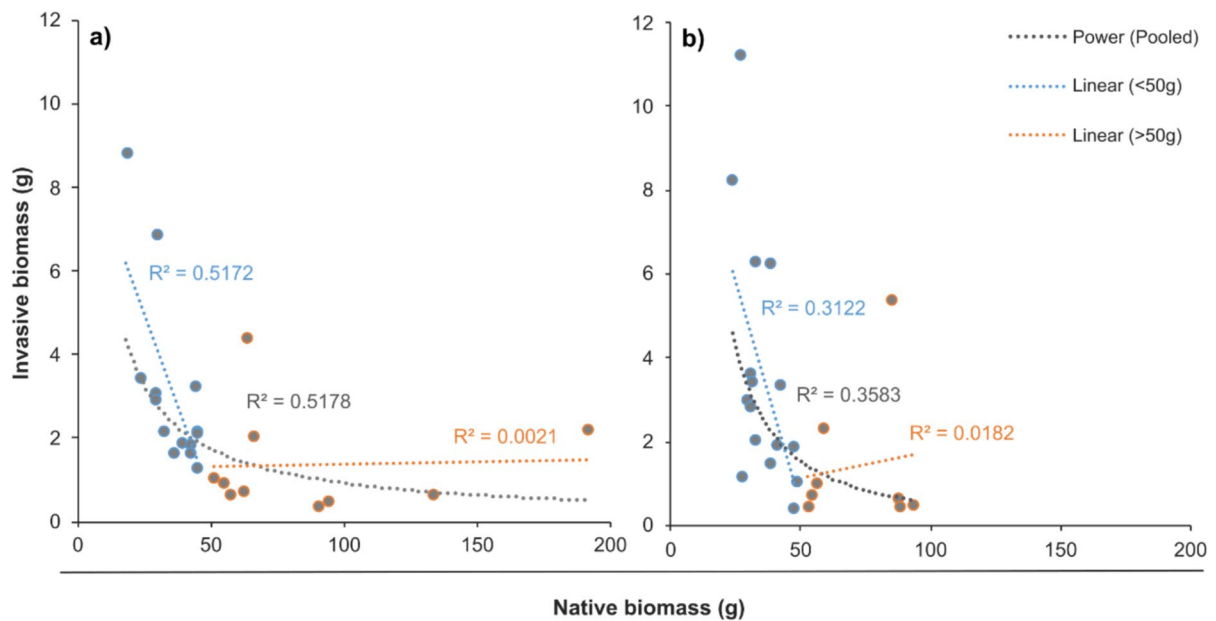


Fig. 4 Relationship between the above-ground biomass of **a** *P. dilatatum* and **b** *E. curvula* and the pooled above-ground native biomass. Data are further partitioned into two categories:

less than 50g of invasive biomass, greater than 50g of invasive biomass. Linear and power regression trend lines for partitioned and pooled data, respectively, are displayed

High richness mesocosms are more likely to contain a native species with greater resource acquisition which inhibits the invader, but it also predicts that there is likely a native species with inhibitory allelopathic effects on germinating grass (Wardle 2001). Allelochemical activity has been identified in many of our experimental native species' congeners (i.e. *Acacia*—Fatonbi et al. 2009; *Eremophila*—Sadgrove et al. 2021; *Melaleuca*—Baumann and Hewitt 2023; *Geranium*—Dennehy et al. 2011) but the use of allelopathy in our study species remains unknown. Similarly, the floristic richness of south-eastern Australian woodlands is positively associated with fungal diversity (Barrett et al. 2009), suggesting that in high richness mesocosms there may be an increased probability of invasive grass seed encountering a parasitic or pathogenic fungi which inhibits its germination. Differences in species' susceptibility to allelochemicals and fungal pathogens may underlie the strength of richness' effects on propagule success and the discrepancies observed between *P. dilatatum* and *E. curvula*. As this study presents one of the first experimental investigations into the effects of native community richness on an invaders' germination success, these findings present basic evidence upon which

future studies may elucidate the presence of these drivers and their mechanisms of action.

Leaf morphological response of invaders

As predicted, both *P. dilatatum* and *E. curvula* displayed significant morphological differences between light and richness treatments, consistent with the tendency for invasive plants to exhibit phenotypic plasticity in response to low-resource environments (Richards et al. 2006; Firn et al. 2012). Shade-induced increases in SLA are well documented (Evans and Pooter 2001; Liu et al. 2016; Gruntman et al. 2019) and here, specific leaf area increased by ~40% and ~30% for shaded *P. dilatatum* and *E. curvula*, respectively. By increasing SLA in low light environments, plants reduce the density of photosynthetic machinery per unit area (Tardella et al. 2017), therefore utilizing diffuse radiation more efficiently and achieving greater growth in these environments (Fynn et al. 2011). However, the observed SLA of *P. dilatatum* was approximately four times greater than *E. curvula* across the treatment groups and indicates supports our hypothesised differences in light resource acquisition between invasive species. Biomass gains

in shaded individuals of *P. dilatatum* may have manifested as a higher mean relative leaf area, indicating fewer but larger individuals establishing through time. As a result of lower survival, there were only smaller differences in the final biomass between light intensity treatments.

Conversely, *E. curvula* had much greater biomass in low richness mesocosms and in sunny conditions, suggesting these kinds of environments which mimic restoration communities have lowest resistance to invasion. Plants in this environment had higher relative leaf area, lower SLA and less plant mortality. Lower SLA leaves utilise high irradiance more efficiently (Tardella et al. 2017), yielding a greater competitive advantage in full sun as reflected in *E. curvula*'s higher overall biomass in this environment compared to *P. dilatatum*, but a greater discrepancy in biomass between light-intensity treatments.

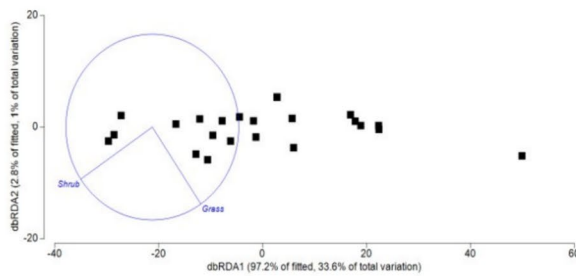
Importantly, the SLA of both species increased significantly in high richness mesocosms indicating a shift towards a more competitive, ruderal strategy potentially resulting from increased competition in these assemblages. It is unknown, however, whether competition-mediated increases in SLA are also adaptive in origin or occurs passively as a consequence of decreased resource abundance and thus, decreased resource allocation to leaf architecture (Xu et al. 2009). Regardless, the higher SLA plasticity observed in *P. dilatatum* in response to full sun may indicate a stress-tolerance strategy underpinning invasion success in this species, whilst the greater biomass accumulation of *E. curvula* in full sun suggests it may utilise a contrasting, resource-acquisition strategy (Conti et al. 2018).

Sampling and complementarity effects

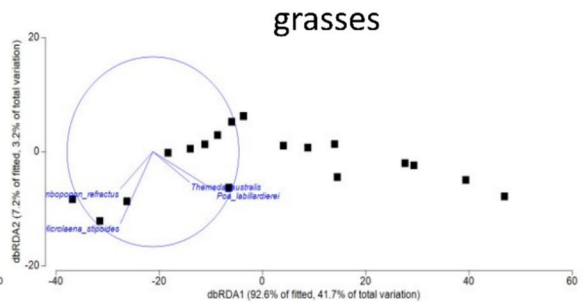
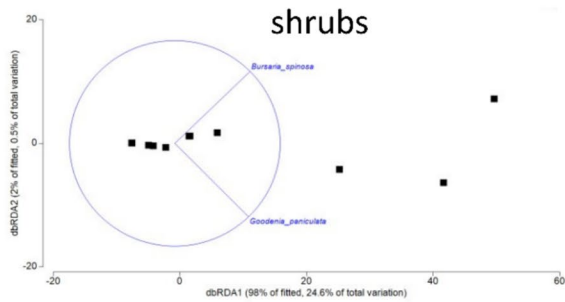
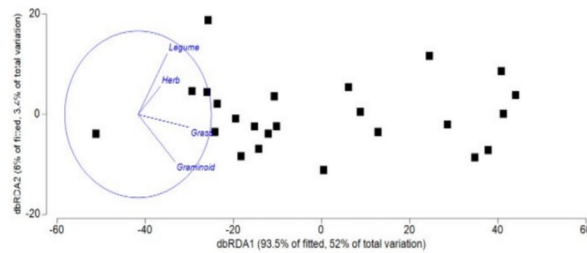
The biomass of both invasive grasses was significantly reduced in high richness mesocosms as predicted by the 'diversity-resistance hypothesis' (Elton 1958) and repeatedly observed in other, small scale, experimental studies (see Levine et al. 2004). We found some evidence that some species were more competitive and contribute to overall community resistance, but there was also evidence of niche-filling with the presence of a number of functional groups having influence.

For both species, shrubs had an overall positive effect on biomass of invasive species. Two reasons may be pertinent here. A positive correlation between the growth of native and invasive flora may reflect a facilitatory, 'portfolio effect' (Schindler et al. 2010). Small statured woody plants may enhance the establishment of an invader by ameliorating undesirable microclimatic or soil conditions, increasing an invader's realised spatial niche (Bruno et al. 2003; Griffith 2010). Where the abiotic environment of the mesocosms in full sun was considerably harsher than shaded treatments (i.e. increased solar radiation, ambient temperature, wind exposure), there was no significant difference in strength of the relationship between native shrub and *P. dilatatum* biomass between light intensity treatments (Appendix 2) suggesting this mechanism is unlikely. Rather, a positive relationship between shrub and *P. dilatatum* biomass may result from the absence of any meaningful interaction between the groups, as a result of large differences in the realised niches of sympatric shrubs and grasses. Xu et al. (2021) demonstrated that shrubs and grasses share little niche overlap in stable grassland communities, as a result of variation in N/P acquisition strategies and rooting depth. As such, the growth of these groups may positively covary as a result of analogous responses to shared abiotic stressors, where the strength of these abiotic interactions is more significant than the strength of any intraspecific relationship, positive or negative, between the functional groups.

Despite these positive associations, there was still an overall negative effect associated with species-rich mesocosms with evidence of strong influence by some species. Sampling effects are strongest between species which share the same realised or functional niche (MacArthur and Levins 1967; MacDougall et al. 2009) or are taxonomically similar (Fox 1987; Adler et al. 2018) substantiating the finding that increases in grass biomass induced significant decreases in the biomass of both invasive grasses. Indeed, one species alone, *Poa labillarderei*, explained 25% and 26% of the variation in *P. dilatatum* and *E. curvula* biomass, respectively. Competitive exclusion of invasive grasses by their native counterparts is well documented in Australia (Prober and Lunt 2008; 2009) and abroad (Fargione and Tilman 2005; van Klinken and Friedel 2017) and has been attributed to overlap

a) *Paspalum dilatatum*

Species	Marginal test Pseudo F, P	Slope	Prop.
<i>Goodenia paniculata</i>	2.854, 0.084	+ve	0.115
<i>Bursaria spinosa</i>	2.727, 0.09	+ve	0.110
<i>Poa labillardierei</i>	7.456, 0.002	-ve	0.253
<i>Themeda triandra</i>	3.471, 0.048	-ve	0.136
<i>Cymbopogon refractus</i>	2.151, 0.143	+ve	0.089
<i>Microlaena stipoides</i>	2.606, 0.097	+ve	0.106

b) *Eragrostis curvula*

Species	Marginal test Pseudo F, P	Slope	Prop.
<i>Acacia linifolia</i>	1.096, 0.398	+ve	0.047
<i>Geranium solanderi</i>	2.689, 0.085	-ve	0.109
<i>Poa labillardierei</i>	8.021, 0.003	-ve	0.267
<i>Lomandra longifolia</i>	6.075, 0.005	-ve	0.216

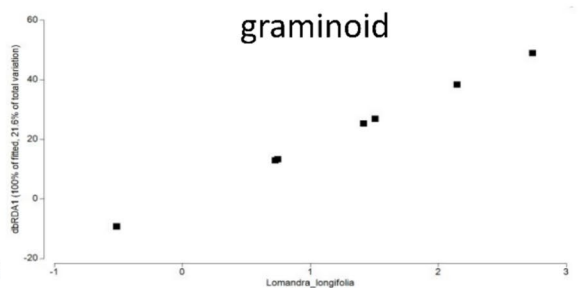
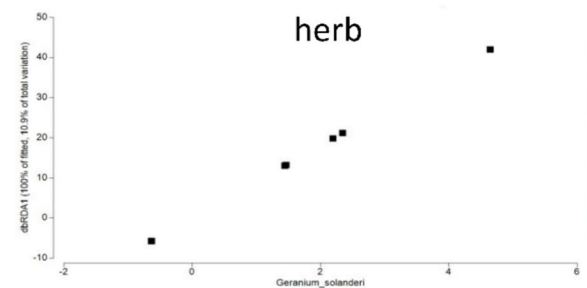
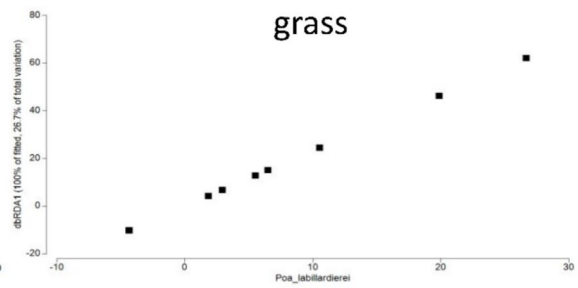
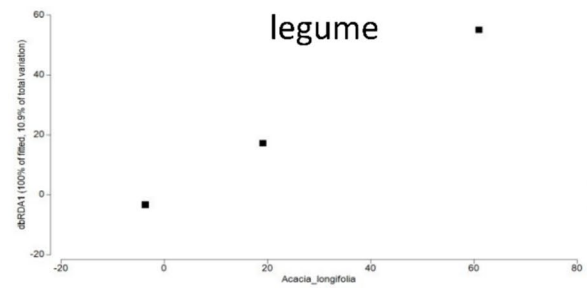


Fig. 5 Distance based redundancy analysis of stepwise models resulting from the best model identified in the distance-based linear modelling of the effects of native species biomass on **a** *P. dilatatum* and **b** *E. curvula* biomass. Results of marginal tests, where an individual species was identified as having a significant individual effect on invasive grass biomass, are tabulated. Prop. is the proportion of total variation explained by the species

in the phenology, rooting depth and nitrogen acquisition of these groups (Fargione 2004). For *P. dilatatum*, there was also positive associations with two other grasses, *Cymbopogon refractus* and *Microlaena stipoides*. Further work will be required to elucidate how such different interactions can arise from similar taxonomic groups.

The biomass of *E. curvula* was best explained by DISTLM models containing species from 4 out of 5 functional groups, suggesting that community-wide complementarity, in either resource-use or functional trait expression is a principal component of ecosystem resistance to invasion by this species. Complementarity between invasive plants and native assemblages in their use of nutrients, water or subterranean space is likely to result in the inhibition of invasive plant growth (MacDougall et al. 2009; Zhu et al. 2015; Byun et al. 2017), particularly in systems where niche pre-emption by native flora has occurred (Mwangi et al. 2006). However, within these functional groups, the main effect was associated with a negative impact by one species in three of the functional groups. Ongoing investigations are required to confirm this pattern of complementarity and the potential for a synergistic competitive effect when these species occur together, rather than in isolation. Without quantifying resource use between richness treatments, the strength of resource-use complementarity in this system remains equivocal, however, clear indications of sampling effects were observed. Similarly, while measures of below-ground biomass were deemed beyond the scope of this study, competition strength differs in magnitude between below and above-ground grassland species (Price et al. 2012; Aoyama et al. 2023, warranting further investigations to elucidate alternative methods of native community resistance.

Ecosystem resistance

Interestingly, the negative relationship between native biomass and the biomass of both invasive species was non-linear with rapid reductions in invasive biomass observed until native biomass exceeded 50 g per mesocosm, after which invasive biomass remained relatively low. This is a possible indication of a 'biotic resistance threshold' in this system (Chakraborty and Li 2010; Diez et al. 2012), that is, a theoretical point at which CPW plant assemblages achieve (or retain) the ability to resist the establishment of *P. dilatatum* and *E. curvula*. The biotic resistance threshold observed here comprises two distinct functional relationships between invasive grass and the recipient community: (1) the potential for invasive grass establishment at low levels of native biomass below the threshold, and (2) the rapid inhibition of invasive grass establishment once native biomass exceeds the threshold. The first part of the relationship may result from incomplete utilisation of limiting resources by native species below the threshold, where less niche overlap limits intraspecific competitive interactions between native and invasive flora, allowing invasion to occur (MacDougall et al. 2009; Byun et al. 2017). The biotic resistance threshold signals a subsequent shift towards a critical point of resource uptake by the native community, beyond which little is left for invaders to exploit. Moreover, as community biomass increases, concurrent increases in interspecific competition strength can be expected to further augment biotic resistance reducing the establishment of invaders (Downing et al. 2012).

Conclusion

Here, we identify evidence for multiple mechanisms which confer invasion resistance manifesting from strong, inhibitory, biotic interactions at the interspecific level (i.e. sampling effects) and community level (i.e. complementarity). We conclude that woodland ecosystems are most resistant to invasion by exotic grasses where the recipient native community is taxonomically rich and highly productive,

minimising the niche space available for invaders to exploit (Byun et al. 2023). However, the results of this study suggest that substantial contributions are made either side of the niche, where high native richness may limit an invader's ability to emerge into a niche as well as their capacity to exploit a niche post-establishment, particularly where resources (i.e. light) are already limited.

As such, attempts to restore or ameliorate woodland ecosystems impacted by exotic grass invasion should focus on measures designed to rapidly increase the diversity and biomass of native flora, as reductions in the establishment success of new individuals and fitness of existing populations are likely to be realised, concurrently. However, landscape-scale, in-situ studies will be required to confirm how the interspecific interactions identified here, and their significance in applied restoration efforts, change in response to scale-dependent variation in disturbance history, resource availability and herbivore pressure (Chen et al. 2021; Wang et al. 2022; Morrison et al. 2023). Similarly, further experimental inquiry which examines the effect of native community richness on the trait expression and germination success of invaders from additional functional groups, and across varied ecosystem types

will be necessary to confirm these as important mechanisms of plant invasion resistance.

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Author contributions All authors contributed to the study conception and design. Mesocosm preparation and data collection were performed by Charles Gluskie. Data analysis was performed by Charles Gluskie and Kris French. The first draft of the manuscript was written by Charles Gluskie and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data on the invasive and native species recorded during this study and presented herein, are included within this paper and its Supplementary Information files.

Appendix

See Tables 2 and 3.

Table 2 Definitions of the floristic functional groups used in this experiment and their constituent pool of species

Functional group	
<i>i) Graminoids – Herbaceous, grass-like flora with narrow leaves and extended culms</i>	
<i>Caesia parviflora</i> R.Br. var. <i>parviflora</i>	Anthericaceae
<i>Dianella longifolia</i> R.Br. var. <i>longifolia</i>	Phormiaceae
<i>Dianella revoluta</i> R.Br.	Phormiaceae
<i>Jucus usitatus</i> L.A.S.Johnson	Juncaeae
<i>Laxmannia gracilis</i> R.Br.	Asparagaceae
<i>Lomandra longifolia</i> Labill	Asparagaceae
<i>ii) Herbs – Small statured (< 1 m tall) flora which do not develop persistent woody tissue</i>	
<i>Coronodium rutidolepis</i> (DC.) N.G. Walsh	Asteraceae
<i>Dichondra repens</i> J.R.Forst. & G.Forst	Convolvulaceae
<i>Eremophila debilis</i> (Andrews) Chinnock	Scrophulariaceae
<i>Geranium solanderi</i> Carolin	Geraniaceae
<i>Lobelia purpureascens</i> R.Br.	Campanulaceae
<i>Viola hederacea</i> Labill	Violaceae
<i>Wahlenbergia stricta</i> (R.Br.) Sweet	Campanulaceae
<i>iii) Grasses – Any flora from the family Poaceae</i>	
<i>Bothriochloa macra</i> (Steud.) S.T.Blake	Poaceae
<i>Cymbopogon refractus</i> (R.Br.) A.Camus	Poaceae
<i>Dicanthum sericeum</i> (R.Br.) A.Camus	Poaceae
<i>Dichelachne micrantha</i> (Cav.) Domin	Poaceae
<i>Microlaena stipoides</i> (Labill.) R.Br. var. <i>stipoides</i>	Poaceae
<i>Poa labillardierei</i> Steud	Poaceae
<i>Rytidosperma longifolium</i> (R.Br.) Connor & Edgar	Poaceae
<i>Themeda australis</i> (R.Br.) Stapf	Poaceae
<i>iv) Legumes – Any flora from the family Fabaceae</i>	
<i>Acacia linifolia</i> (Vent.) Willd	Fabaceae; Mimosoideae
<i>Acacia longifolia</i> (Andrews) Willd	Fabaceae; Mimosoideae
<i>Daviesia genistifolia</i> A.Cunn ex Benth	Fabaceae; Faboideae
<i>Dillwynia retorta</i> (J.C.Wendl.) Druce	Fabaceae; Faboideae
<i>Pultenaea daphnoides</i> J.C.Wendl	Fabaceae; Faboideae
<i>Pultenaea villosa</i> Willd	Fabaceae; Faboideae
<i>Kennedia rubicunda</i> Vent	Fabaceae; Faboideae
<i>v) Shrubs – Woody, multi-stemmed perennial plant < 6 m tall</i>	
<i>Bursaria spinose</i> Cav	Pittosporaceae
<i>Hakea dactyloides</i> (Gaertn.) Cav	Proteaceae
<i>Goodenia paniculata</i> Sm	Goodeniaceae
<i>Kunzea ambigua</i> (Sm.) Druce	Myrtaceae
<i>Melaleuca thymifolia</i> Sm	Myrtaceae
<i>Pomax umbellata</i> (Gaertn.) Sol. ex A.Rich	Rubiaceae

Table 3 Results of a two-way ANCOVA examining the effect of light treatment and native shrub biomass on invasive grass biomass

Response variable				
Source of variation	<i>P. dilatatum</i>			
	df	MS	F	p
<i>a) Invasive biomass</i>				
Light	1	0.805	0.277	0.605
Native shrub biomass	1	25.75	8.849	0.008**
Light × Native shrub biomass	1	1.131	0.389	0.540
Residuals	23	91.56		

As there was no significant interaction between light intensity and shrub biomass on the biomass of either *P. dilatatum* or *E. curvula*, it was concluded that the positive effect of shrub biomass on invasive grass biomass was not due to an interaction with the climatic constituents of the experiment

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