

# Alien grass disrupts reproduction and post-settlement recruitment of co-occurring native vegetation: a mechanism for diversity decline in invaded forest?

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**Abstract** Invasive plants significantly threaten native plant biodiversity, yet the mechanisms by which they drive species losses and maintain their own dominance are poorly known. We examined the effects of alien grass invasion (*Stenotaphrum secundatum*) on (1) abundance and frequency of occurrence, (2) reproductive effort (flowering) and output (fruit production) and (3) soil seed banks for three focal native plants that are characteristic of endangered coastal forest of south-eastern Australia. First, we sampled and compared the foliage cover abundance and frequency (proportion of sites occupied) of the focal natives across invaded and non-invaded (reference) sites ( $n = 20$ ). We then intensively sampled reproductive effort and output (range of 5–9 sites per species), and density of propagules within

the soil (using a standard glasshouse ‘emergence’ method;  $n = 26$ ) for each species. Invasion was associated with reduced population sizes of all species within the standing vegetation but did not affect population frequency (i.e. proportion of sites where each species was present). Reproductive effort and output were about 75 % lower at invaded than native sites for all species. However, invasion had no effect on propagule densities of the focal natives within the seed bank, despite the substantial reduction in their reproduction. This indicates that the ultimate driver of population declines across invaded landscapes is post-settlement recruitment limitation from the seed bank (e.g. low rates of germination and seedling survival) rather than a reduction in the arrival and storage of propagules at invaded sites. Removal of *Stenotaphrum* alone might thus be sufficient to stimulate the recovery of native populations from the seed bank.

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*Stenotaphrum secundatum*

## Abbreviation

SLA Specific leaf area

## Introduction

Alien plant invaders are considered amongst the greatest threats to the biodiversity, structure and function of

indigenous plant communities at local and global scales (Vitousek et al. 1996, 1997; Mack et al. 2000). Recent comprehensive reviews (e.g. Gaertner et al. 2009; Vilà et al. 2011), as well as community-scale manipulative experiments (e.g. Green and Galatowitsch 2002; e.g. Flory and Clay 2010) have clearly shown that invasion is associated with significant reductions in native plant diversity and altered vegetation communities, yet there is less information on the mechanisms by which such changes are driven. To date, the majority of studies that seek to identify impact mechanisms have focused primarily on either direct competitive effects of invaders on the growth and persistence of co-occurring native plants, usually at small scales (see review by Daehler 2003), or indirect effects on native populations via changes to key ecosystem-level processes, such as disturbance regimes and nutrient cycling (see review by Levine et al. 2003). There is growing evidence that declining native populations are also driven by limited species recruitment (that is, the germination of propagules and the growth and survival of subsequent seedlings) at invaded sites, leading to the reduced viability, persistence and replacement of resident populations in invaded habitats, and ultimately declines in vegetation diversity (Ens and French 2008; Galbraith-Kent and Handel 2008).

Current evidence suggests that there are two main pathways by which invaders drive recruitment limitation of co-resident plant populations: first, by reducing the reproduction of co-occurring native plants through either direct competition for resources (D'Antonio et al. 1998), or disruption of pollinator services and/or pollen quality (Bjerknes et al. 2007; Morales and Traveset 2009). This, in turn, may reduce the density of propagules within the seed bank (especially for species with short distance dispersal strategies, whose declining reserves of seed may not be supplemented by immigrant seed from adjacent, non-invaded populations) and ultimately the number of propagules available for recruitment into the standing vegetation (Vilà and Gimeno 2007; Gioria and Osborne 2009). Second, invaders can limit the post-settlement recruitment by inhibiting the germination of propagules (e.g. Ens et al. 2009) or the subsequent survival of emergent recruits (e.g. Gorchov and Trisel 2003; Miller and Gorchov 2004). The relative importance of these processes to overall declines in native plant populations across invaded landscapes remains unknown, since they are most often studied in isolation.

We used invasion of an endangered coastal forest community by the alien turf-grass *Stenotaphrum secundatum* (Walter) Kuntze (hereafter termed *Stenotaphrum* for brevity) as a model to test whether native plant population declines in invaded communities are driven by either limited production of propagules or their dispersal to and storage within soil seed banks. *Stenotaphrum* is a stoloniferous, C<sub>4</sub> grass (Poaceae), native to the tropical and subtropical Atlantic coastlines of Africa and the Americas (Sauer 1972). It is widely used throughout eastern Australia as an urban and recreational turf grass, particularly in coastal areas. Recent research has shown that invaded forest has significantly fewer native species, both in the standing vegetation and seed bank, and lower rates of woody plant recruitment than non-invaded forest (Gooden and French 2014a, b), but it is unknown whether such declines are due to a reduction in the fitness and reproductive output of resident natives.

Specifically, we compared invaded with non-invaded (reference) sites to simultaneously examine effects of *Stenotaphrum* invasion on the (1) reproductive effort and output, (2) storage of propagules in the soil seed bank and (3) abundance and frequency of occurrence within the standing vegetation of three target native species: *Tetragonia tetragonioides* (Pall.) Kuntze (Aizoaceae), *Baumea juncea* (R.Br.) Palla (Cyperaceae) and *Juncus kraussii* Hochst (Juncaceae). Simultaneous examination of responses to invasion at each of these three key life-history stages will enable us to identify the point at which the invader limits recruitment and drives population declines. These species were chosen as they are characteristic of the swamp forest community (Tozer et al. 2010), are morphologically and phylogenetically distinct, and have different modes of pollination and propagule dispersal (Appendix S1 in Supplementary Material). Furthermore, we predicted that impacts of *Stenotaphrum* invasion will vary amongst the target species as a function of their different modes of pollination, seed dispersal and growth habit: i.e. populations of species which are insect-pollination and have the capacity for long-distance dispersal, such as *T. tetragonioides*, will be relatively less likely to decline in response to invasion because any in situ loss of propagules might be supplemented by immigrant ones from adjacent non-invaded sites. An understanding of such life-history traits may thus enable prediction of species' responses to invasion.

## Methods

### Study area and habitat

Each of the three studies consisted of comparisons (using standard comparative protocols outlined by Adair and Groves 1998) of each of the target species between *Stenotaphrum*-invaded and non-invaded (hereafter termed 'native') reference sites located within remnant stands of an endangered swamp oak floodplain forest community (Tozer et al. 2010), located along the southern coastline of New South Wales (NSW), south-eastern Australia, between Sydney (33°51' 54"S; 151°12'20"E) and Eden (37°03'55"S; 149°54'04"E). The study region has a warm temperate climate with mean annual rainfall of between 700 and 1,000 mm at Eden and Sydney, respectively, and mean annual temperatures ranging from 16 °C in winter to 25 °C in summer (Bureau of Meteorology 2012, 2013). The swamp forest community occurs on marine-derived, waterlogged sandy loams, bordering coastal estuaries and brackish floodplains. It has a very simple structure, characterised by a dense upper canopy dominated by the nitrogen-fixing tree *Casuarina glauca* Sieber ex Spreng, a very sparse shrub layer, and a semi-continuous, species-rich groundcover of forbs and graminoids (Tozer et al. 2010). The community is listed as endangered in NSW (Tozer et al. 2010; NSW Office of Environment and Heritage 2013).

### Description of focal species

*Juncus kraussii* ssp. *australiensis* (hereafter referred to as *Juncus* for brevity) is a stout, tussock-forming, shortly rhizomatous, perennial graminoid, which grows commonly in damp, waterlogged, saline swamps and forests of south-eastern and western Australian coastlines (Harden 1993). Inflorescences are borne singly on a culm and arranged in compound cymes of discrete clusters of fertile flowers, with each cluster consisting of usually 4–6 flowers; each flower develops into a multi-seeded capsule (Pellow et al. 2009; Appendix S1, S2 in Supplementary Material). Seeds are small and most likely dispersed by wind (Benson and McDougall 2002). Seeds sink immediately in water, and during periods of inundation are likely to settle near the parent plant (Clarke and Hannon 1970).

*Baumea juncea* (hereafter *Baumea*) is a slender, rhizomatous, extensively spreading, perennial graminoid, which grows commonly in brackish or saline swamps on sandy soils along the south-eastern and western Australian coastlines (Harden 1993). Flowers are arranged in spikelets, and each spikelet contains only one bisexual, fertile flower, which develops into a single nut (hereafter termed seed); spikelets are few and arranged in erect, paniculate inflorescences borne singly on a slender culm (Pellow et al. 2009; Appendix S1, S2 in Supplementary Material). Seeds are large and are usually shed directly beneath the parent plant, with little capacity for long-distance dispersal (Thorsen et al. 2009).

*Tetragonia tetragonioides* (hereafter *Tetragonia*) is a broad-leaved, succulent, prostrate, spreading, short-lived perennial forb, arising from a slender taproot (Pellow et al. 2009; Appendix S1, S2 in Supplementary Material). It is very widespread and common throughout eastern Australia across a variety of habitats, predominately coastal shrublands, forests, estuaries and the margins of salt marsh, but also in arid areas of western New South Wales and Queensland (Pellow et al. 2009). Flowers are bisexual, usually solitary in leaf axils, and comprise a single, large, multi-locular ovary with up to 10 ovules, each with the potential to develop into a seed (Gray 1997; Pellow et al. 2009; Appendix S1 in Supplementary Material). The fleshy fruit may be ingested and dispersed by birds (Thorsen et al. 2009), but trials (Gooden Unpublished data) have shown that dried fruit collected from beneath parent plants and from flood-deposited wrack can float on seawater for at least 30 days, which is sufficient time for it to disperse many tens to hundreds of metres from parent plants. Tests on morphologically-similar fruit of a congener species, *T. decumbens* Mill., reveal buoyancy of greater than 2 years (Heligers 2007).

### Assessment of species' frequency of occurrence and abundance in the standing vegetation

To determine the effects of *Stenotaphrum* invasion on the frequency of occurrence (i.e. presence or absence) and abundance of the three target species, a subset of 20 extensively *Stenotaphrum*-invaded and 20 native sites were haphazardly selected from a pool of sites that had been surveyed in a previous study of *Stenotaphrum* invasion in the coastal swamp forest

(for details of site selection and survey protocols, see Gooden and French 2014b). Infestations of *Stenotaphrum* at each invaded site were spatially extensive, covering an area of greater than 400 m<sup>2</sup>, with a foliage cover abundance of *Stenotaphrum* of  $\geq 80\%$ .

A 10 m  $\times$  10 m quadrat was established at each site: at invaded sites, quadrats were positioned randomly within the centre of each patch of *Stenotaphrum*, with quadrat edges at least 2 m from the edge of the patch; at native sites, quadrats were randomly positioned in native vegetation that contained less than 5 % foliage cover of *Stenotaphrum*. In each quadrat, we recorded the presence or absence of each target species, and, where present, estimated each species' abundance using a modified Braun-Blanquet cover abundance index (Poore 1955; Mason and French 2007): "1", <5 % and single plant; "2", <5 % and uncommon; "3", <5 % and common; "4", 5–20 %; "5", 21–50 %; "6", 51–75 %; "7", 76–100 %. Surveys were done between September 2010 and March 2011.

#### Seed bank sampling

Effects of *Stenotaphrum* invasion on the frequency and abundance of propagules of each target species within the soil seed bank were assessed using a seedling emergence glasshouse experiment, following protocols developed by Poiani and Johnson (1988) and Mason et al. (2007). Between September and December 2010, whilst the target species were fruiting, but before they had shed seed, we randomly collected 10 soil cores (corer dimensions: diameter, 63 mm; depth, 100 mm) from 2 m  $\times$  2 m quadrats that were established within 26 *Stenotaphrum*-invaded and 26 native sites interspersed randomly across the study region. Infestations of *Stenotaphrum* at each invaded site covered an area of greater than 100 m<sup>2</sup>, with a foliage cover abundance of  $\geq 80\%$ , and native sites were dominated by native vegetation, with less than 5 % foliage cover of *Stenotaphrum*.

Soil cores from each site were bulked, sieved through a 6 mm  $\times$  6 mm mesh to remove stones, woody debris and rhizomatous material, and spread evenly to a depth of approximately 20 mm over a 1:1 vermiculite/perlite base within 340 mm  $\times$  290 mm propagation trays (Gooden and French 2014a). Sieved residue was carefully inspected for *Tetragonia* fruit, which were reintegrated as necessary back into each

soil sample. Trays were allocated randomly within glasshouses located at the University of Wollongong's Ecological Research Centre (34°24'16.90"S, 150°52'17.98"E). Seedling emergence was assessed fortnightly for the first 3 months, then monthly thereafter for 1 year (September 2010 to September 2011). All seedlings were removed from trays once identified and counted. 10 control trays containing only the vermiculite/perlite mixture were randomly interspersed amongst sample trays to control for contaminant seeds within the glasshouses (no contaminants were detected). Trays were watered twice daily for 5 min using tap water expelled from misters housed 50 cm above each tray. The positions of trays within the glasshouses were changed randomly once a fortnight.

#### Measurement of species' size and reproduction

To assess the effects of invasion on the morphological and reproductive traits of the target species, six reproductively mature (flowering stage) plants were sampled from 5 to 9 sites where the species were present (Appendix S1 in Supplementary Material). At each site, three plants were haphazardly sampled from within patches of *Stenotaphrum* and three from adjacent native vegetation. Infestations of *Stenotaphrum* covered an area of greater than 400 m<sup>2</sup>, with foliage cover abundance of *Stenotaphrum* of  $\geq 80\%$ . Sampling was done between July and October 2011 in order to sample fruit that had developed during the previous flowering seasons.

A 1 m  $\times$  1 m plot was positioned around each plant. The above-ground biomass of each species was measured by clipping all plant material rooted within each plot at the soil surface, then bagging and drying the vegetative biomass to constant weight (5 days at 60 °C; mass recorded to  $\pm 0.01$  g). For *Tetragonia*, we also assessed the effects of invasion on specific leaf area (SLA), which is the ratio of a leaf's surface area (and thus capacity to intercept light) to the mass invested in its construction (Westoby 1998). An increase in SLA may occur in response to competition with an invader in order for a native to increase the capture of diminishing light resources whilst keeping the costs of leaf construction to a minimum (Westoby 1998). We calculated SLA by randomly selecting up to 10 fully expanded, undamaged leaves per plot, measuring their surface area (cm<sup>2</sup>) using a portable

leaf area metre (LI-COR Inc. Model LI-3000A), drying leaves to constant weight (as above; mass recorded to  $\pm 0.001$  g), then dividing surface area by dry weight (Westoby 1998). The mean SLA of the 10 leaves per plot was used in subsequent analyses.

The total reproductive output for each species was assessed in the field by counting and bagging the total number of fruit for *Tetragonia* and infructescences for *Baumea* and *Juncus* per 1 m<sup>2</sup> plot (Bazzaz et al. 1979; Table 1). The reproductive ‘effort’ invested by plants into fruit production was calculated by dividing the total number of fruit or infructescences by plant biomass (Table 1). Seed set for *Tetragonia* was measured as the number of seeds per fruit (calculated as the mean number of seeds based on measurements of up to 10 fruit per m<sup>2</sup>; Table 1; Appendix S1 in Supplementary Material). *Baumea* seed set was measured as the total number of seeds per m<sup>2</sup>. Furthermore, the glumes that enclose unfertilised flowers persist within *Baumea* inflorescences once seeds begin to develop (B. Gooden pers. obs.; Appendix S1 in Supplementary Material), thus making it possible for us to determine flowering effort (calculated as the mean number of unfertilised flowers and seeds of up to 10 infructescences per m<sup>2</sup>; Table 1, Appendix S1 in Supplementary Material), as well as rates of seed development (calculated as the mean proportion of the original number of flowers that developed into seeds of up to 10 infructescences per m<sup>2</sup>; Table 1). Similarly, the two perianth whorls of *Juncus* flowers persist within inflorescences once fruiting capsules begin to develop (B. Gooden pers. obs.; Appendix S1 in Supplementary Material), thus allowing us to determine the total flowering effort (calculated as the average number of flowers within 20 randomly selected floral clusters of up to five randomly selected infructescences per m<sup>2</sup>, Table 1), as well as fruit set (calculated as the mean proportion of the original number of flowers per floral cluster per infructescence per m<sup>2</sup> that developed into fruiting capsules). For *Juncus*, we also measured the size of each infructescence (calculated as the mean number of floral clusters of up to five randomly selected infructescences).

#### Data analysis

Differences in the likelihood of species’ occurrence between invaded and native habitats within both the standing vegetation ( $n = 20$ ) and seed bank ( $n = 26$ )

were assessed using binomial generalised linear models. Species were scored as either present (1) or absent (0) from sites. Differences in species’ abundance in the standing vegetation (i.e. percentage foliage cover across each 10 m  $\times$  10 m quadrat) and seed bank (i.e. number of germinants per sampled per 2 m  $\times$  2 m quadrat) between invaded and native habitats were assessed using the non-parametric Kruskal–Wallis test (Zar 1999), since data transformations were unable to satisfy assumption of parametric analyses. Comparisons of abundance were done using data only from the subset of sites from which each species was present.

Effects of invasion (fixed factor with two levels: invaded versus native) and location (random factor: variable number of levels depending on target species, Appendix S1 in Supplementary Material) on the morphological and reproductive traits of the target species (response variables, Table 1) were assessed using general linear mixed models. Since seed and fruit output can be influenced by plant size and rates of reproduction (Metcalf and Kunin 2006; Ens and French 2008), we also included plant biomass and other reproductive traits in the models as covariates. Normality of the data was assessed by inspecting plots of studentised residuals. Data were square root transformed as necessary. Analyses for infructescence size and reproductive success of *Baumea* and *Juncus* included data only from plots where infructescences were detected. All analyses were done using the statistical package JMP<sup>®</sup> (version 9, SAS Institute Inc., Cary, NC, US).

## Results

### Impacts on species’ representation in standing vegetation

*Juncus* was the most common species, occupying about twice as many sites as either *Tetragonia* or *Baumea* (Table 2). There was no significant difference in the likelihood of occurrence within the standing vegetation between invaded and native habitats for any species. However, at sites where they occurred, the percentage foliage cover was significantly lower (over fourfold) for *Baumea* and *Juncus* in invaded than native habitats, whilst the cover of *Tetragonia* was



**Table 1** Summary of morphological and reproductive traits (response variables) measured for each species, including the measurement units and a list of the predictor variables used to model the variation for each trait in general linear mixed models

Species Response variable	Units
<i>Tetragonia tetragonioides</i>	
Plant biomass	g biomass m <sup>-2</sup>
Fruit output	Number of fruit m <sup>-2</sup>
Fruiting effort	Number of fruit g biomass <sup>-1</sup> m <sup>-2</sup>
Seed set	Mean number of seeds fruit <sup>-1</sup>
Specific leaf area	Leaf area cm <sup>2</sup> leaf dry weight g <sup>-1</sup> m <sup>-2</sup>
<i>Baumea juncea</i>	
Plant biomass	g biomass m <sup>-2</sup>
Infructescence output	Number of infructescences m <sup>-2</sup>
Infructescence effort	Number of infructescences g biomass <sup>-1</sup> m <sup>-2</sup>
Seed output	Number of seeds m <sup>-2</sup>
Seeding effort	Number of seeds g biomass <sup>-1</sup> m <sup>-2</sup>
Flowering effort	Number of floral units (i.e. seed + flowers) infructescence <sup>-1</sup> m <sup>-2</sup>
Seed set	Proportion of floral units developing into seed: [# seed/(# seed + flowers)] infructescence <sup>-1</sup> m <sup>-2</sup>
<i>Juncus kraussii</i>	
Plant biomass	g biomass m <sup>-2</sup>
Infructescence output	Number of infructescences m <sup>-2</sup>
Infructescence effort	Number of infructescences g biomass <sup>-1</sup> m <sup>-2</sup>
Infructescence size	Number of clusters infructescence <sup>-1</sup> m <sup>-2</sup>
Cluster size	Number of floral units (i.e. capsules + flowers) cluster <sup>-1</sup> infructescence <sup>-1</sup> m <sup>-2</sup>
Fruit set	Proportion of floral units developing into capsules: [# capsules/(# capsules + flowers)] infructescence <sup>-1</sup> m <sup>-2</sup>

similar across both habitats (Table 2). *Baumea* was the most abundant species in terms of percentage cover at locations in which it occurred, with *Tetragonia* lowest in cover and *Juncus* intermediate.

#### Impacts on species' representation in seed bank

Invasion by *Stenotaphrum* was associated with a significant reduction in the occurrence of *Baumea* germinants in the soil seed bank but no effect of invasion on occurrence was evident for either *Juncus* or *Tetragonia* (Table 2). Similar to patterns within the standing vegetation, *Juncus* was the most common species within the seed bank. At sites where seeds were detected, germinant density did not vary significantly between invaded and native habitats for any species (Table 2).

#### Impacts on species' size and reproduction

A total of 120 reproductively mature plants were examined in detail for responses to *Stenotaphrum* invasion. Specifically, for *Tetragonia*, we sampled approximately 1,650 seeds from 300 fruit from 30 plants; for *Baumea*, we inspected approximately 1,620 flowers from 360 infructescences from 36 plants; and for *Juncus*, we inspected approximately 6,700 flowers from 2,700 floral clusters, and 270 infructescences from 54 plants.

Invasion was associated with significantly lower biomass and fruit output (i.e. total number of fruit per m<sup>2</sup>) of *Tetragonia*, both of which were approximately 75 % lower in invaded than native habitats (Table 3; Fig. 1a, b). Invasion had no effect, however, on fruiting effort (i.e. number of fruit produced per g plant

**Table 2** Summary of results for differences in species occurrence (binomial generalised linear models) and abundance (Kruskal–Wallis tests) within the standing vegetation and seed bank between *Stenotaphrum*-invaded and native habitats

Source Response variable Species	Invasion category		$\chi^2$	P
	Native	Invaded		
Standing vegetation ( $n = 20$ )				
Occurrence (% sites occupied)				
<i>Tetragonia</i>	30	40	0.4286	0.5127
<i>Baumea</i>	30	40	0.4286	0.5127
<i>Juncus</i>	70	75	0.1223	0.7266
Abundance (mean $\pm$ SE% foliage cover)				
<i>Tetragonia</i>	7.42 ( $\pm$ 2.29)	6.69 ( $\pm$ 4.76)	0.9019	0.3423
<i>Baumea</i>	57.58 ( $\pm$ 10.56)	13.13 ( $\pm$ 4.91)	8.7450	0.0031*
<i>Juncus</i>	17.07 ( $\pm$ 3.98)	4.3 ( $\pm$ 1.11)	15.0113	0.0001*
Seed bank ( $n = 26$ )				
Occurrence (% sites occupied)				
<i>Tetragonia</i>	23	19	0.1131	0.7367
<i>Baumea</i>	42	15	4.5027	0.0338*
<i>Juncus</i>	50	58	0.3036	0.5817
Germinant density (mean $\pm$ SE no. of germinants)				
<i>Tetragonia</i>	1.83 ( $\pm$ 0.54)	4.00 ( $\pm$ 2.76)	0.0447	0.8325
<i>Baumea</i>	7.27 ( $\pm$ 2.04)	7.25 ( $\pm$ 2.69)	0.0697	0.7918
<i>Juncus</i>	60.46 ( $\pm$ 24.37)	14.73 ( $\pm$ 7.78)	1.9477	0.1628

Analyses on abundance in the standing vegetation (% foliage cover) and seed bank (number of germinants per site) were done using data only from sites where each species was present  
\* Statistical significance

biomass), seed set (i.e. mean number of seed per fruit) or mean SLA (Table 3; Fig. 1c–e).

There was a significant negative effect of invasion on the biomass and fruit output (i.e. total number of infructescences per  $m^2$ ) for *Baumea*, which were both approximately 80 % lower in invaded than native habitats (Table 3; Fig. 2a, b). Seed output (i.e. total number per  $m^2$ ) was also significantly lower on average in invaded habitats, despite considerable variation in seed densities within native habitats across locations (note large standard errors for seed output in native habitats; Fig. 2d). This variability and large difference in mean seed output between invaded and native habitats was driven mainly by extremely high seed output for plants at one location, 'Nangudga' (mean  $\pm$  SE seed output for all plants regardless of invasion: Nangudga =  $827 \pm 347$  seeds  $m^{-2}$ ; all other locations combined =  $12 \pm 3$  seeds  $m^{-2}$ ). However, *Baumea* plants from invaded habitats still produced significantly fewer seed overall when data from 'Nangudga' were removed from the analysis (mean  $\pm$  SE seed output: native habitat =  $19 \pm 6$  seeds  $m^{-2}$ ; invaded habitat =  $5 \pm 2$  seeds  $m^{-2}$ ; Table 3). Fruiting and seeding effort, measured as the number of infructescences and seed, respectively,

produced per g plant biomass, were unaffected by invasion, both when data from Nangudga were included and excluded from models (Table 3; Fig. 2c, e). Overall, flowering effort (i.e. total number of seeds and undeveloped flowers per infructescence) and seed set (i.e. proportion of the original number of these flowers that developed into seeds) did not differ between invaded and native habitats (Fig. 2f, g). As with seed output, however, the mean ( $\pm$ SE) seed set of plants from 'Nangudga' was substantially higher (i.e.  $66 \pm 4$  %) than other locations ( $13 \pm 2$  % combined); when data from 'Nangudga' were removed from the model, plants from invaded habitats were found to have significantly lower rates of seed set than those from native habitats (Table 3; Fig. 2h).

The biomass and fruit output of *Juncus* were also significantly lower in invaded than native habitats (Table 3; Fig. 3a, b). Invasion had no effect on fruiting effort, infructescence size (i.e. number of floral clusters per infructescence) or fruit set (Table 3; Fig. 3c–f). There was a trend ( $P = 0.0913$ ), however, towards greater flowering effort, as measured by the total number of capsules and undeveloped flowers per cluster, for plants in native than invaded habitats. There was a significant negative effect of plant

**Table 3** Summary of general linear mixed models testing for the effects of *Stenotaphrum* invasion on plant morphological and reproductive attributes for three species: *Tetragonia tetragonioides*, *Baumea juncea* and *Juncus kraussii*

Species Response variable	DF	F	P	Figure reference
<i>Tetragonia tetragonioides</i>				
Plant biomass	1, 29	45.4943	0.0025*	Fig. 1a
Fruit output	1, 29	35.4818	0.0040*	Fig. 1b
Fruiting effort	1, 29	0.3913	0.5655	Fig. 1c
Seed set	1, 29	0.3194	0.6022	Fig. 1d
Specific leaf area	1, 29	1.3142	0.3156	Fig. 1e
<i>Baumea juncea</i> (all sites)				
Plant biomass	1, 35	22.7970	0.0050*	Fig. 2a
Infructescence output	1, 35	7.7308	0.0389*	Fig. 2b
Infructescence effort	1, 35	3.5322	0.1190	Fig. 2c
Seed output	1, 35	4.6370	0.0385*	Fig. 2d
Seeding effort	1, 35	1.2776	0.3110	Fig. 2e
Flowering effort	1, 35	2.7188	0.1420	Fig. 2f
Seed set	1, 35	2.1434	0.1826	Fig. 2g
<i>Baumea juncea</i> (Nangudga removed)				
Plant biomass	1, 29	20.5900	0.0105*	
Infructescence output	1, 29	5.2813	0.0292*	
Infructescence effort	1, 29	3.3450	0.0781	
Seed output	1, 29	9.3487	0.0049*	
Seeding effort	1, 29	1.3260	0.2592	
Flowering effort	1, 29	2.8068	0.1050	
Seed set	1, 29	4.5018	0.0428*	Fig. 2h
<i>Juncus kraussii</i>				
Plant biomass	1, 53	20.0759	0.0021*	Fig. 3a
Infructescence output	1, 53	12.0869	0.0084*	Fig. 3b
Infructescence effort	1, 53	0.1106	0.7480	Fig. 3c
Infructescence size	1, 49	0.2129	0.6469	Fig. 3d
Cluster size	1, 49	3.4517	0.0913	Fig. 3e
Fruit set	1, 49	1.3072	0.2811	Fig. 3f

\* Statistical significance

biomass on flowering effort ( $r^2 = 0.12$ ,  $P = 0.01$ ), and a significant positive relationship between flowering effort and fruit set ( $r^2 = 0.24$ ,  $P = 0.0003$ ).

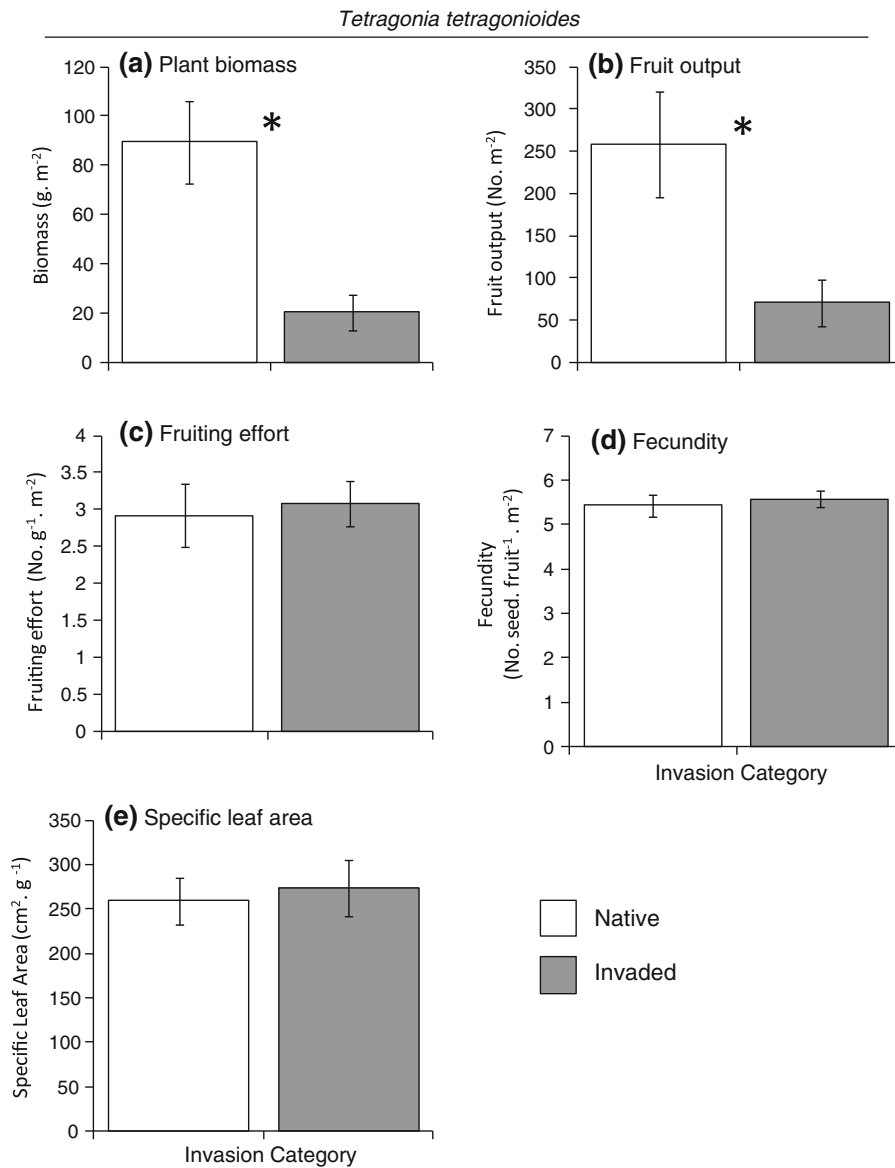
## Discussion

Invasion by the alien grass *Stenotaphrum secundatum* had no effect on the frequency of any of the three focal native species within the swamp forest community, as measured by the differences in their likelihood of detection between invaded and native sites. However, *Baumea* and *Juncus* were less abundant (and all species lower in biomass) at invaded sites within which they were detected, indicating future reductions

in frequency in response to *Stenotaphrum* invasion. *Stenotaphrum* invasion was associated with substantial reductions in the reproductive output of all natives, but had no apparent effect on the frequency or density of propagules for most species (except *Baumea*) within the soil seed bank. This finding suggests that *Stenotaphrum* maintains small populations of most native species by primarily limiting their recruitment into the community, rather than propagule supplies.

However, it is possible that *Stenotaphrum* invasion and reductions in both native plant abundance and reproduction were coincidental, such that the invader proliferated within microsites unsuitable for the native species. However, previous studies by Gooden and French (2014a, b) have shown that invaded and non-





**Fig. 1** Mean ( $\pm$ SE) **a** plant biomass, **b–d** reproduction and **e** specific leaf area for *Tetragonia tetragonioides* in native and *Stenotaphrum*-invaded plots ( $n = 15$ ). Note differences in y-

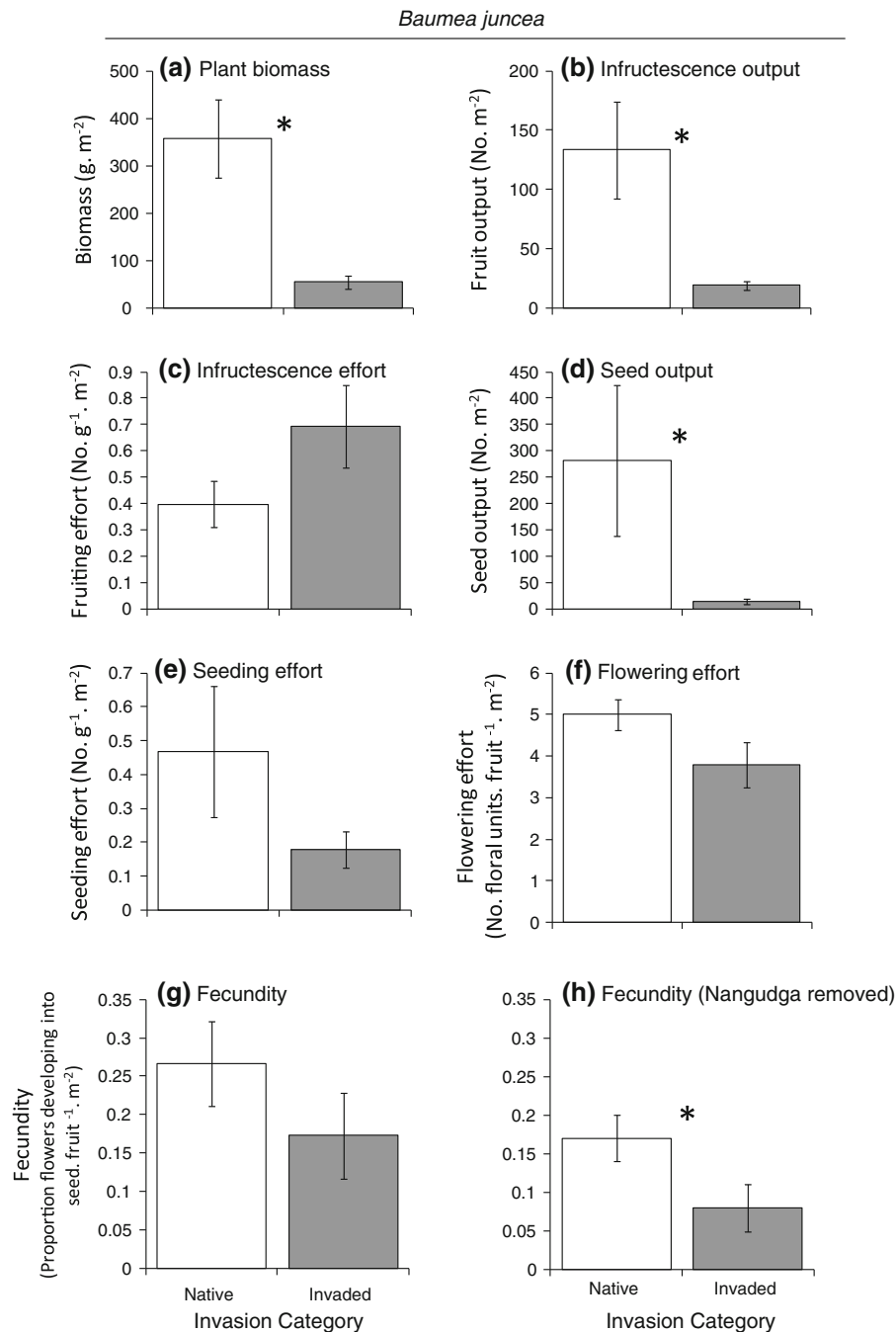
axis units between figure plates. Asterisks denote significantly different means

invaded patches of forest are similar in terms of levels of landscape and local disturbances (e.g. fire severity, canopy openness and anthropogenic land use). Furthermore, we found that within a particular site, invaded and non-invaded patches did not differ in available soil nutrients (unpublished data available on request). Given a similar *potential* for the representation of species between invaded and non-invaded patches because of similar seed bank densities, we conclude that invasion was indeed the likely cause of

disrupted native populations. This could be resolved through longitudinal or experimental studies (Adair and Groves 1998).

#### Impacts on reproduction

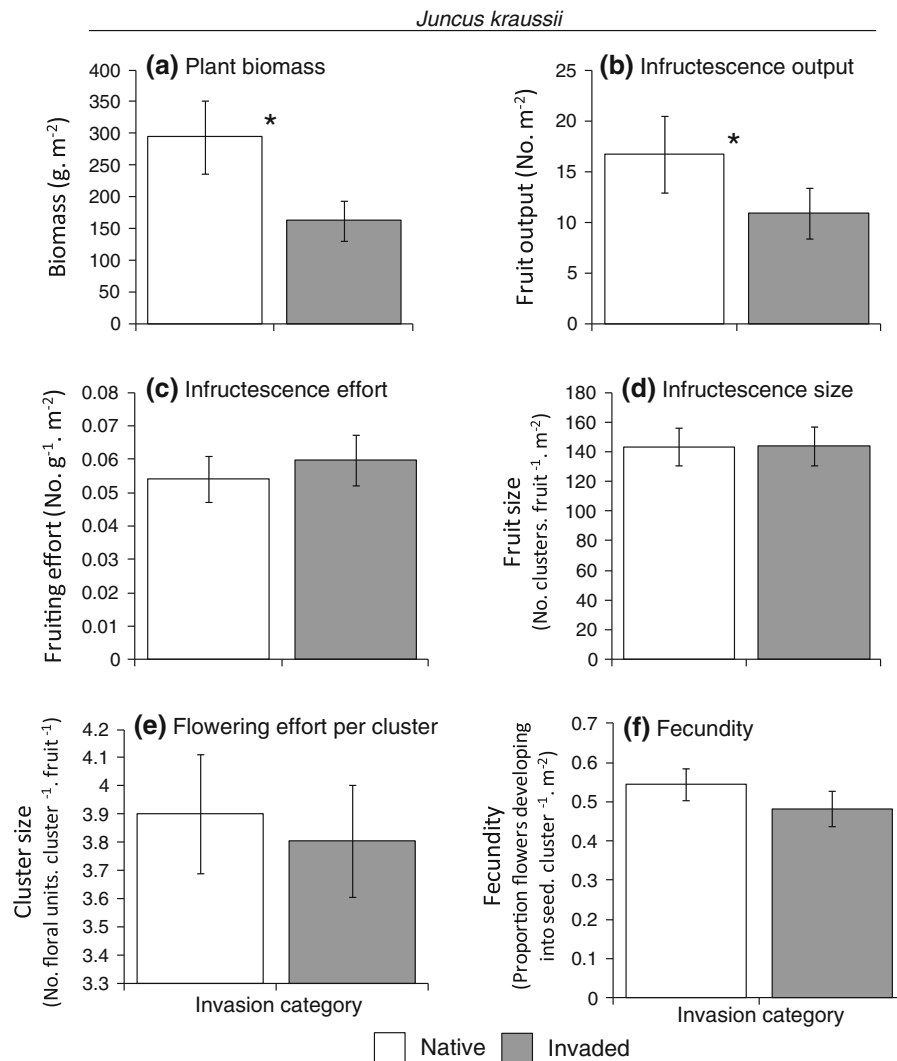
*Stenotaphrum* invasion significantly affected the reproduction of all three species, with focal plants producing at least 75 % less fruit on average in invaded than native sites. Our results contrast strongly



**Fig. 2** Mean ( $\pm$ SE) **a** plant biomass and **b–h** reproduction for *Baumea juncea* in native and *Stenotaphrum*-invaded plots ( $n = 18$ ). Note differences in y-axis units between figure plates. Asterisks denote significantly different means

with the majority of other studies, which show that invasion has generally little effect on the reproduction of co-occurring natives (Badano and Pugnaire 2004; Totland et al. 2006; Denoth and Myers 2007; Ens and French 2008; Ferrero et al. 2013). In studies where

negative impacts of invaders on the reproductive success of natives have been detected (see reviews by Bjercknes et al. 2007; Morales and Traveset 2009 and examples by Gould and Gorchov 2000 and Miller and Gorchov 2004), such effects occurred through



**Fig. 3** Mean ( $\pm$ SE) **a** plant biomass and **b–f** reproduction for *Juncus kraussii* in native and *Stenotaphrum*-invaded plots ( $n = 25$ ). Note differences in y-axis units between figure plates. Asterisks denote significantly different means

competition for pollinator services and interspecific pollen transfer. Generally, in studies of wind-pollinated systems, where interference of native pollinator networks by the invader is unlikely to occur, we have found no other evidence that the reproductive success of natives is affected by the alien species. Indeed, a similar study by Minchinton et al. (2006) on impacts of invasion by the rhizomatous, wind-pollinated grass *Phragmites australis* into north American marshes found that two native forbs produced more seeds when grown within *P. australis* infestations.

Although the overall output of *Tetragonia* and *Juncus* fruit was lower in invaded than native sites,

there was no evidence that invasion affected their reproductive ‘effort’ or per capita investment in reproductive structures (i.e. number of fruit per g plant biomass), or the ‘size’ of each fruit produced, as measured, for example, by the number of floral clusters comprising each *Juncus* infructescence. Likewise, the number of viable seed per fruit was similar for *Tetragonia* between invaded and native sites. These findings indicate that the impact of invasion on reproductive output for these species was due to a decrease in body size and the subsequent number of fruit that each plant could produce as a result of resource competition, rather than pollen limitation or

inhibited fertilisation of available flowers. If such effects occurred as a result of competition with *Stenotaphrum* for soil resources, then removal of *Stenotaphrum* may be sufficient to facilitate the regeneration of resident plants and an increase in reproductive output, as demonstrated elsewhere by invader removal experiments (e.g. D'Antonio et al. 1998; Gould and Gorchov 2000).

Similarly, *Stenotaphrum* invasion negatively affected the biomass and reproductive output of *Baumea* plants, and had no effect on the species' reproductive effort, as measured by both the per capita production of infructescences and number of original floral units produced per infructescence. However, unlike *Juncus* and *Tetragonia*, there was a significant negative effect of invasion on the seed set of *Baumea* at most sites, as measured by the proportion of original flowers that developed into seed. This could have occurred through either (1) a limited supply of suitable pollen to *Baumea* plants isolated within *Stenotaphrum* infestations, which for wind-pollinated species declines rapidly with increasing distance from pollen donors and at low population densities (Davis et al. 2004; Friedman and Barrett 2009); (2) contamination of stigmatic surfaces by heterospecific pollen (possibly by *Stenotaphrum*) (Nielsen et al. 2008; Matsumoto et al. 2010) and/or (3) abortion of fertilised ovules as a result of competition with *Stenotaphrum*. The exact mechanism is unknown, but warrants further investigation.

Impacts on seed banks: are populations propagule or recruitment limited?

Despite substantial reductions in the reproductive output for all species, there was generally little effect of *Stenotaphrum* invasion on the soil seed banks, although this varied amongst the three species. As expected, *Juncus* and *Tetragonia*, which can disperse long distances via wind and water, respectively, were equally likely to occur and had similar seed densities between invaded and native sites. It is likely that immigration rates of *Juncus* and *Tetragonia* propagules from neighbouring populations were sufficiently high to buffer against reduced local inputs from plants co-occurring with *Stenotaphrum*. Conversely, *Baumea*, which typically sheds and stores propagules directly beneath the parent plant, with little capacity for long-distance dispersal, was less likely to have propagules represented in seed banks of invaded sites,

which was probably a direct result of its reduced abundance and reproductive success within *Stenotaphrum* infestations. These results confirm those from a previous study by Gooden and French (2014a), which found that the number of species with short distance dispersal strategies was significantly lower in swamp forest seed banks at sites invaded by *Stenotaphrum*, whilst the richness of wind and water-dispersed species was similar between invaded and native reference sites.

A comparison of results between our reproduction and seed bank studies demonstrates that there are two contrasting mechanisms by which alien plants maintain low populations of natives within invaded communities: (1) post-settlement recruitment limitation, rather than limited availability of propagules within the seed bank (e.g. *Juncus* and *Tetragonia*), and (2) limited reproductive success, leading to depleted seed banks and a reduction in the number of propagules available for recruitment (e.g. *Baumea*). Whilst impacts of invasion on the reproductive success of *Juncus* and *Tetragonia* were evident, a reduction in their fruit set alone is unlikely to have led to a decline in populations, since there were sufficiently high numbers of propagules in the seed bank available for recruitment; thus, the primary mechanism of population reduction is likely to be at the post-settlement stage, through either inhibited propagule germination or survival of young germinants. In a similar study on impacts of the alien pasture grass *Pennisetum ciliare* (buffelgrass) on native columnar cactus populations in Mexican thorn scrub, Morales-Romero and Molina-Freaner (2008) found no effect of invasion on the flowering effort, pollination and reproductive output of cactus plants, but significantly lower rates of their recruitment and seedling survival within buffelgrass pastures.

#### Conclusions and research directions

Our results clearly show that invasion by an alien grass is associated with significant reductions in the abundance and reproduction of co-occurring native plant species within an endangered swamp forest community. Our study provides a rare example of reproductive impacts within a system where the invader and resident natives do not compete for pollinator services for effective fertilisation, unlike those investigated elsewhere (Traveset and Richardson 2006; Morales

and Traveset 2009). Our findings suggest that impacts on reproduction may be a general effect of *Stenotaphrum* invasion within coastal communities, which for most species is driven by reductions in the body size of resident plants and the absolute number of reproductive structures that they are able to produce. Despite this, limited reproduction is unlikely to be the ultimate cause of population declines for most species, particularly those with long-distance dispersal strategies, since invasion had little impact on the supply and storage of propagules within the seed bank. We speculate, therefore that the primary mechanism of population decline for most species is post-settlement recruitment limitation, rather than a reduction in the availability of propagules for recruitment. A key hypothesis requiring further investigation is that limited reproduction is relatively more important than recruitment limitation as a mechanism of population decline in response to alien plant invasion for species with short rather than long-distance dispersal strategies.

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