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

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.

Keywords

Disturbance, Exotic species, Propagule dispersal, Reproduction, Seed bank, *Stenotaphrum secundatum*

Disciplines

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

3

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10

11

12 **Declaration of authorship:** This study forms a component of BG's PhD research at the
13 University of Wollongong. BG and KF conceived and designed the study. BG completed all
14 field and laboratory sampling (but see acknowledgements). BG, KF and SR analysed the
15 data. BG wrote the manuscript. KF and SR provided editorial advice. No other persons are
16 entitled to authorship.

17

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21

22

1

2 **Abstract**

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4 they drive species losses and maintain their own dominance are poorly known. We examined
5 the effects of alien grass invasion (*Stenotaphrum secundatum*) on (1) abundance and
6 frequency of occurrence, (2) reproductive effort (flowering) and output (fruit production) and
7 (3) soil seed banks for three focal native plants that are characteristic of endangered coastal
8 forest of south-eastern Australia. First, we sampled and compared the foliage cover
9 abundance and frequency (proportion of sites occupied) of the focal natives across invaded
10 and non-invaded (reference) sites ($n = 20$). We then intensively sampled reproductive effort
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12 standard glasshouse 'emergence' method; $n = 26$) for each species. Invasion was associated
13 with reduced population sizes of all species within the standing vegetation but did not affect
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20 reduction in the arrival and storage of propagules at invaded sites. Removal of *Stenotaphrum*
21 alone might thus be sufficient to stimulate the recovery of native populations from the seed
22 bank.

23 **Abstract word count:** 246

- 1 **Keywords:** Disturbance; exotic species; propagule dispersal; reproduction; seed bank;
- 2 *Stenotaphrum secundatum*
- 3 **Abbreviations:** SLA = specific leaf area
- 4 **Running head:** Invasion limits native plant recruitment

1

2 **Introduction**

3 Alien plant invaders are considered amongst the greatest threats to the biodiversity,
4 structure and function of indigenous plant communities at local and global scales (Vitousek et
5 al. 1996; Vitousek et al. 1997; Mack et al. 2000). Recent comprehensive reviews (e.g.
6 Gaertner et al. 2009; Vilà et al. 2011) as well as community-scale manipulative experiments
7 (e.g. Green & Galatowitsch 2002; e.g. Flory & Clay 2010) have clearly shown that invasion
8 is associated with significant reductions in native plant diversity and altered vegetation
9 communities, yet there is less information on the mechanisms by which such changes are
10 driven. To date, the majority of studies that seek to identify impact mechanisms have focused
11 primarily on either direct competitive effects of invaders on the growth and persistence of co-
12 occurring native plants, usually at small scales (see review by Daehler 2003), or indirect
13 effects on native populations via changes to key ecosystem-level processes, such as
14 disturbance regimes and nutrient cycling (see review by Levine et al. 2003). There is growing
15 evidence that declining native populations are also driven by limited species recruitment(that
16 is, the germination of propagules and the growth and survival of subsequent seedlings) at
17 invaded sites, leading to the reduced viability, persistence and replacement of resident
18 populations in invaded habitats, and ultimately declines in vegetation diversity (Ens & French
19 2008; Galbraith-Kent & Handel 2008).

20 Current evident suggests that there are two main pathways by which invaders drive
21 recruitment limitation of co-resident plant populations: first, by reducing the reproduction of
22 co-occurring native plants through either direct competition for resources (D'Antonio et al.
23 1998), or disruption of pollinator services and/or pollen quality (Bjerknes et al. 2007;
24 Morales & Traveset 2009). This, in turn, may reduce the density of propagules within the

1 seed bank (especially for species with short distance dispersal strategies, whose declining
2 reserves of seed may not be supplemented by immigrant seed from adjacent, non-invaded
3 populations) and ultimately the number of propagules available for recruitment into the
4 standing vegetation (Vilà & Gimeno 2007; Gioria & Osborne 2009). Second, invaders can
5 limit the post-settlement recruitment by inhibiting the germination of propagules (e.g. Ens et
6 al. 2009) or the subsequent survival of emergent recruits (e.g. Gorchov & Trisel 2003; Miller
7 & Gorchov 2004). The relative importance of these processes to overall declines in native
8 plant populations across invaded landscapes remains unknown, since they are most often
9 studied in isolation.

10 We used invasion of an endangered coastal forest community by the alien turf-grass
11 *Stenotaphrum secundatum* (Walter) Kuntze (hereafter termed *Stenotaphrum* for brevity) as a
12 model to test whether native plant population declines in invaded communities are driven by
13 either limited production of propagules or their dispersal to and storage within soil seed
14 banks. *Stenotaphrum* is a stoloniferous, C₄ grass (Poaceae), native to the tropical and
15 subtropical Atlantic coastlines of Africa and the Americas (Sauer 1972). It is widely used
16 throughout eastern Australia as an urban and recreational turf grass, particularly in coastal
17 areas. Recent research has shown that invaded forest has significantly fewer native species,
18 both in the standing vegetation and seed bank, and lower rates of woody plant recruitment
19 than non-invaded forest (Gooden & French in press-b, a), but it is unknown whether such
20 declines are due to a reduction in the fitness and reproductive output of resident natives.

21 Specifically, we compared invaded with non-invaded (reference) sites to
22 simultaneously examine effects of *Stenotaphrum* invasion on the (1) reproductive effort and
23 output, (2) storage of propagules in the soil seed bank and (3) abundance and frequency of
24 occurrence within the standing vegetation of three target native species: *Tetragonia*

1 *tetragonioides* (Pall.) Kuntze (Aizoaceae), *Baumea juncea* (R.Br.) Palla (Cyperaceae) and
2 *Juncus kraussii* Hochst (Juncaceae). Simultaneous examination of responses to invasion at
3 each of these three key life-history stages will enable us to identify the point at which the
4 invader limits recruitment and drives population declines. These species were chosen as they
5 are characteristic of the swamp forest community (Tozer et al. 2010), are morphologically
6 and phylogenetically distinct, and have different modes of pollination and propagule dispersal
7 (Appendix S1). Furthermore, we predicted that impacts of *Stenotaphrum* invasion will vary
8 amongst the target species as a function of their different modes of pollination, seed dispersal
9 and growth habit: i.e. populations of species which are insect-pollination and have the
10 capacity for long-distance dispersal, such as *T. tetragonioides*, will be relatively less likely to
11 decline in response to invasion because any in situ loss of propagules might be supplemented
12 by immigrant ones from adjacent non-invaded sites. An understanding of such life-history
13 traits may thus enable prediction of species' responses to invasion.

14 **Methods**

15 Study area and habitat

16 Each of the three studies consisted of comparisons (using standard comparative
17 protocols outlined by Adair & Groves 1998) of each of the target species between
18 *Stenotaphrum*-invaded and non-invaded (hereafter termed “native”) reference sites located
19 within remnant stands of an endangered swamp oak floodplain forest community (Tozer et al.
20 2010), located along the southern coastline of New South Wales (NSW), south-eastern
21 Australia, between Sydney (33° 51' 54" S; 151° 12' 20" E) and Eden (37° 03' 55" S; 149°
22 54' 04" E). The study region has a warm temperate climate with mean annual rainfall of
23 between 700 and 1000 mm at Eden and Sydney, respectively, and mean annual temperatures
24 ranging from 16°C in winter to 25°C in summer (Bureau of Meteorology 2012, 2013). The

1 swamp forest community occurs on marine-derived, waterlogged sandy loams, bordering
2 coastal estuaries and brackish floodplains. It has a very simple structure, characterised by a
3 dense upper canopy dominated by the nitrogen-fixing tree *Casuarina glauca* Sieber ex
4 Spreng, a very sparse shrub layer, and a semi-continuous, species-rich groundcover of forbs
5 and graminoids (Tozer et al. 2010). The community is listed as endangered in NSW (Tozer et
6 al. 2010; NSW Office of Environment and Heritage 2013).

7
8 Description of focal species

9 *Juncus kraussii* ssp. *australiensis* (hereafter referred to as *Juncus* for brevity) is a
10 stout, tussock-forming, shortly rhizomatous, perennial graminoid, which grows commonly in
11 damp, waterlogged, saline swamps and forests of south eastern and western Australian
12 coastlines (Harden 1993). Inflorescences are borne singly on a culm and arranged in
13 compound cymes of discrete clusters of fertile flowers, with each cluster consisting of usually
14 4-6 flowers; each flower develops into a multi-seeded capsule (Pellow et al. 2009; Appendix
15 S1, Appendix S2). Seeds are small and most likely dispersed by wind (Benson & McDougall
16 2002). Seeds sink immediately in water, and during periods of inundation are likely to settle
17 near the parent plant (Clarke & Hannon 1970).

18 *Baumea juncea* (hereafter *Baumea*) is a slender, rhizomatous, extensively spreading,
19 perennial graminoid, which grows commonly in brackish or saline swamps on sandy soils
20 along the south-eastern and western Australian coastlines (Harden 1993). Flowers are
21 arranged in spikelets, and each spikelet contains only one bisexual, fertile flower, which
22 develops into a single nut (hereafter termed seed); spikelets are few and arranged in erect,
23 panicle inflorescences borne singly on a slender culm (Pellow et al. 2009; Appendix S1,

1 Appendix S2). Seeds are large and are usually shed directly beneath the parent plant, with
2 little capacity for long distance dispersal (Thorsen et al. 2009).

3 *Tetragonia tetragonioides* (hereafter *Tetragonia*) is a broad-leaved, succulent,
4 prostrate, spreading, short-lived perennial forb, arising from a slender taproot (Pellow et al.
5 2009; Appendix S1, Appendix S2). It is very widespread and common throughout eastern
6 Australia across a variety of habitats, predominately coastal shrublands, forests, estuaries and
7 the margins of salt marsh, but also in arid areas of western New South Wales and Queensland
8 (Pellow et al. 2009). Flowers are bisexual, usually solitary in leaf axils, and comprise a
9 single, large, multi-locular ovary with up to 10 ovules, each with the potential to develop into
10 a seed (Gray 1997; Pellow et al. 2009; Appendix S1). The fleshy fruit may be ingested and
11 dispersed by birds (Thorsen et al. 2009), but trials (B. Gooden, Unpublished data) have
12 shown that dried fruit collected from beneath parent plants and from flood-deposited wrack
13 can float on seawater for at least 30 days, which is sufficient time for it to disperse many tens
14 to hundreds of metres from parent plants. Tests on morphologically-similar fruit of a
15 congener species, *T. decumbens* Mill., reveal buoyancy of greater than two years (Heligers
16 2007).

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

18 To determine the effects of *Stenotaphrum* invasion on the frequency of occurrence
19 (i.e. presence or absence) and abundance of the three target species, a subset of 20
20 extensively *Stenotaphrum*-invaded and 20 native sites were haphazardly selected from a pool
21 of sites that had been surveyed in a previous study of *Stenotaphrum* invasion in the coastal
22 swamp forest (for details of site selection and survey protocols, see Gooden & French in
23 press-b). Infestations of *Stenotaphrum* at each invaded site were spatially extensive, covering
24 an area of greater than 400 m², with a foliage cover abundance of *Stenotaphrum* of ≥ 80 %.

1 A 10 m × 10 m quadrat was established at each site: at invaded sites, quadrats were
2 positioned randomly within the centre of each patch of *Stenotaphrum*, with quadrat edges at
3 least 2 m from the edge of the patch; at native sites, quadrats were randomly positioned in
4 native vegetation that contained less than 5 % foliage cover of *Stenotaphrum*. In each quadrat
5 we recorded the presence or absence of each target species, and, where present, estimated
6 each species' abundance using a modified Braun-Blanquet cover abundance index (Poore
7 1955; Mason & French 2007): "1", < 5% and single plant; "2", < 5 % and uncommon; "3", <
8 5 % and common; "4", 5-20 %; "5", 21-50 %; "6", 51-75 %; "7", 76-100 %. Surveys were
9 done between September 2010 and March 2011.

10 Seed bank sampling

11 Effects of *Stenotaphrum* invasion on the frequency and abundance of propagules of
12 each target species within the soil seed bank were assessed using a seedling emergence
13 glasshouse experiment, following protocols developed by Poiani and Johnson (1988) and
14 Mason et al. (2007). Between September and December 2010, whilst the target species were
15 fruiting, but before they had shed seed, we randomly collected 10 soil cores (corer
16 dimensions: diameter, 63 mm; depth, 100 mm) from 2 m × 2 m quadrats that were
17 established within 26 *Stenotaphrum*-invaded and 26 native sites interspersed randomly across
18 the study region. Infestations of *Stenotaphrum* at each invaded site covered an area of greater
19 than 100 m², with a foliage cover abundance of ≥ 80 %, and native sites were dominated by
20 native vegetation, with less than 5 % foliage cover of *Stenotaphrum*.

21 Soil cores from each site were bulked, sieved through a 6 mm × 6 mm mesh to
22 remove stones, woody debris and rhizomatous material, and spread evenly to a depth of
23 approximately 20 mm over a 1:1 vermiculite/perlite base within 340 mm × 290 mm
24 propagation trays (Gooden & French In press-a). Sieved residue was carefully inspected for

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

11 Measurement of species' size and reproduction

12 To assess the effects of invasion on the morphological and reproductive traits of the
13 target species, six reproductively mature (flowering stage) plants were sampled from between
14 5-9 sites where the species were present (Appendix S1). At each site, three plants were
15 haphazardly sampled from within patches of *Stenotaphrum* and three from adjacent native
16 vegetation. Infestations of *Stenotaphrum* covered an area of greater than 400 m², with foliage
17 cover abundance of *Stenotaphrum* of ≥ 80 %. Sampling was done between July and October
18 2011 in order to sample fruit that had developed during the previous flowering seasons.

19 A 1 m \times 1 m plot was positioned around each plant. The above-ground biomass of
20 each species was measured by clipping all plant material rooted within each plot at the soil
21 surface, then bagging and drying the vegetative biomass to constant weight (5 days at 60°C;
22 mass recorded to ± 0.01 g). For *Tetragonia*, we also assessed the effects of invasion on
23 specific leaf area (SLA), which is the ratio of a leaf's surface area (and thus capacity to
24 intercept light) to the mass invested in its construction (Westoby 1998). An increase in SLA

1 may occur in response to competition with an invader in order for a native to increase the
2 capture of diminishing light resources whilst keeping the costs of leaf construction to a
3 minimum (Westoby 1998). We calculated SLA by randomly selecting up to 10 fully
4 expanded, undamaged leaves per plot, measuring their surface area (cm^2) using a portable
5 leaf area meter (LI-COR Inc. Model LI-3000A), drying leaves to constant weight (as above;
6 mass recorded to ± 0.001 g), then dividing surface area by dry weight (Westoby 1998). The
7 mean SLA of the 10 leaves per plot was used in subsequent analyses.

8 The total reproductive output for each species was assessed in the field by counting
9 and bagging the total number of fruit for *Tetragonia* and infructescences for *Baumea* and
10 *Juncus* per 1 m^2 plot (Bazzaz et al. 1979; Table 1). The reproductive ‘effort’ invested by
11 plants into fruit production was calculated by dividing the total number of fruit or
12 infructescences by plant biomass (Table 1). Seed set for *Tetragonia* was measured as the
13 number of seeds per fruit (calculated as the mean number of seeds based on measurements of
14 up to 10 fruit per m^2 ; Table 1, Appendix S1). *Baumea* seed set was measured as the total
15 number of seeds per m^2 . Furthermore, the glumes that enclose unfertilised flowers persist
16 within *Baumea* inflorescences once seeds begin to develop (B. Gooden pers. obs.; Appendix
17 S1), thus making it possible for us to determine flowering effort (calculated as the mean
18 number of unfertilised flowers and seeds of up to 10 infructescences per m^2 ; Table 1,
19 Appendix S1) as well as rates of seed development (calculated as the mean proportion of the
20 original number of flowers that developed into seeds of up to 10 infructescences per m^2 ;
21 Table 1). Similarly, the two perianth whorls of *Juncus* flowers persist within inflorescences
22 once fruiting capsules begin to develop (B. Gooden pers. obs.; Appendix S1), thus allowing
23 us to determine the total flowering effort (calculated as the average number of flowers within
24 20 randomly selected floral clusters of up to 5 randomly selected infructescences per m^2 ,

1 Table 1) as well as fruit set (calculated as the mean proportion of the original number of
2 flowers per floral cluster per infructescence per m² that developed into fruiting capsules). For
3 *Juncus* we also measured the size of each infructescence (calculated as the mean number of
4 floral clusters of up to 5 randomly selected infructescences).

5 Data analysis

6 Differences in the likelihood of species' occurrence between invaded and native
7 habitats within both the standing vegetation ($n = 20$) and seed bank ($n = 26$) were assessed
8 using binomial generalised linear models. Species were scored as either present (1) or absent
9 (0) from sites. Differences in species' abundance in the standing vegetation (i.e. percentage
10 foliage cover across each 10 m \times 10 m quadrat) and seed bank (i.e. number of germinants per
11 sampled per 2 m \times 2 m quadrat) between invaded and native habitats were assessed using the
12 non-parametric Kruskal-Wallis test (Zar 1999), since data transformations were unable to
13 satisfy assumption of parametric analyses. Comparisons of abundance were done using data
14 only from the subset of sites from which each species was present.

15 Effects of invasion (fixed factor with two levels: invaded versus native) and location
16 (random factor: variable number of levels depending on target species, Appendix S1) on the
17 morphological and reproductive traits of the target species (response variables, Table 1) were
18 assessed using general linear mixed models. Since seed and fruit output can be influenced by
19 plant size and rates of reproduction (Metcalf & Kunin 2006; Ens & French 2008), we also
20 included plant biomass and other reproductive traits in the models as covariates. Normality of
21 the data was assessed by inspecting plots of studentised residuals. Data were square root
22 transformed as necessary. Analyses for infructescence size and reproductive success of
23 *Baumea* and *Juncus* included data only from plots where infructescences were detected. All

1 analyses were done using the statistical package JMP[®] (version 9, SAS Institute Inc., Cary,
2 NC, US).

3 **Results**

4 Impacts on species' representation in standing vegetation

5 *Juncus* was the most common species, occupying about twice as many sites as either
6 *Tetragonia* or *Baumea* (Table 2). There was no significant difference in the likelihood of
7 occurrence within the standing vegetation between invaded and native habitats for any
8 species. However, at sites where they occurred, the percentage foliage cover was significantly
9 lower (over four-fold) for *Baumea* and *Juncus* in invaded than native habitats, whilst the
10 cover of *Tetragonia* was similar across both habitats (Table 2). *Baumea* was the most
11 abundant species in terms of percentage cover at locations in which it occurred, with
12 *Tetragonia* lowest in cover and *Juncus* intermediate.

13 Impacts on species' representation in seed bank

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

20 Impacts on species' size and reproduction

21 A total of 120 reproductively mature plants were examined in detail for responses to
22 *Stenotaphrum* invasion. Specifically, for *Tetragonia*, we sampled approximately 1650 seeds

1 from 300 fruit from 30 plants; for *Baumea*, we inspected approximately 1620 flowers from
2 360 infructescences from 36 plants; and for *Juncus*, we inspected approximately 6700
3 flowers from 2700 floral clusters, and 270 infructescences from 54 plants.

4 Invasion was associated with significantly lower biomass and fruit output (i.e. total
5 number of fruit per m²) of *Tetragonia*, both of which were approximately 75% lower in
6 invaded than native habitats (Table 3, Fig. 1a,b). Invasion had no effect, however, on fruiting
7 effort (i.e. number of fruit produced per g plant biomass), seed set (i.e. mean number of seed
8 per fruit) or mean SLA (Table 3, Fig. 1c,d,e).

9 There was a significant negative effect of invasion on the biomass and fruit output
10 (i.e. total number of infructescences per m²) for *Baumea*, which were both approximately
11 80% lower in invaded than native habitats (Table 3, Fig. 2a,b). Seed output (i.e. total number
12 per m²) was also significantly lower on average in invaded habitats, despite considerable
13 variation in seed densities within native habitats across locations (note large standard errors
14 for seed output in native habitats; Fig 2d). This variability and large difference in mean seed
15 output between invaded and native habitats was driven mainly by extremely high seed output
16 for plants at one location, “Nangudga” (mean \pm SE seed output for all plants regardless of
17 invasion: Nangudga = 827 ± 347 seeds. m⁻²; all other locations combined = 12 ± 3 seeds. m⁻²).
18 However, *Baumea* plants from invaded habitats still produced significantly fewer seed
19 overall when data from “Nangudga” were removed from the analysis (mean \pm SE seed
20 output: native habitat = 19 ± 6 seeds. m⁻²; invaded habitat = 5 ± 2 seeds. m⁻²; Table 3).
21 Fruiting and seeding effort, measured as the number of infructescences and seed,
22 respectively, produced per g plant biomass, were unaffected by invasion, both when data
23 from Nangudga were included and excluded from models (Table 3, Fig. 2c,e). Overall,
24 flowering effort (i.e. total number of seeds and undeveloped flowers per infructescence) and

1 seed set (i.e. proportion of the original number of these flowers that developed into seeds) did
2 not differ between invaded and native habitats (Fig. 2f,g). As with seed output, however, the
3 mean (\pm SE) seed set of plants from “Nangudga” was substantially higher (i.e. 66 ± 4 %) than
4 other locations (13 ± 2 % combined); when data from “Nangudga” were removed from the
5 model, plants from invaded habitats were found to have significantly lower rates of seed set
6 than those from native habitats (Table 3, Fig. 2h).

7 The biomass and fruit output of *Juncus* were also significantly lower in invaded than
8 native habitats (Table 3, Fig. 3a,b). Invasion had no effect on fruiting effort, infructescence
9 size (i.e. number of floral clusters per infructescence) or fruit set (Table 3, Fig. 3c,d,e,f).
10 There was a trend ($P = 0.0913$), however, towards greater flowering effort, as measured by
11 the total number of capsules and undeveloped flowers per cluster, for plants in native than
12 invaded habitats. There was a significant negative effect of plant biomass on flowering effort
13 ($r^2 = 0.12$, $P = 0.01$), and a significant positive relationship between flowering effort and fruit
14 set ($r^2 = 0.24$, $P = 0.0003$).

15 **Discussion**

16 Invasion by the alien grass *Stenotaphrum secundatum* had no effect on the frequency
17 of any of the three focal native species within the swamp forest community, as measured by
18 differences in their likelihood of detection between invaded and native sites. However,
19 *Baumea* and *Juncus* were less abundant (and all species lower in biomass) at invaded sites
20 within which they were detected, indicating future reductions in frequency in response to
21 *Stenotaphrum* invasion. *Stenotaphrum* invasion was associated with substantial reductions in
22 the reproductive output of all natives, but had no apparent effect on the frequency or density
23 of propagules for most species (except *Baumea*) within the soil seed bank. This finding

1 suggests that *Stenotaphrum* maintains small populations of most native species by primarily
2 limiting their recruitment into the community, rather than propagule supplies.

3 However, it is possible that *Stenotaphrum* invasion and reductions in both native plant
4 abundance and reproduction were coincidental, such that the invader proliferated within
5 microsites unsuitable for the native species. However, previous studies by Gooden & French
6 (2014a,b) have shown that invaded and non-invaded patches of forest are similar in terms of
7 levels of landscape and local disturbances (e.g. fire severity, canopy openness and
8 anthropogenic land use). Furthermore, we found that within a particular site, invaded and
9 non-invaded patches did not differ in available soil nutrients (unpublished data available on
10 request). Given a similar *potential* for the representation of species between invaded and non-
11 invaded patches because of similar seed bank densities, we conclude that invasion was indeed
12 the likely cause of disrupted native populations. This could be resolved through longitudinal
13 or experimental studies (Adair & Groves 1998).

14 Impacts on reproduction

15 *Stenotaphrum* invasion significantly affected the reproduction of all three species,
16 with focal plants producing up to 75% less fruit on average in invaded than native sites. Our
17 results contrast strongly with the majority of other studies, which show that invasion has
18 generally little effect on the reproduction of co-occurring natives (Badano & Pugnaire 2004;
19 Totland et al. 2006; Denoth & Myers 2007; Ens & French 2008; Ferrero et al. 2013). In
20 studies where negative impacts of invaders on the reproductive success of natives have been
21 detected (see reviews by Bjerknes et al. 2007; Morales & Traveset 2009 and examples by
22 Gould & Gorchov 2000 and Miller & Gorchov 2004), such effects occurred through
23 competition for pollinator services and interspecific pollen transfer. Generally, in studies of
24 wind-pollinated systems, where interference of native pollinator networks by the invader is

1 unlikely to occur, we have found no other evidence that the reproductive success of natives is
2 affected by the alien species. Indeed, a similar study by Minchinton et al. (2006) on impacts
3 of invasion by the rhizomatous, wind-pollinated grass *Phragmites australis* into north
4 American marshes found that two native forbs produced more seeds when grown within *P.*
5 *australis* infestations.

6 Although the overall output of *Tetragonia* and *Juncus* fruit was lower in invaded than
7 native sites, there was no evidence that invasion affected their reproductive ‘effort’ or per
8 capita investment in reproductive structures (i.e. number of fruit per g plant biomass), or the
9 ‘size’ of each fruit produced, as measured, for example, by the number of floral clusters
10 comprising each *Juncus* infructescence. Likewise, the number of viable seed per fruit was
11 similar for *Tetragonia* between invaded and native sites. These findings indicate that the
12 impact of invasion on reproductive output for these species was due to a decrease in body
13 size and the subsequent number of fruit that each plant could produce as a result of resource
14 competition, rather than pollen limitation or inhibited fertilisation of available flowers. If
15 such effects occurred as a result of competition with *Stenotaphrum* for soil resources, then
16 removal of *Stenotaphrum* may be sufficient to facilitate the regeneration of resident plants
17 and an increase in reproductive output, as demonstrated elsewhere by invader removal
18 experiments (e.g. D'Antonio et al. 1998; Gould & Gorchov 2000).

19 Similarly, *Stenotaphrum* invasion negatively affected the biomass and reproductive
20 output of *Baumea* plants, and had no effect on the species’ reproductive effort, as measured
21 by both the per capita production of infructescences and number of original floral units
22 produced per infructescence. However, unlike *Juncus* and *Tetragonia*, there was a significant
23 negative effect of invasion on the seed set of *Baumea* at most sites, as measured by the
24 proportion of original flowers that developed into seed. This could have occurred through

1 either (1) a limited supply of suitable pollen to *Baumea* plants isolated within *Stenotaphrum*
2 infestations, which for wind-pollinated species declines rapidly with increasing distance from
3 pollen donors and at low population densities (Davis et al. 2004; Friedman & Barrett 2009);
4 (2) contamination of stigmatic surfaces by heterospecific pollen (possibly by *Stenotaphrum*)
5 (Nielsen et al. 2008; Matsumoto et al.) and/or (3) abortion of fertilised ovules as a result of
6 competition with *Stenotaphrum*. The exact mechanism is unknown, but warrants further
7 investigation.

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

9 Despite substantial reductions in the reproductive output for all species, there was
10 generally little effect of *Stenotaphrum* invasion on the soil seed banks, although this varied
11 amongst the three species. As expected, *Juncus* and *Tetragonia*, which can disperse long
12 distances via wind and water, respectively, were equally likely to occur and had similar seed
13 densities between invaded and native sites. It is likely that immigration rates of *Juncus* and
14 *Tetragonia* propagules from neighbouring populations were sufficiently high to buffer against
15 reduced local inputs from plants co-occurring with *Stenotaphrum*. Conversely, *Baumea*,
16 which typically sheds and stores propagules directly beneath the parent plant, with little
17 capacity for long distance dispersal, was less likely to have propagules represented in seed
18 banks of invaded sites, which was probably a direct result of its reduced abundance and
19 reproductive success within *Stenotaphrum* infestations. These results confirm those from a
20 previous study by Gooden & French (In press-a), which found that the number of species
21 with short distance dispersal strategies was significantly lower in swamp forest seed banks at
22 sites invaded by *Stenotaphrum*, whilst the richness of wind and water dispersed species was
23 similar between invaded and native reference sites.

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

17 Conclusions and research directions

18 Our results clearly show that invasion by an alien grass is associated with significant
19 reductions in the abundance and reproduction of co-occurring native plant species within an
20 endangered swamp forest community. Our study provides a rare example of reproductive
21 impacts within a system where the invader and resident natives do not compete for pollinator
22 services for effective fertilisation, unlike those investigated elsewhere (Traveset &
23 Richardson 2006; Morales & Traveset 2009). Our findings suggest that impacts on
24 reproduction may be a general effect of *Stenotaphrum* invasion within coastal communities,

1 which for most species is driven by reductions in the body size of resident plants and the
2 absolute number of reproductive structures that they are able to produce. Despite this, limited
3 reproduction is unlikely to be the ultimate cause of population declines for most species,
4 particularly those with long distance dispersal strategies, since invasion had little impact on
5 the supply and storage of propagules within the seed bank. We speculate, therefore, that the
6 primary mechanism of population decline for most species is post-settlement recruitment
7 limitation, rather than a reduction in the availability of propagules for recruitment. A key
8 hypothesis requiring further investigation is that limited reproduction is relatively more
9 important than recruitment limitation as a mechanism of population decline in response to
10 alien plant invasion for species with short rather than long distance dispersal strategies.

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17

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31

32 **Supplementary Information list**

33 Appendix S1. Morphological, taxonomic and reproductive characteristics of study species.

34 Appendix S2. Photographs of species' reproductive features.

35

1

2

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.

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

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. 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.

Source	Invasion category		χ^2	<i>P</i>
Response variable				
Species	Native	Invaded		
Standing vegetation (<i>n</i> = 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 (<i>n</i> = 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

* Statistical significance

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 tetragonoides*, *Baumea juncea* and *Juncus kraussii*.

<i>Species</i>	<i>DF</i>	<i>F</i>	<i>P</i>	Figure reference
Response variable				
<i>Tetragonia tetragonoides</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	4.637	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

List of figure captions

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.

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.

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.

Tetragonia tetragonioides

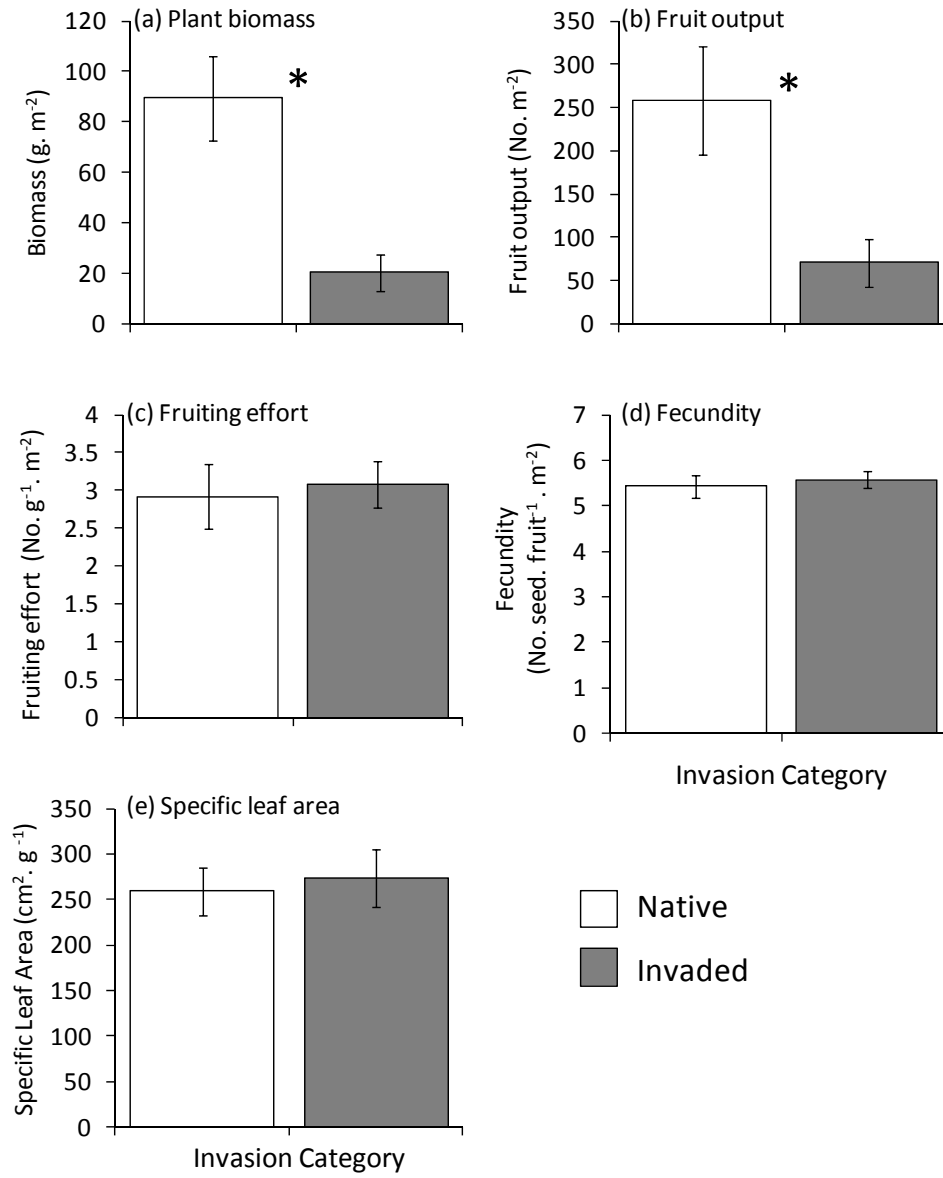


Figure 1

Baumea juncea

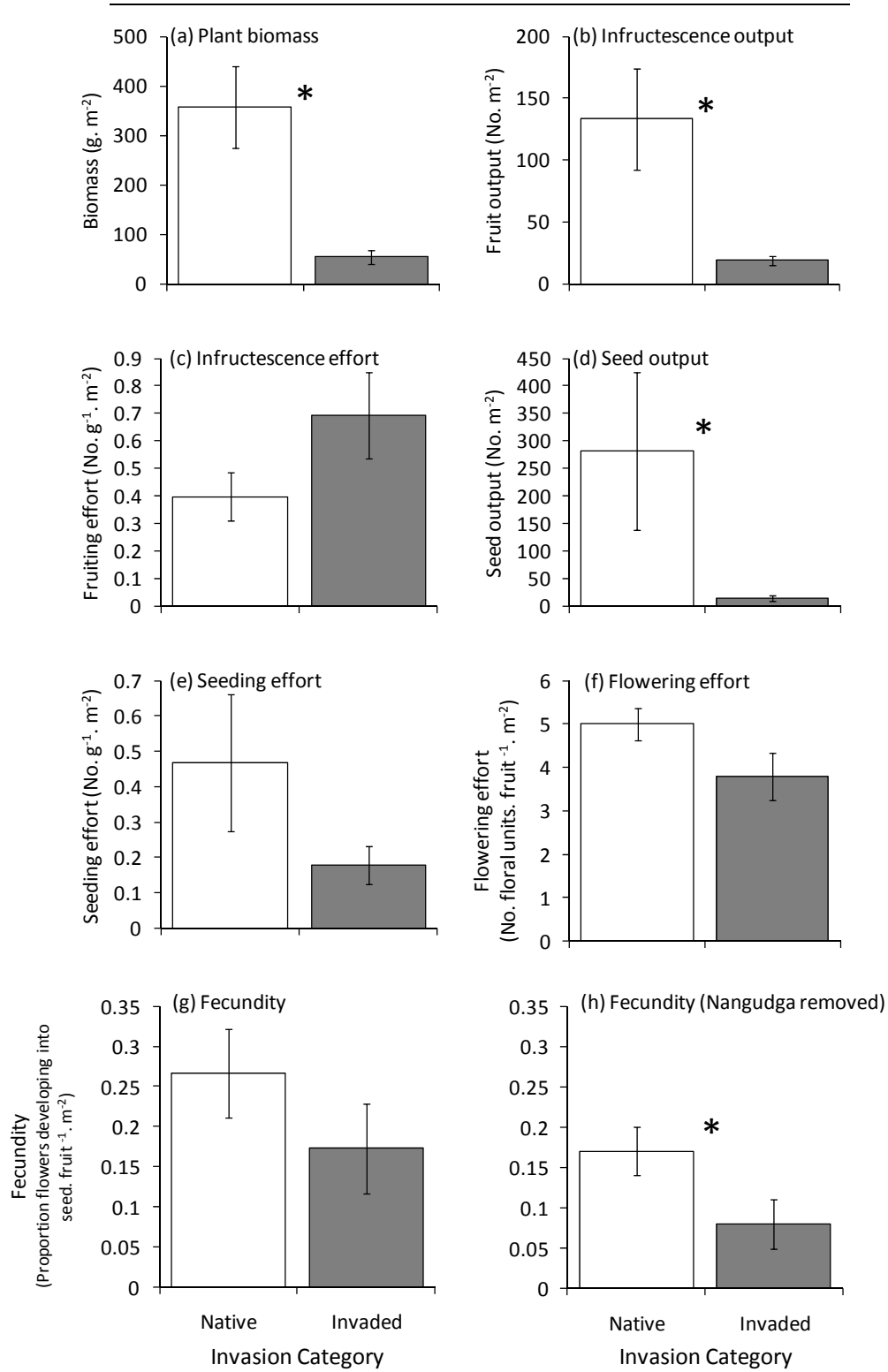


Figure 2

Juncus kraussii

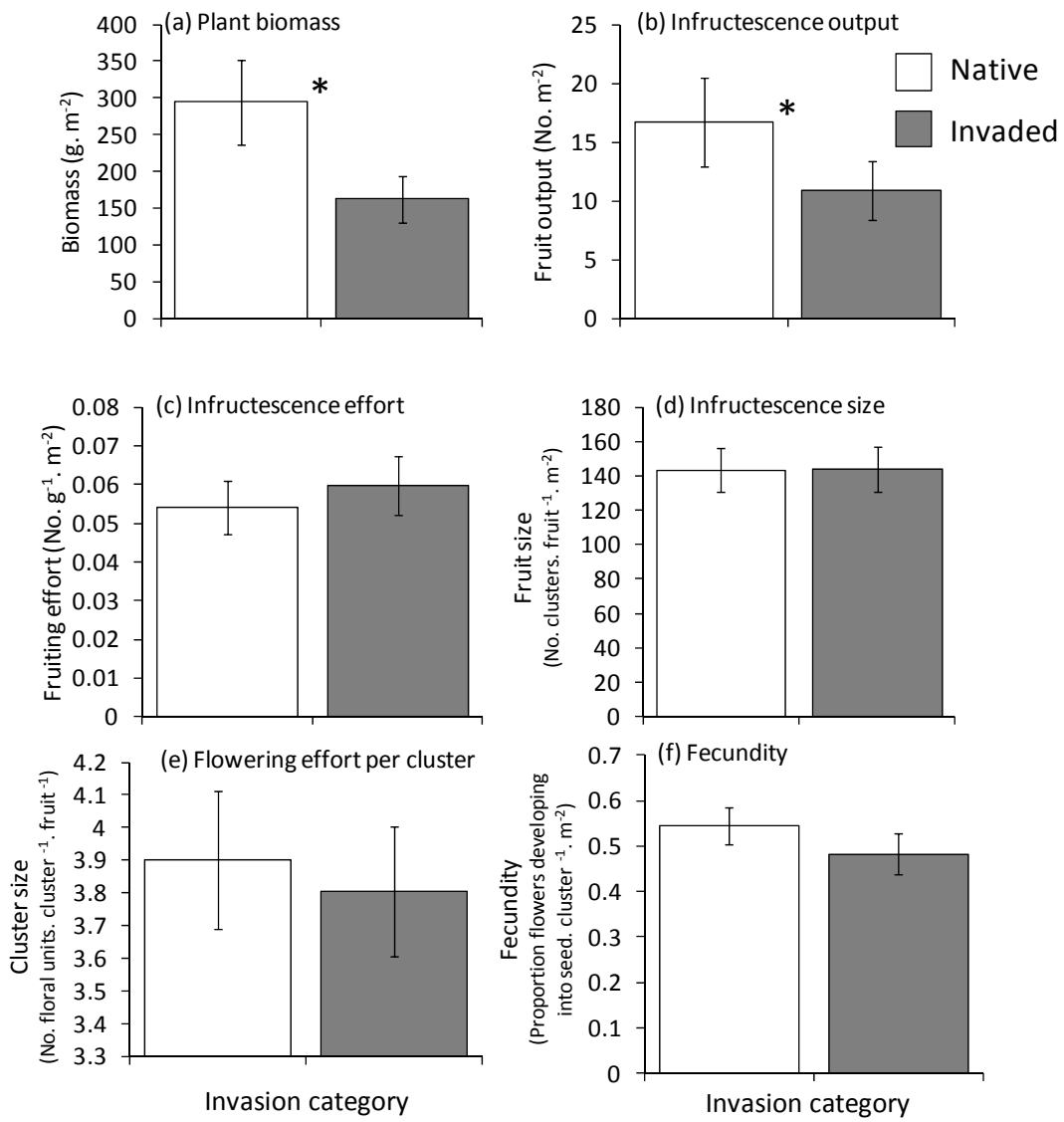


Figure 3

Supporting Information to the paper Gooden, B., French, K. & Robinson, S. A. Alien grass disrupts reproduction and post-settlement recruitment of co-occurring native vegetation: a mechanism for diversity decline in invaded forest? *Plant Ecology*

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Appendix S1. Morphological, taxonomic and reproductive characteristics of the study species, including the number and location of sites from which samples were gathered.

<i>Species</i>	Class (Family)	Growth habit	Flower phenology	Morphology of reproductive organs	Seed characteristics^a	Dispersal strategy	No. of sample locations	Sample location^b
<i>Tetragonia tetragonioides</i> (Pall.) Kuntze	Magnoliopsida (Aizoaceae)	Prostrate, short-lived perennial.	Throughout year; maximum fruiting during winter and spring (pers. obs.).	Styles 5–10; ovary 2–8 locular with up to 10 ovules; fruit fleshy, sub-globose, 10–12 mm diameter, woody, multiple seed.	Seeds numerous per fruit, pyriform, light brown; 1000 seed weight 31.8 g.	Fleshy fruit dispersed by birds (Thorsen et al. 2009), but floats when dry and dispersed principally by water and wrack across study region (pers. obs.).	5	Puckeys, Primbee, Windang, Wallaga, Cuttagee
<i>Baumea juncea</i> (R.Br.) Palla	Liliopsida (Cyperaceae)	Extensively spreading perennial with long rhizome.	October to January (Clifford & Drake 1985).	Inflorescence a panicle, 15–80 mm long; flowers bisexual, arranged in spikelets; reproductive organs enclosed in glumes, perianth absent.	Single seed per nut; single nut produced per flower; 1000 seed weight 4.1 g.	Large nuts are shed beneath parent plants, but may be ingested and spread by wetland birds (Rea & Ganf 1994; B. Gooden, pers. obs.).	6	Squires Way, Primbee, Kioloa, Dalmeny, Nangudga, Wallaga
<i>Juncus kraussii</i> Hochst.	Liliopsida (Juncaceae)	Tussock-forming, shortly rhizomatous perennial.	Spring to summer (Pellow et al. 2009).	Inflorescence a compound cyme, > 100 mm long; flowers borne in clusters; ovary 1–3	Multiple seed per capsule; 1000 seed weight 0.02 g.	Seeds sink immediately in water and thus not water dispersed (Grant et al. 2003); dispersed principally by wind	9	Puckeys, Primbee, Commerong, Currarong, Sanctuary Point,

locular; fruit a
capsule.

(Clifford & Drake
1985); seed
mucilaginous when wet
and may be transported
on animal fur/feathers
or in mud (Clifford &
Drake 1985; Lichstein
et al. 2004).

Sussex Inlet,
Kioloa,
Nangudga,
Wallaga

^a Seed sizes calculated as average weights of 1000 seeds; data obtained from Royal Botanic Gardens Kew Seed Information Database (1989).

^b Geographical location of sample sites, in order of north to south (latitude, longitude): Squires Way (34°23'52.20"S; 150°54'9.10"E), Puckeys (34°24'25.20"S; 150°53'46.60"E), Primbee (34°30'15.10"S; 150°52'25.10"E), Windang (34°32'18.29"S; 150°51'33.51"E), Commerong (34°51'56.70"S; 150°44'46.10"E), Currarong (35° 1'7.60"S; 150°48'51.90"E), Sanctuary Point (35° 6'19.20"S; 150°38'24.30"E), Sussex Inlet (35° 8'57.62"S; 150°35'37.01"E), Kioloa (35°32'46.50"S; 150°22'56.50"E), Dalmeny (36° 9'43.26"S; 150° 7'18.21"E), Nangudga (36°14'48.21"S; 150° 8'15.45"E), Wallaga Lake (36°21'56.10"S; 150° 4'7.80"E), Cuttagee (36°29'24.02"S; 150° 3'4.02"E).

Appendix S2. Photographic examples of arrangements of reproductive structures for (a-b) *Juncus kraussii*, (c) *Baumea juncea* and (d-e) *Tetragonia tetragonioides*: (a) section of a highly fecund *Juncus* infructescence with 7 clusters of fruiting capsules, each bearing multiple seeds; (b) section of a *Juncus* infructescence with 5 clusters of mainly unfertilised or aborted flowers; (c) *Baumea* infructescence bearing 5 unfertilised or aborted floral spikelets and 2 seeds; (d) axial position of solitary fruit on *Tetragonia* stem and (e) transverse section of *Tetragonia* fruit with 6 seeds.

