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1-1-2014

### Impacts of alien grass invasion in coastal seed banks vary amongst native growth forms and dispersal strategies

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## Impacts of alien grass invasion in coastal seed banks vary amongst native growth forms and dispersal strategies

### Abstract

Alien plant invaders frequently reduce biodiversity of native communities, but the mechanisms of impact remain poorly understood. We used the seedling emergence method to assess impacts of invasion by an alien, clonal grass (*Stenotaphrum secundatum*) on endangered coastal swamp forest seed banks of eastern Australia. We asked: do impacts vary amongst native plant growth forms and dispersal strategies, and are impacts driven by propagule or recruitment limitation? Invasion was associated with significant reductions in seed bank species richness and increased dissimilarity between the seed bank and standing vegetation. The rate of species loss was more than two times greater within the standing vegetation than seed bank, however, indicating that the primary mechanism of community change is limited recruitment from the seed bank rather than a reduction in the arrival and storage of propagules to invaded sites. Overall, species losses were observed for herbs, graminoids and vertebrate-dispersed species, whilst wind and water dispersed and woody species were unaffected by invasion. Overall, seed banks were substantially richer than the standing vegetation across both invaded and non-invaded sites, indicating a high potential for unassisted reestablishment of a species-rich standing vegetation from the seed bank following *S. secundatum* removal, although one unlikely to resemble the original community in structure, function and identity of species. Differential impacts across functional groups may result in regenerating communities relatively dominated by woody species, which may prevent subsequent recolonisation by herbs and graminoids. Monitoring will be required to identify whether these and other species require assisted reintroduction.

### Keywords

Plant community change, plant invasion, recruitment dynamics, St. Augustine grass, *Stenotaphrum secundatum* (Walter) Kuntze

### Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

### Publication Details

Gooden, B. & French, K. (2014). Impacts of alien grass invasion in coastal seed banks vary amongst native growth forms and dispersal strategies. *Biological Conservation*, 171 114-126.

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**Title:**

Impacts of alien grass invasion in coastal seed banks vary amongst native growth forms and dispersal strategies

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15 **Abstract**

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36 **Abstract word count: 247**

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## 39 **1. Introduction**

40 Alien plant invaders are well known drivers of plant community change, being frequently  
41 associated with local extinctions of resident flora and altered ecosystem functions (Ehrenfeld  
42 2010; Mason et al. 2009). The majority of research has focused on impacts to visible  
43 components of plant communities, such as the diversity (Bell et al. 1997; Vilà et al. 2011),  
44 structure (Mason and French 2008), reproductive output (e.g. Miller and Gorchoff 2004;  
45 Morales-Romero and Molina-Freaner 2008) and propagule dispersal (e.g. Gosper et al. 2006)  
46 of the standing vegetation. There is very poor understanding, however, of how invasion  
47 influences the post-dispersal recruitment processes that regulate vegetation communities,  
48 such as the arrival, incorporation and storage of propagules within the seed bank (but see  
49 Holmes 2002; Mason et al. 2007), and their emergence and establishment in the standing  
50 vegetation.

51 Seed banks of the soil and associated litter are particularly important in the regulation of plant  
52 community assembly processes, since they comprise a large component of the suite of species  
53 available for recruitment into the standing vegetation and allow for the persistence and  
54 turnover of sexually reproducing species at a particular locality (Chambers and MacMahon  
55 1994; Roberts 1981). Seed banks are considered to be ‘reservoirs of biodiversity’ (Vilà and  
56 Gimeno 2007) and the primary mechanism by which many communities recover following  
57 stochastic disturbances that cause damage to the standing vegetation (Davies et al. 2013;  
58 Kalamees and Zobel 2002; Vosse et al. 2008). Their diversity is thus considered an important  
59 determinant of a community’s resilience to environmental change (Vilà and Gimeno 2007).  
60 Furthermore, seed banks can act as intergenerational reservoirs of genetic diversity, buffering  
61 small, transient and threatened populations from local extinction (Godefroid et al. 2011;  
62 Honnay et al. 2008). Impacts of invasive plants on the seed bank thus have important  
63 implications for the persistence, recoverability and future diversity of resident vegetation

64 following invader management (Fourie 2008; Vosse et al. 2008), and will inform whether  
65 restoration intervention will be necessary to facilitate community recovery (Mason et al.  
66 2007).

67 Invasion can disrupt seed inputs by competitively reducing reproductive rates of adult plants  
68 in the standing vegetation (e.g. Miller and Gorchoff 2004) and the supply of propagules to  
69 invaded sites. Upon arrival, propagules may be physically intercepted and prevented from  
70 reaching the seed bank if the invader increases the density of foliage or litter at the soil  
71 surface (Chambers and MacMahon 1994). Surprisingly, to the best of our knowledge,  
72 trapping of propagules by litter as a mechanism for seed bank disruption has not as yet been  
73 investigated, despite invasion, particular by alien grasses, frequently causing an increase in  
74 rates of litter accumulation (Coleman and Levine 2007; Evans et al. 2001). If, however,  
75 propagules are able to become successfully incorporated within the seed bank, the invader  
76 may prevent their recruitment into the standing vegetation by chemically inhibiting  
77 germination (Ens et al. 2009), changing the abiotic conditions required for recruitment (Farrer  
78 and Goldberg 2009) or increasing rates of seed predation and disease (Beckstead et al. 2010).

79 Native biodiversity responses to alien plant invasion are typically investigated in terms of  
80 changes to the absolute number of resident species (i.e. richness; Vilà et al. 2011), but it is  
81 increasingly recognised that species losses vary across different plant functional groups (see  
82 review by Mason et al. 2009). Differential species losses amongst functional groups, such as  
83 growth form (Gooden et al. 2009a; Gooden et al. 2009b) or dispersal strategy (Mason and  
84 French 2008), in response to invasion may be more important than absolute reductions in  
85 richness, since functional diversity is strongly linked to key ecosystem processes, such as  
86 productivity, strata complexity, nutrient cycling and light availability (Mouillot et al. 2011).  
87 Functional group responses to invasion have only rarely been examined in the seed bank (but  
88 see Mason and French 2008; Mason et al. 2007), yet any differential responses are likely to

89 have strong effects on the emergent structure and composition of regenerating communities  
90 following invader control if some groups are more depauperate in species than others  
91 (priority effects; Mason et al. 2013). Furthermore, an examination of functional responses  
92 may indicate the mechanisms by which invasion drives community change; for example,  
93 relatively greater losses of vertebrate-dispersed than wind or water-dispersed species from  
94 invaded communities could indicate that community change is driven indirectly via impacts  
95 on assemblages and feeding behaviours of resident vertebrate dispersers, such as birds  
96 (Mason and French 2008).

97 We used a seedling emergence study to investigate the effects of invasion by the alien grass  
98 *Stenotaphrum secundatum* (Walter) Kuntze on soil stored seed banks in endangered coastal  
99 swamp forests of south-eastern Australia. *S. secundatum* is a perennial, C<sub>4</sub>, stoloniferous,  
100 clonal grass (Poaceae), originating from the tropical and subtropical Atlantic coastlines of  
101 Africa and the Americas (Sauer 1972). Invasive populations along the eastern Australian  
102 coastline have been present since at least the late 1800s (first naturalised specimen collected  
103 from Sydney in 1882; Atlas of Living Australia 2013), were most likely derived from a sterile  
104 triploid variant (Long and Bashaw 1961) that originated from South Africa (Mullen and  
105 Shelton 1996; Sauer 1972), and which spread vegetatively from adventitious stolons. The  
106 contribution of newly-developed, commercial fertile cultivars to invasive populations is  
107 unknown. In Australia, *S. secundatum* is associated with substantial reductions of species  
108 diversity and altered compositions of coastal forest as well as increased rates of litter  
109 accumulation (Gooden and French in press). This species has received no attention as a  
110 potential threat to the environment, probably because it is widely used throughout Australia  
111 as a valuable amenity turf grass of urban and recreational areas, but is considered to pose a  
112 high risk to native communities across coastal Australia and Oceania (Daehler et al. 2004;  
113 Pacific Islands Ecosystems at Risk 2005).

114 Specifically, we asked:

115 1. What are the effects of invasion on the diversity and composition of the native seed  
116 bank, and do responses vary amongst species with different growth forms and  
117 dispersal strategies?

118 2. What are the relative contributions of seeds in litter and soil to the seed bank?  
119 Considering that *S. secundatum* invasion doubles the biomass and depth of litter, is  
120 there evidence that alien litter interferes with the accumulation of propagules in the  
121 soil?

122 3. Based on the condition of the seed bank, what is the likely mechanism of community  
123 change associated with invasion: limited supply of propagules to the seed bank or  
124 limited recruitment into the standing vegetation?

125 Furthermore, in order to predict the capacity for unassisted community regeneration from  
126 the seed bank following invader management (Holmes and Cowling 1997), we asked:

127 4. How similar are compositions of the standing vegetation and seed bank, and are  
128 similarities lower at invaded sites?

129 5. What is the richness and abundance of other alien species in the seed bank?

## 130 **2. Methods**

### 131 2.1. Study area and habitat

132 The study was located in remnant stands of Swamp Oak Floodplain Forest (sensu Tozer et al.  
133 2010), an endangered ecological community (NSW Office of Environment & NSW Office of  
134 Environment and Heritage 2013), along approximately 500 km of the southern coastline of  
135 New South Wales (NSW), south eastern Australia, between Sydney (33° 51' 54" S; 151° 12'  
136 20" E) and Eden (37° 03' 55" S; 149° 54' 04" E). The community is characterised by the



137 dominant nitrogen-fixing tree *Casuarina glauca*, with a sparse shrub layer and a dense  
138 groundcover of herbs and graminoids, such as *Cyperus*, *Baumea* and *Juncus* species, that are  
139 typical of swamp and marsh vegetation of estuaries and coastal lagoons of eastern Australia  
140 (Clarke 1983; Tozer et al. 2010). The community is restricted to coastal embayments and  
141 estuaries on waterlogged soils below 10 m ASL (Tozer et al. 2010). For details of the  
142 structural and floral attributes of the endangered community, climatic and geological  
143 characteristics and map of the study region, see Tozer et al. (2010).

144 Impacts of *S. secundatum* invasion on the litter and soil seed banks were assessed using a  
145 correlative, multi-site comparative procedure (Adair and Groves 1998; Mason and French  
146 2007), whereby the assemblage of emergent seedlings from samples collected from 26  
147 patches of extensively-invaded forest were compared with those from 26 patches of non-  
148 invaded reference forest dominated by native species. Seed banks were sampled from 2 m × 2  
149 m plots at the same sites and times (between September 2010 and March 2011) as surveys of  
150 the standing vegetation that were carried out previously by Gooden and French (in press).  
151 Infestations of *S. secundatum* at each invaded site covered an area of greater than 100 m<sup>2</sup>,  
152 with a foliage cover abundance of ≥ 80%; non-invaded sites were dominated by native  
153 vegetation, with less than 5% foliage cover of *S. secundatum*. Sites were randomly  
154 interspersed, separated on average by 5.5 km, and evenly distributed across a gradient of  
155 anthropogenic land use in the surrounding matrix to ensure that impacts of *S. secundatum*  
156 were not confounded by extrinsic habitat disturbances (Gooden and French in press).  
157 Furthermore, invaded and non-invaded sites shared similar biological, physical and  
158 disturbance characteristics (e.g. a similar richness of alien species, tree densities and covers  
159 of the herb, shrub and tree canopy layers in the standing vegetation, as well as similar fire  
160 histories and covers of urban and vegetated land in the surrounding landscape matrix)  
161 (Gooden and French in press). These characteristics were included in statistical models as

162 explanatory variables (see section 2.4.2) in order to assess community and landscape effects  
163 on the seed banks.

## 164 2.2. Sampling and seedling emergence

165 Effects of *S. secundatum* invasion on the density and richness of viable propagules within the  
166 seed bank were assessed using a seedling emergence glasshouse experiment, following  
167 protocols developed by Poiani and Carter Johnson (1988) and Mason et al. (2007). Although  
168 seedling emergence studies cannot be relied upon to detect dormant seed, it is a useful  
169 method for rapidly assessing the ecologically viable component of the seed bank and the  
170 species that are thus likely to contribute to the regenerating community following control of  
171 invasive species (Brown 1992). Within each 2 m × 2 m plot we carefully collected leaf litter  
172 from within 10 random subplots of 100 mm × 100 mm, avoiding the soil surface beneath.  
173 Soil was sampled from a different set of 10 random points (excluding litter), using cores of  
174 diameter 63 mm and depth of 100 mm. Soil and litter cores were bulked on site to reduce  
175 within-site variability. Soil was sieved through a 6 mm × 6 mm mesh to remove stones,  
176 woody debris and other contaminants. We also recorded the number of native and alien  
177 species within the standing vegetation in 20 m × 20 m quadrats surrounding each 2 m × 2 m  
178 plot.

179

180 Soil and litter samples were spread evenly to a depth of approximately 20 mm over a  
181 propagation medium of 1:1 vermiculite/perlite within 340 mm × 290 mm propagation trays,  
182 which were positioned randomly within glasshouses located at the University of  
183 Wollongong's Ecological Research Centre (34°24'16.90"S, 150°52'17.98"E). Tap water was  
184 applied to each tray twice daily for 5 minutes from misters housed 50 cm above each tray.  
185 The positions of trays within the glasshouses were changed randomly once per fortnight.  
186 Seedling emergence was assessed once per fortnight for the first three months, then monthly

187 thereafter for one year. Seedlings were removed from trays upon identification, or transferred  
188 to individual pots and grown until identification could be achieved. Species nomenclature  
189 followed Harden (1990, 1991, 1992, 1993). We interspersed 10 control trays (containing only  
190 the vermiculite/perlite base) amongst samples to control for contaminant seeds within the  
191 glasshouses.

### 192 2.3. Functional groups

193 Emergent species from the seed bank were recorded as either native or alien to the study  
194 region. Alien species were defined as those introduced from other regions within Australia or  
195 other countries (Mason and French 2007). Native species were then assigned to one of two  
196 broad dispersal strategies, either 'short' or 'long', following French et al. (2008). Short  
197 distance dispersal was assigned if either no dispersal mechanism could be identified, or if  
198 seeds were capable of moving only up to 10 m from the parent plant (e.g. ballistic or ant  
199 dispersal). Species using long distance dispersal strategies were those capable of moving  
200 seeds in the order of tens to hundreds of metres or more (Mason and French 2008). Long  
201 distance dispersers were further divided into one of four categories: water, wind, endo- and  
202 exo-zoochory (Mason and French 2008). Species' dispersal strategies were determined  
203 through literature searches (Benson and McDougall 1993-2005; Harden 1990, 1991, 1992,  
204 1993; Thorsen et al. 2009; Westoby et al. 1990).

205 Species were assigned to one of four growth forms: herbs, graminoids, climbers and woody  
206 species. These forms were chosen as they are the main contributors to the structure of the  
207 swamp forest community (Tozer et al. 2010), and any differential effects of *S. secundatum*  
208 invasion amongst these groups are thus likely to result in significant shifts in the  
209 community's structure and productivity. Herbs were considered to be non-woody, usually  
210 broad-leaved forbs growing to below 50 cm in height; graminoids were monocotyledonous  
211 grasses and grass-allies, including sedges and rushes; climbers included trailers, twiners,

212 climbers and scramblers that require other vegetation for structural support; woody species  
213 included shrubs and trees growing to above 50 cm in height. Growth forms were determined  
214 through inspection of species habits in the field as well as descriptions within Harden (1990,  
215 1991, 1992, 1993).

## 216 2.4. Data analysis

### 217 2.4.1. Comparison of the seed bank and standing vegetation

218 Similarities in the assemblage of native species between the standing vegetation and seed  
219 bank (i.e. litter and soil combined) were assessed by comparing numbers of species, as well  
220 as Sørensen's quotient of similarity (Sørensen 1948), calculated as follows:  $QS = [2C/(A +$   
221  $B)] \times 100$ , where A and B are the number of respective species in the seed bank and standing  
222 vegetation, and C is the number of species common to both assemblages. Two-way analyses  
223 of variance (ANOVA) were used to assess differences in native and alien species richness  
224 (response variables) between the seed bank and standing vegetation across both *S.*  
225 *secundatum* invaded and non-invaded habitats. A one-way ANOVA was used to compare the  
226 seed bank-standing vegetation QS between *S. secundatum* invaded and non-invaded habitats.

227 Compositional differences between the seed bank and standing vegetation were assessed  
228 using distance-based permutational multivariate analysis of variance (PERMANOVAs)  
229 (Anderson 2001), performed with the statistical packages PRIMER 6 (Clarke and Gorley  
230 2006) and PERMANOVA+ B (Anderson and Gorley 2007). PERMANOVAs were done  
231 using Bray-Curtis similarity indices, calculated using species presence/absence data for all  
232 possible combinations of sample pairs (McArdle and Anderson 2001). Sites containing no  
233 species were removed from analyses as Bray-Curtis indices cannot be calculated using '0'  
234 values. Compositional differences were assessed visually by generating non-metric  
235 multidimensional scaling ordination plots (Clarke 1993). Similarity percentage (SIMPER)

236 analysis was used to identify the species contributing most strongly to the compositional  
237 differences between the seed bank and standing vegetation (Clarke 1993).

#### 238 2.4.2. Impacts of invasion on the seed bank

239 General linear models (GLMs) were used to assess the effects of *S. secundatum* invasion, as  
240 well as the extrinsic physical, biological and disturbance characteristics of the surrounding  
241 community and landscape (i.e. predictor variables) that were measured previously by Gooden  
242 and French (in press) on the germinant density and richness of native and alien species within  
243 the litter, soil and total (i.e. litter and soil combined) seed banks (i.e. response variables). Our  
244 modelling approach followed the procedure outlined by Field (2010) and was performed  
245 using the statistical package JMP® 9 (SAS Institute Inc. 2010):

- 246 1. Multicollinearity amongst predictors was assessed by generating a matrix of Pearson  
247 correlation coefficients (Quinn and Keough 2002); three uncorrelated community-  
248 level predictors (i.e. number of native species of the standing vegetation within the  
249 400 m<sup>2</sup> quadrat, and percentage cover of ground and upper canopy vegetation layers)  
250 and one landscape-level predictor (i.e. percentage cover of vegetation in the matrix  
251 surrounding each site) were included in models (Gooden and French in press). Date of  
252 collection (i.e. number of days since first sample was collected) and latitudinal  
253 position (i.e. decimal degrees south) were also included as covariates to account for  
254 sampling effects.
- 255 2. GLMs were constructed using a backwards step-wise elimination procedure, whereby  
256 non-significant predictors ( $P > 0.05$ ) were successively removed from a complete  
257 model (i.e. all predictors and their first-order interactions included). Model fit was  
258 verified at each stage of variable elimination by calculating Akaike's Information

259 Criterion (Akaike 1974). Normality of the data and homogeneity of variances  
260 amongst treatments were assessed by inspecting plots of studentised residuals.

261 3. GLMs were also done to assess the variation in native species richness within each of  
262 the dispersal and growth forms functional groups in response to invasion and the other  
263 extrinsic environmental predictors measured previously by Gooden and French (in  
264 press). Poisson regression, using the same backwards step-wise selection procedure as  
265 for GLMs, was used to model the response of woody species richness to invasion, as  
266 such species were rare, and data transformations were unable to improve normality of  
267 the data.

268 PERMANOVAs were used to assess the differences in seed bank compositions of native and  
269 alien species between *S. secundatum* invaded and non-invaded habitats. Analyses were done  
270 using both species abundance (i.e. germinant density) and presence/absence data. Analyses  
271 using presence/absence data allowed us to detect the contributions of rare and less abundant  
272 species to community change. SIMPER analysis was used to identify the species contributing  
273 most strongly to the compositional differences between non-invaded and invaded sites.

274 Dead or unidentifiable germinants were removed from analyses. The mean percentage of  
275 germinants across seed bank samples that died and could not be identified to species level  
276 was only 0.85%, and did not vary significantly between invaded and non-invaded seed bank  
277 samples (t-test:  $t_{1,52} = 1.69$ ,  $P = 0.1$ ). Thus, we considered that excluding these data was  
278 unlikely to influence our results.

### 279 **3. Results**

280 3.1. Compositional similarities between the native standing vegetation and seed bank

281 In total, 142 native species were recorded from the emergent seed bank (113 species) and  
282 standing vegetation (74 species) across the 26 native and 26 invaded sites (Appendix 1).  
283 Approximately 66 (58%) and 29 (39%) of the species were unique to the seed bank and  
284 standing vegetation, respectively. A two-way ANOVA revealed that the mean ( $\pm$  SE) native  
285 species richness pooled across all sites ( $n = 52$ ) was significantly higher in the seed bank  
286 ( $10.75 \pm 0.67$  species) than the standing vegetation ( $4.3 \pm 0.63$  species) (Table 1). This  
287 difference in species richness was consistent in both invaded and non-invaded site categories,  
288 as indicated by the non-significant interaction term between invasion category (i.e. invaded  
289 vs. non-invaded habitats) and sample type (i.e. soil vs. standing vegetation) in the model  
290 (Table 1). Species richness combined across the seed bank and standing vegetation also  
291 varied significantly between invaded ( $5.2 \pm 0.58$  species) and non-invaded ( $9.8 \pm 0.57$   
292 species) habitats (Table 1; but see section 3.2. for details of invasion effects within the seed  
293 bank and Gooden and French (in press) for details on invader effects on the standing  
294 vegetation).

295 The native standing vegetation and seed bank assemblages were strongly dissimilar based on  
296 the identity (i.e. presence/absence) of species (PERMANOVA: pseudo  $F_{1,98} = 16.93$ ,  $P =$   
297  $0.001$ ; Fig. 1). Across all sites, the mean ( $\pm$  SE) Sørensen's quotient of similarity (SQ)  
298 between the seed bank and standing vegetation was  $17.7 (\pm 2.2)$  %. The degree of similarity  
299 between the standing vegetation and seed bank was, however, significantly lower for sites  
300 invaded by *S. secundatum* than non-invaded reference sites, with respective mean ( $\pm$  SE) SQ  
301 values of  $9.9 (\pm 2.8)$  % and  $25.2 (\pm 2.8)$  % (one-way ANOVA:  $F_{1,51} = 14.96$ ,  $P = 0.0003$ ).

302 The seed bank assemblage was more homogeneous than the standing vegetation, since sites  
303 were more tightly clustered within the nMDS (Fig. 1).

304 The species contributing most strongly to compositional differences between the seed bank  
305 and standing vegetation were typically graminoids and herbs with long distance dispersal

306 mechanisms (SIMPER analysis; Table 2). In almost all cases, these species occupied a  
307 greater percentage of sites in the seed bank, yet were rarely represented in the standing  
308 vegetation (except for two species, *Phragmites australis* and *Parsonsia straminea*, which  
309 were common in the standing vegetation but absent from the seed bank). Subsequent site  
310 inspections (up to four visits per site over two years following the initial sampling of the seed  
311 bank and standing vegetation) revealed that only nine (14%) of the 66 species unique to the  
312 seed bank germinated and became established in the standing vegetation at only seven (13%)  
313 sites. This indicates that the low similarity between the seed bank and standing vegetation is a  
314 potentially long-term trend rather than an artefact of the timing of our sampling, and that the  
315 seed bank is in the very least a poor short-term (and perhaps long-term) predictor of the  
316 standing vegetation. However, longer term monitoring will be necessary to determine the  
317 temporal scale over which the seed bank contributes to the standing vegetation.

### 318 3.2. Impacts of invasion on the native seed bank

319 In total, 9393 germinants, consisting of 113 native and 40 alien species, were recorded from  
320 the combined litter and soil seed banks (none were detected in control trays). Over 86% of  
321 germinants were native in origin, and the majority of these were recorded from non-invaded  
322 reference sites not invaded by *S. secundatum* (see below for details of invader effects). The  
323 litter contributed very little to both the native and alien species seed banks, with only 6% of  
324 native and 9% of alien germinants emerging from the litter. Likewise, for both native and  
325 alien species, the litter seed bank consisted of 70% fewer species than the soil seed bank.

326 There were no species unique to the litter seed bank.

327 In total, 8100 native germinants were recorded from the combined litter and soil seed banks.  
328 The richness and germinant density of native species in the litter seed bank were unaffected  
329 by *S. secundatum* invasion (Table 3; Fig. 2). However, both the richness and density of native



330 germinants in the soil seed bank were significantly lower at sites invaded by *S. secundatum*  
331 than non-invaded sites (Table 3; Fig. 2). There was also a significant decrease in germinant  
332 density with increasing latitude south, and a positive association between species richness in  
333 the soil seed bank and the richness of the standing vegetation in the surrounding forest  
334 community (i.e. 20 m × 20 m plot). However, the richness and density of germinants were  
335 not affected by any other of the disturbance or environmental attributes of the surrounding  
336 community or landscape that were included in the models as explanatory variables (Table 3).

337 The native seed bank community (litter and soil combined), based on the identity of species  
338 (i.e. presence/absence data), varied significantly between invaded and non-invaded sites  
339 (average Bray-Curtis dissimilarity of 72.4%; pseudo  $F_{1,52} = 1.794$ ,  $P = 0.033$ ). Compositions  
340 also differed significantly when the germinant densities of species were considered (average  
341 Bray-Curtis dissimilarity of 88.34%; pseudo  $F_{1,52} = 1.629$ ,  $P = 0.025$ ), yet this only increased  
342 the magnitude of compositional differences by about 16 %, indicating that the main driver of  
343 community differentiation associated with invasion was a change to the identity and/or  
344 frequency of occurrence of species.

345 SIMPER analysis revealed that only six species (i.e. 5% of the total number of species  
346 detected in the seed bank) contributed up to 50% to the compositional differences between  
347 invaded and non-invaded sites, and that, overall, such compositional change was driven by  
348 reduced germinant density following *S. secundatum* invasion (Table 4).

### 349 3.3. Functional effects of *S. secundatum* invasion on the native seed bank

350 The seed bank assemblage across all sites was dominated by species with long rather than  
351 short distance dispersal strategies (Fig. 3). Of the long distance dispersers, the majority were  
352 water dispersed. The majority of species were either herbs or graminoids; there were very  
353 few woody and climbing species represented in the seed bank.

354 Overall, the richness of species within both short (unassisted, ant and ballistic combined) and  
355 long (wind, water and vertebrate combined) distance dispersal categories was significantly  
356 lower (by about 32%) in invaded than non-invaded sites (Table. 5; Fig. 3). However, the  
357 richness of water and wind dispersed species was unaffected by *S. secundatum* invasion. The  
358 richness of wind dispersed species was negatively related to the percentage cover of ground  
359 layer plants in the standing vegetation in the surrounding community and declined  
360 significantly within increasing latitudinal position of sites. The richness of both endo- and  
361 exo-zoochorously dispersed species was significantly lower in invaded than non-invaded  
362 sites. The magnitude of species loss associated with *S. secundatum* invasion was relatively  
363 larger for exozoochorous species (more than 70% reduction in richness) than for  
364 endozoochorous species (35% reduction in richness).

365 Species richness was significantly lower (by about 35%) for herb and graminoid growth  
366 forms in invaded than non-invaded sites, however the richness of woody tree and shrub  
367 species was unaffected by invasion (Table. 5; Fig. 3). The effects of invasion on climbing  
368 species richness could not be determined because only four species emerged from soil  
369 collected from four locations (all of which were non-invaded sites), and each species was  
370 represented by only one germinant.

371 The disturbance and environmental attributes of the surrounding community and landscape  
372 that were included in the GLMs as explanatory variables did not affect the richness of species  
373 within any dispersal group or growth form (Table 5).

#### 374 3.4. Alien species and potential for secondary invasion

375 In total, 49 alien species (excluding *S. secundatum*) were recorded from across the 52 sites  
376 (Appendix 1). A two-way ANOVA revealed that the standing vegetation had significantly  
377 fewer alien species than the seed bank, with respective means ( $\pm$  SE) of 1.23 ( $\pm$  0.20) and

378 4.17 ( $\pm 0.41$ ) species, but that alien species richness was unaffected by *S. secundatum*  
379 invasion (Table 6).

380 In total, 1293 alien germinants, representing 40 species, were recorded from the seed bank,  
381 92% of which emerged from soil samples. The density of alien germinants in both the litter  
382 and soil was unaffected by *S. secundatum* invasion (Table 7; Fig. 4). However, density in the  
383 litter was positively associated with alien species richness and the percentage ground layer  
384 cover of the standing vegetation in the surrounding community, but negatively associated  
385 with the date of collection. Alien germinant density in the soil was positively associated with  
386 the percentage cover of standing vegetation in the surrounding landscape matrix, but only for  
387 sites invaded by *S. secundatum*.

388 Although the litter comprised very few alien germinants (i.e. 8%) compared with the soil,  
389 alien species richness in the litter was significantly greater in sites invaded by *S. secundatum*  
390 than non-invaded sites (Table 7; Fig. 4). Alien species richness in the soil was unaffected by  
391 *S. secundatum* invasion, but was positively associated with alien species richness and the  
392 percentage cover of ground and upper canopy layers of the standing vegetation in the  
393 surrounding community (i.e. 20  $\times$  20 m plot). Alien richness declined with sampling date in  
394 both the litter and soil. *S. secundatum* contributed very little to the assemblage of alien  
395 species in the seed bank: only 24 *S. secundatum* germinants (i.e. 2% of the total number of  
396 alien germinants) were recorded from eight invaded sites, and none from non-invaded sites.

397 *S. secundatum* invasion had no effect on the composition of the alien species seed bank  
398 (PERMANOVA: presence/absence, pseudo  $F_{1,51} = 1.861$ ,  $P = 0.07$ ; germinant density,  
399 pseudo  $F_{1,51} = 1.398$ ,  $P = 0.112$ ).

#### 400 **4. Discussion**

401 4.1. Impacts of invasion on the seed bank: is the community propagule or recruitment  
402 limited?

403 Invasion by *S. secundatum* was associated with significant but moderate (i.e. 30%) losses of  
404 native species from the seed bank, and an increase in the compositional dissimilarities  
405 between the seed bank and standing vegetation. Those species still present in invaded seed  
406 banks generally had lower propagule densities than in non-invaded seed banks, signalling  
407 potential future reductions in diversity in response to invasion. Our results contrast with most  
408 other seed bank studies, which show that invasion by alien plants generally has little effect on  
409 biodiversity attributes of seed banks (e.g. Adams and Engelhardt 2009; Biggerstaff and Beck  
410 2007; Giantomasi et al. 2008; e.g. Mason et al. 2007; Vilà and Gimeno 2007; Wearne and  
411 Morgan 2004). Generally, we found little effect of landscape context, such as the cover of  
412 indigenous vegetation surrounding sites, or environmental condition of the community, such  
413 as the cover of different canopy strata, on responses of seed bank communities to invasion.  
414 However, across both invaded and non-invaded habitats, there was a decline in native  
415 germinant densities with increasing latitude south, and a positive effect of vegetation richness  
416 in the surrounding forest community on seed bank richness, implying that broader  
417 community condition buffers losses of species from seed banks in *S. secundatum* infestations.

418 There are two main mechanisms by which *S. secundatum* invasion could have lowered seed  
419 bank diversity: either by (1) lowering rates of propagule supply to infested sites through  
420 either reductions in reproductive output of mature resident plants or visitation rates of key  
421 seed dispersers (e.g. Ens and French 2008; Morales-Romero and Molina-Freaner 2008), or  
422 (2) competitively interfering with propagule viability and emergence as a result of residual  
423 allelochemicals (e.g. Ens et al. 2009) or pathogens (Beckstead et al. 2010) within the soil or  
424 modifications to soil chemistry (Novoa et al. 2013). The relative importance of these  
425 mechanisms in driving low rates of germinant emergence is unknown since the seedling

426 emergence method used here is unable to detect the presence of dormant or unviable  
427 propagules in the seed bank (Brown 1992; Poiani and Carter Johnson 1988).

428 A recent study by Gooden and French (in press) found that 2 m × 2 m plots of vegetation  
429 infested with *S. secundatum* has about 80% fewer species than non-invaded forest, which is a  
430 rate of species loss more than two times greater than is evident for the seed bank. This trend  
431 indicates that although species losses from the seed bank do occur, the strongest driver of  
432 community change following *S. secundatum* invasion is reduced species recruitment into the  
433 standing vegetation. Indeed, propagules of *Casuarina glauca*, the dominant canopy tree  
434 within the community, were present in the seed bank at high densities across all sites, but  
435 invaded vegetation had more than 85% fewer seedlings than non-invaded forest (Gooden and  
436 French in press), signalling a substantial shift in the physical structure of the forest.

#### 437 4.2. No effect of alien litter on the seed bank

438 Across all habitats, litter contributed very little to the complement of species within the seed  
439 bank (6% of native germinants), none of which were unique to the litter. This was surprising  
440 considering that litter, often in the form of floating wrack, is a known repository for a variety  
441 of marsh and swamp species (Minchinton 2002), and has been shown in woodland systems to  
442 contain as much as 25% of germinants (Fisher et al. 2009). Despite *S. secundatum* doubling  
443 the biomass and depth of litter in the forest (Gooden and French in press), richness and  
444 density of germinants in the litter seed bank did not vary between invaded and non-invaded  
445 habitats. This indicates that the addition of *S. secundatum* litter at the soil surface does not  
446 inhibit propagules from entering the soil seed bank. However, litter may still influence  
447 recruitment from the seed bank, subsequently driving greater rates of species loss from the  
448 standing vegetation, by altering the abiotic conditions required for seed germination, such as  
449 light, temperature and moisture (Facelli and Pickett 1991), which have been demonstrated as

450 important controls on species recruitment in other ecosystems invaded by alien grasses (e.g.  
451 Coleman and Levine 2007; Holdredge and Bertness 2011). The relative importance of litter  
452 versus direct competition with *S. secundatum* on recruitment from the seed bank could be  
453 assessed using manipulative litter and shoot removal experiments (e.g. Coleman and Levine  
454 2007; Minchinton et al. 2006).

#### 455 4.3. Do impacts on seed bank diversity vary across growth forms or dispersal strategies?

456 Impacts of invasion on species richness in the seed bank varied amongst both native plant  
457 growth forms and dispersal strategies. Although woody trees and shrubs were the least  
458 speciose growth form in the seed bank, they were equally represented in both invaded and  
459 non-invaded habitats. Herb and graminoid growth forms, however, had significantly fewer  
460 species in invaded seed banks. This trend contrasts with an invasion study by Mason et al.  
461 (2007) which found that the seed banks of coastal hind dune woodlands invaded by the  
462 woody shrub *Chrysanthemoides monilifera* ssp. *rotundata* had similar levels of graminoid  
463 and herb richness, but had about 75% fewer tree species than sparsely-invaded dunes.

464 Relative differences in the dominance of growth forms in the seed bank may have important  
465 consequences for the structure of emergent communities following invader management, if  
466 priority species moderate the success of subsequent immigrant species (termed priority  
467 effects; Ladd and Facelli 2008; Mason et al. 2013). In swamp forest, the relative loss of herbs  
468 and graminoids from *S. secundatum*-invaded sites may result in an emergent community  
469 dominated by juvenile woody trees and shrubs. Woody ‘priority’ species could interfere with  
470 the recolonisation of sites by herbs and graminoids after removal of *S. secundatum* by  
471 competitively pre-empting resources (most probably light) or changing the abiotic conditions  
472 required for their establishment (Mason et al. 2013). This represents a potential indirect

473 legacy effect of *S. secundatum* on the community, leading to continued absences of herb and  
474 graminoid species from the standing vegetation even once the invader has been removed.

475 Overall, *S. secundatum* invasion was associated with losses of species with both short and  
476 long distance dispersal strategies; however, within the long distance dispersal group, species  
477 losses were driven by a reduction in the number of vertebrate dispersed species, not of those  
478 dispersed passively by either wind or water. Losses of vertebrate dispersed species might  
479 have resulted from reduced occupancy of invaded sites by frugivorous birds or macropods,  
480 such as swamp wallaby (*Wallabia bicolor*), red-necked wallaby (*Macropus rufogriseus*) and  
481 eastern grey kangaroo (*Macropus giganteus*), which are very abundant throughout the study  
482 region (pers. obs.) and important dispersers of indigenous flora (Clifford and Drake 1985;  
483 Willson et al. 1989). Such vertebrate species may have avoided invaded areas because of the  
484 low abundance of native plants upon which to forage, the reduction in woody shrubs used for  
485 roosting, or if *S. secundatum* is relatively less palatable than native plants and thus not  
486 attractive to them as a food source. Many species with short distance dispersal mechanisms  
487 that are absent from both the seed bank and standing vegetation may be unable to re-establish  
488 spontaneously following invader removal, and may need to be actively reintroduced by land  
489 managers. Likewise, many vertebrate-dispersed species may be delayed in re-establishing at  
490 invaded sites if the dispersers continue to avoid infestations after the removal of *S.*  
491 *secundatum*.

492 4.4. What is the potential for unassisted community regeneration from the seed bank  
493 following invader management?

494 The seed bank and standing vegetation assemblages varied substantially, with only 17% of  
495 species on average per site being shared between them. Such low levels of similarity are  
496 consistent with other seed bank studies (e.g. Holmes and Cowling 1997; Mason et al. 2007;

497 Vilà and Gimeno 2007). However, in contrast to other coastal plant communities (e.g. Mason  
498 and French 2008; Mason et al. 2007), this difference was driven primarily by a significantly  
499 greater number of unique species within the seed bank, rather than a loss of characteristic  
500 species of the standing vegetation from the seed bank. Indeed, many species considered to be  
501 characteristic of the community, e.g. *Juncus kraussii*, *Casuarina glauca*, *Lobelia anceps*,  
502 *Baumea juncea* (Tozer et al. 2010), were well represented in the seed bank, often at high  
503 propagule densities and more common than in the standing vegetation. Since over 80% of  
504 species unique to the seed bank never emerged into the standing vegetation, it is likely that  
505 the seed bank functions as a propagule sink (at least in the absence of soil disturbance), and  
506 that vegetation diversity of the swamp forest is limited by low rates of post-settlement  
507 recruitment, rather than reductions in the arrival of propagules to sites or their storage within  
508 the seed bank. Although *S. secundatum* invasion was associated with significant reductions in  
509 seed bank species richness, invaded seed banks still contained significantly more species,  
510 most of which were unique, than the overall standing vegetation. In general, therefore, we  
511 consider that there is a high potential for unassisted reestablishment of a species-rich standing  
512 vegetation from the seed bank, although one that is unlikely to resemble the characteristic  
513 community in either structure, function or the identity of species.

514

515 There are several implications that emerge from our study for the restoration of native  
516 vegetation following removal of *S. secundatum*. First, several functional groups, such as  
517 herbs, graminoids and vertebrate dispersed species, may require supplemented reintroduction  
518 as their propagules are poorly represented in invaded seed banks. Regenerating communities  
519 are likely to be underrepresented in herbs and graminoids, and relatively dominated by  
520 woody species. Since woody species are relatively long-lived, their potential dominance of  
521 regenerating vegetation might cause long-term shifts in vegetation structure and diversity by



522 preventing the recolonisation of herbaceous species. Species reintroductions may be more  
523 necessary in sites with southern geographical location as well as those with low species  
524 richness in the broader forest community.

525 Alien species contributed strongly to the seed bank, representing about 30% of the total  
526 number of species recorded; thus, there is a significant threat of secondary plant invasion to  
527 the regenerating community. The risk of secondary invasion could be reduced by controlling  
528 *S. secundatum* towards the end of summer when the richness of secondary invaders in the soil  
529 is lower than in spring, as well as using chemical application to dense infestations, rather than  
530 manually removing stolons, in order to limit disturbance of the litter and soil, which has been  
531 shown to increase weed emergence elsewhere (e.g. Mason and French 2007). Furthermore,  
532 whilst seed banks represent the regeneration potential of a community following invader  
533 removal (Holmes and Cowling 1997), the contribution of the seed bank and the restoration  
534 trajectory of the regenerating community will be influenced strongly by the removal regime  
535 (e.g. intensive mechanical versus extensive chemical removal; Mason and French 2007).  
536 Long-term monitoring of regenerating vegetation will be required to identify those species  
537 unable to recolonise sites, and which thus require supplemented reintroduction, and to ensure  
538 that secondary invaders do not dominate the emergent vegetation.

## 539 **5. Acknowledgements**

540 We thank S. Robinson, T. Minchinton, T. Mason and K. Maute for helpful discussions that  
541 improved the quality of this manuscript; C. Dunne and K. Reed for assistance in the field, B.  
542 Pellow for assistance with plant specimen identification; M. Batterham for statistical advice.  
543 Financial support was provided by an Ecological Society of Australia student research grant  
544 (2010). Plant surveys were granted under NSW National Park and Wildlife Service Scientific

545 Licence (Number S13163). The manuscript was improved through helpful suggestions from  
546 three anonymous reviewers.

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560 [:414915&sort=occurrence\\_date#tab\\_recordsView](http://biocache.ala.org.au/occurrences/search?q=lsid:urn:lsid:biodiversity.org.au:apni.taxon:414915&sort=occurrence_date#tab_recordsView) (accessed October 2013).
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711 **Figure captions**

712

713 **Figure 1.** Non-metric multidimensional scaling (nMDS) ordination of native species  
714 presence/absence within the standing vegetation ( $n = 46$ , coloured circles) and seed bank ( $n =$   
715  $52$ , clear circles). Points closer together in ordination space indicate relatively more similar  
716 species assemblages based on Bray-Curtis indices of dissimilarity (2D stress: 0.18).

717 **Figure 2.** Average ( $\pm$  SE) differences in germinant density and richness of native species  
718 within litter, soil and total (litter and soil combined) seed banks between *S. secundatum* invaded  
719 ( $n = 26$ ) and non-invaded ( $n = 26$ ) coastal swamp forest habitats. Note the differences in y-axis  
720 units and ranges between figure plates. Asterisks denote significantly different means based on  
721 GLMs.

722 **Figure 3.** Differences in average ( $\pm$  SE) seed bank germinant richness between *S. secundatum*  
723 invaded ( $n = 26$ ) and non-invaded ( $n = 26$ ) coastal swamp forest habitats for species with (a)  
724 short and (b-g) long distance dispersal strategies and (h-j) different growth forms. Asterisks  
725 denote significantly different means based on GLMs.

726 **Figure 4.** Average ( $\pm$  SE) differences in germinant density and richness of alien species within  
727 litter, soil and total (litter and soil combined) seed banks between *S. secundatum* invaded ( $n =$   
728  $26$ ) and non-invaded ( $n = 26$ ) coastal swamp forest habitats. Note the differences in y-axis units  
729 and ranges between figure plates. Asterisks denote significantly different means based on  
730 GLMs.

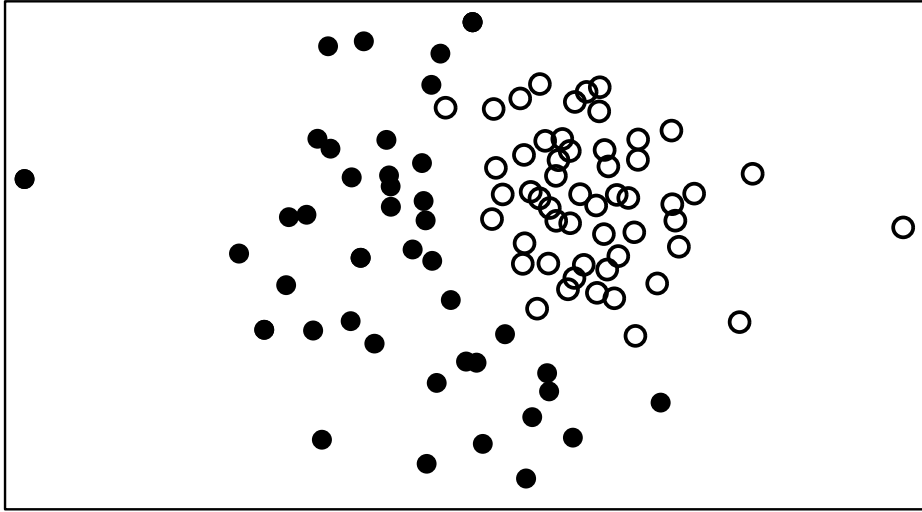
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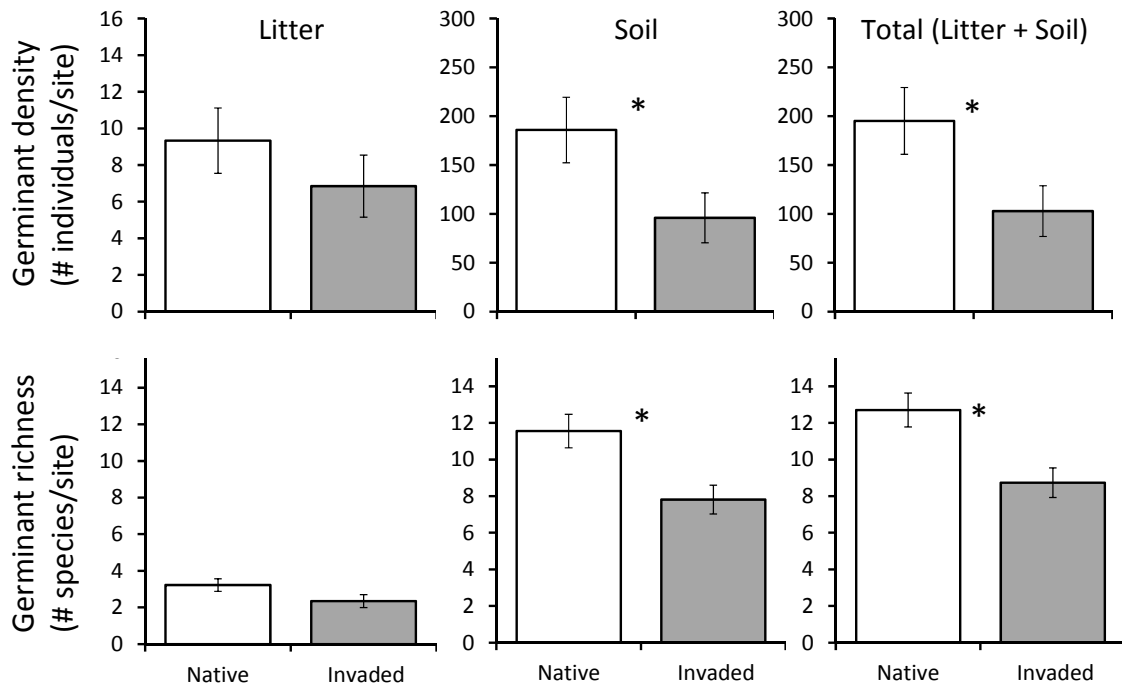
735 Fig. 1.



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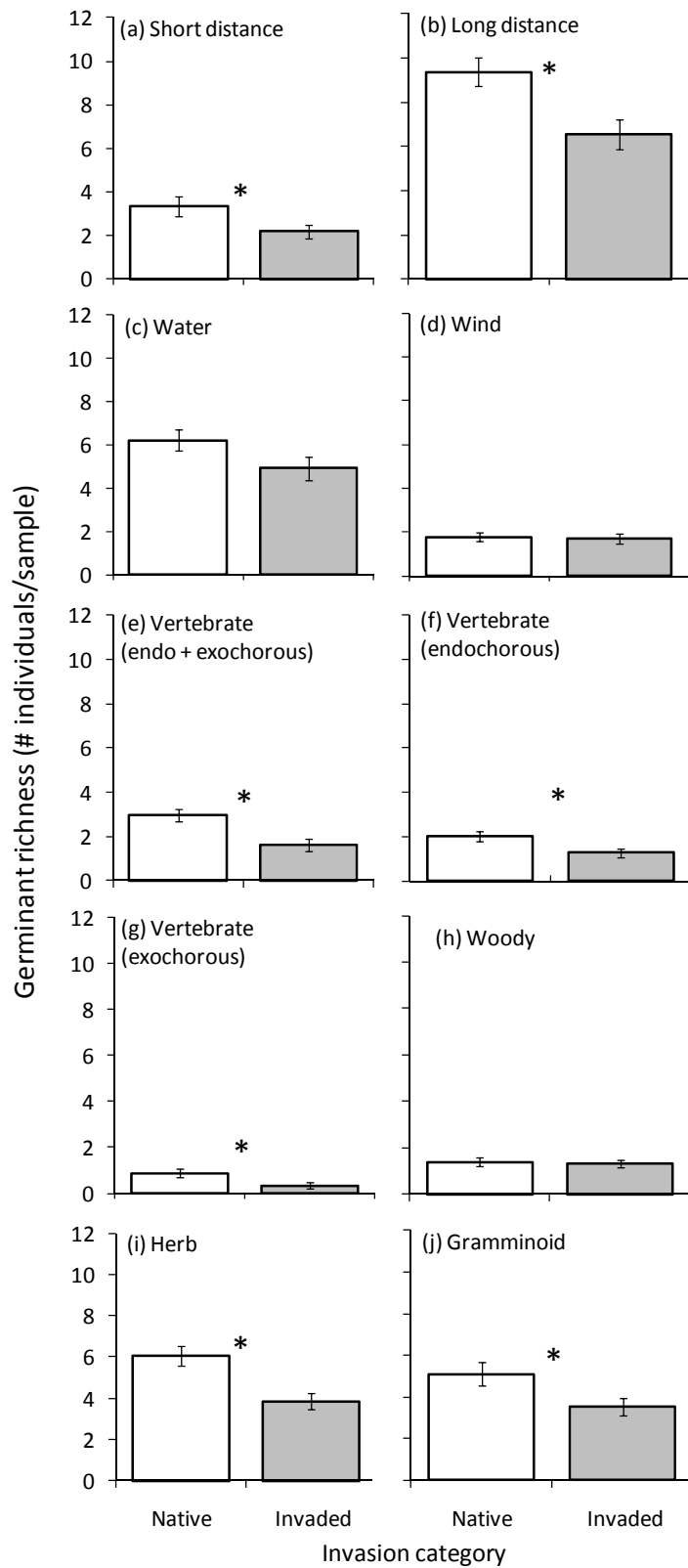
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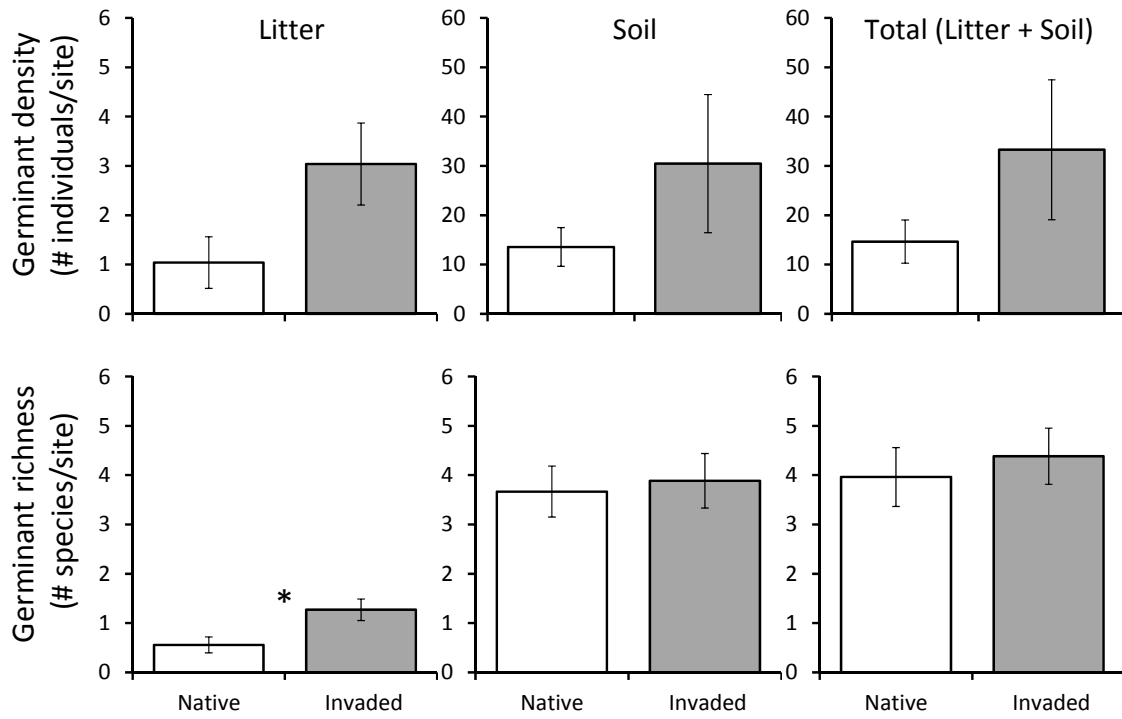
741 Fig. 3.



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748 **Tables**

749

750 **Table 1.** Results of two-way ANOVA for native species richness in response to *S.*

751 *secundatum* invasion (two treatment levels: invaded vs. non-invaded habitats) and sample

752 type (two treatment levels: standing vegetation vs. seed bank). Bold *P*-values denote

753 significant effects.

<b>Source of variation</b>	<b>DF</b>	<b>SS</b>	<b>F</b>	<b>P</b>	<b>r<sup>2</sup></b>
Model	3	1691.4721	32.4376	< <b>0.0001</b>	0.49
Invasion category	1	575.4977	33.1092	< <b>0.0001</b>	
Sample type	1	1107.4838	63.7152	< <b>0.0001</b>	
Invasion category × Sample type	1	12.5404	0.7215	0.3977	
Error	102	1772.9430			

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756 **Table 2.** Summary of SIMPER analysis, showing the cumulative contributions (up to 50%) of native species to the average dissimilarity between the  
 757 standing vegetation and seed bank assemblages.

<i>Species</i>	Growth form	Dispersal	Sites occupied (%)		Average dissimilarity (%)	Diss/SD	Contribution to dissimilarity (%)
			Seed bank (n = 52)	Standing vegetation (n = 46)			
<i>Casuarina glauca</i>	Woody	Wind	89	9	6.17	1.43	6.7
<i>Oxalis perennans</i>	Herb	Ballistic	68	2	4.85	1.11	5.27
<i>Juncus kraussii</i>	Graminoid	Water	55	26	3.89	0.85	4.22
<i>Lobelia anceps</i>	Herb	Vertebrate	53	4	3.6	0.94	3.91
<i>Cynodon dactylon</i>	Graminoid	Water	6	41	3.14	0.73	3.41
<i>Juncus usitatus</i>	Graminoid	Water	45	2	2.97	0.8	3.23
<i>Samolus repens</i>	Herb	Water	25	20	2.61	0.64	2.83
<i>Baumea juncea</i>	Graminoid	Vertebrate	28	20	2.53	0.68	2.74
<i>Oxalis</i> sp.	Herb	Ballistic	36	0	2.47	0.68	2.68
<i>Tetragonia tetragonioides</i>	Herb	Water	21	15	2.24	0.56	2.43
<i>Oplismenus aemulus</i>	Graminoid	Vertebrate	28	20	2.16	0.68	2.34
<i>Parsonsia straminea</i>	Climber	Wind	0	30	2.04	0.59	2.22
<i>Commelina cyanea</i>	Herb	None	13	20	1.99	0.54	2.16
<i>Typha orientalis</i>	Graminoid	Water/Wind	25	0	1.82	0.49	1.98
<i>Phragmites australis</i>	Graminoid	Water/Wind	0	22	1.78	0.46	1.93
<i>Apium prostratum</i>	Herb	Water	19	11	1.74	0.54	1.88

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**Table 3.** Results of general linear models of richness and density of native germinants in the (a) litter, (b) soil and (c) total (litter and soil combined) seed banks in coastal swamp forest invaded by the alien turf grass *S. secundatum*. Values in bold indicate significant effects. Models presented provide the ‘best fit’ for each response variable based on the backwards step-wise elimination procedure, where the elimination of non-influential predictors at each step was verified using the Akaike Information Criterion (AIC).

Seed bank sample type Response variable <sup>a</sup> Predictor variable	DF	SS	F	P	r <sup>2</sup>	Direction of response
<b>(a) Litter seed bank</b>						
<i>Density</i>						
Model non-significant	1	81.936	1.019	0.318	0.020	
<i>Richness</i>						
Model non-significant	1	10.166	3.151	0.082	0.058	
<b>(b) Soil seed bank</b>						
<i>Density</i>						
Model	3	297354.8	4.737	<b>0.006</b>	0.225	
Invasion category	1	159676.37	7.631	<b>0.008</b>		Non-invaded > Invaded; Fig. 2.
Ground cover (%)	1	76142.64	3.639	0.062		
Latitude	1	142490.77	6.810	<b>0.012</b>		Decreasing native germinant density in soil with increasing latitude across all sites.
Error	48	1025271.0				
<i>Richness</i>						
Model	3	500.772	12.100	<b>&lt;0.0001</b>	0.426	
Invasion category	1	71.848	5.208	<b>0.027</b>		Non-invaded > Invaded; Fig. 2.
Native community richness	1	124.838	9.049	<b>0.004</b>		Positive relationship between native germinant richness in soil and native richness of standing vegetation in surrounding community across all sites.
Invasion category × Native community richness	1	55.484	4.022	0.051		
Error	48	675.983				
<b>(c) Total seed bank (litter + soil)</b>						
<i>Density</i>						
Model	2	228833.8	4.994	<b>0.011</b>	0.167	
Invasion category	1	129224.67	5.640	<b>0.021</b>		Non-invaded > Invaded; Fig. 2.



Latitude	1	115803.87	5.055	<b>0.029</b>		Decreasing total native germinant density with increasing latitude across all sites.
Error	49	1145520.2				
<i>Richness</i>						
Model	2	470.076	15.267	<b>&lt;0.0001</b>	0.379	
Invasion category	1	64.815	4.210	<b>0.045</b>		Non-invaded > Invaded; Fig. 2.
Native community richness	1	261.009	16.955	<b>0.0001</b>		Positive relationship between total native germinant richness and native richness of standing vegetation in surrounding community across all sites.
Error	49					

<sup>a</sup> Density = number of germinants/site; Richness = number of species/sample/site.

**Table 4.** Summary of SIMPER analyses, showing the cumulative contributions (up to 50%) of native species within the seed bank to the average dissimilarity between *S. secundatum* invaded and non-invaded sites, based on (a) germinant densities and (b) species presence/absence.

Data source <i>Species</i>	Growth form	Dispersal	Invasion category <sup>a</sup>		Av. Dissimilarity	Diss/SD	Contribution (%)	Cumulative cont. (%)
			Native (n = 26)	Invaded (n = 26)				
<b>(a) Germinant density; average dissimilarity between non-invaded and invaded categories= 88.34 %</b>								
<i>Lobelia anceps</i>	Herb	Vertebrate	23.11	13.04	11.52	0.72	13.04	13.04
<i>Juncus kraussii</i>	Graminoid	Water	28.32	8.5	9.95	0.56	11.26	24.3
<i>Juncus usitatus</i>	Graminoid	Water	23.43	14.62	8.22	0.59	9.3	33.61
<i>Cyperus polystachyos</i>	Graminoid	None	17.04	14.31	6.03	0.47	6.82	40.43
<i>Oxalis perennans</i>	Herb	Ballistic	9.07	6.08	6.02	0.62	6.81	47.24
<i>Isolepis habra</i>	Graminoid	Water	22.86	1.04	4.33	0.34	4.9	52.14
<b>(b) Germinant presence/absence; average dissimilarity between non-invaded and invaded categories = 72.40 %</b>								
<i>Lobelia anceps</i>	Herb	Vertebrate	61	46	2.67	0.93	3.68	3.68
<i>Juncus kraussii</i>	Graminoid	Water	54	58	2.6	0.91	3.59	7.27
<i>Oxalis spp.</i>	Herb	Ballistic	46	23	2.53	0.88	3.49	10.76
<i>Juncus usitatus</i>	Graminoid	Water	46	42	2.5	0.92	3.45	14.21
<i>Oxalis perennans</i>	Herb	Ballistic	71	65	2.36	0.81	3.26	17.48
<i>Baumea juncea</i>	Graminoid	Vertebrate	43	15	2.28	0.83	3.15	20.63
<i>Samolus repens</i>	Herb	Water	32	19	2.12	0.72	2.93	23.56
<i>Oplismenus aemulus</i>	Graminoid	Vertebrate	43	15	2.11	0.84	2.91	26.47
<i>Typha orientalis</i>	Graminoid	Wind/Water	21	27	1.88	0.71	2.6	29.07
<i>Cyperus polystachyos</i>	Graminoid	None	25	27	1.84	0.74	2.54	31.61
<i>Apium prostratum</i>	Herb	Water	32	8	1.79	0.7	2.48	34.08
<i>Isolepis habra</i>	Graminoid	Water	25	23	1.77	0.7	2.45	36.53
<i>Tetragonia tetragonoides</i>	Herb	Water	21	19	1.68	0.65	2.33	38.86
<i>Chenopodium glaucum</i>	Herb	Vertebrate	29	15	1.68	0.7	2.32	41.18

<i>Mimulus repens</i>	Herb	Water	29	12	1.64	0.65	2.26	43.44
<i>Centella asiatica</i>	Herb	None	32	8	1.62	0.68	2.24	45.68
<i>Oxalis exilis</i>	Herb	Ballistic	18	12	1.36	0.55	1.88	47.56
<i>Bacopa monnieri</i>	Herb	Vertebrate	18	15	1.35	0.59	1.87	49.43
<i>Viola hederacea</i>	Herb	Ant	21	12	1.26	0.6	1.74	51.18

<sup>a</sup> Values are (a) mean number of germinants per site and (b) percentage of sites occupied per species.

**Table 5.** Results of general linear models for native germinant richness within (a) herb, woody and graminoid growth forms and (b) seven dispersal strategies in seed banks of coastal forest invaded by the alien turf grass *S. secundatum*. Note that results for Poisson regression are presented for woody species richness. Values in bold indicate significant effects. Models presented provide the ‘best fit’ for each response variable based on the backwards step-wise elimination procedure, where the elimination of predictors at each step was verified using the Akaike Information Criterion (AIC).

<b>Plant functional category</b>							
<i>Response variable</i>							
<b>Predictor variable</b>	<b>DF</b>	<b>SS</b>	<b>F</b>	$\chi^2$	<b>P</b>	$r^2$	<b>Direction of response</b>
<b>(a) Growth form</b>							
<i>Herb</i>							
Model	1	63.577	12.551		<b>0.001</b>	0.197	
Invasion category	1	63.577	12.551		<b>0.001</b>		Non-invaded > Invaded; Fig. 3i.
Error	50	258.348					
<i>Woody (Poisson)</i>							
Model non-significant	1			0.0361	0.849		
<i>Graminoid</i>							
Model	1	32.759	4.576		<b>0.037</b>	0.082	
Invasion category	1	32.759	4.576		<b>0.037</b>	0.082	Non-invaded > Invaded; Fig. 3j.
Error	50	365.128					
<b>(b) Dispersal mechanism</b>							
<i>Short distance</i>							
Model	1	2.311	5.489		<b>0.023</b>	0.097	
Invasion category	1	2.311	5.489		<b>0.023</b>		Non-invaded > Invaded; Fig. 3a.
Error	50	21.479					
<i>Long distance (total)</i>							
Model	1	106.223	9.201		<b>0.004</b>	0.153	
Invasion category	1	106.223	9.201		<b>0.004</b>		Non-invaded > Invaded; Fig. 3b.
Error	50	588.758					
<i>Water</i>							
Model non-significant	1	23.644	3.576		0.064	0.066	
<i>Wind</i>							

Model	2	15.071	7.977	<b>0.001</b>	0.242	
Ground cover (%)	1	7.985	8.453	<b>0.005</b>		Negative relationship between richness of wind dispersed species and cover of ground layer vegetation in surrounding community across all sites.
Latitude	1	4.973	5.264	<b>0.026</b>		Negative relationship between richness of wind dispersed species and latitude.
Error	49					
<i>Vertebrate (total)</i>						
Model	1	24.053	12.132	<b>0.001</b>	0.192	
Invasion category	1	24.053	12.132	<b>0.001</b>		Non-invaded > Invaded; Fig. 3e.
Error	50	101.117				
<i>Vertebrate (endozoochory)</i>						
Model	1	7.808	6.629	<b>0.013</b>	0.115	
Invasion category	1	7.808	6.629	<b>0.013</b>		Non-invaded > Invaded; Fig. 3f.
Error	50	60.078				
<i>Vertebrate (exozoochory)</i>						
Model	2		11.127	<b>0.004</b>		
Invasion category	1		6.607	<b>0.010</b>		Non-invaded > Invaded; Fig. 3g.
Collection date	1		4.607	<b>0.032</b>		Reduced likelihood of exozoochorous species occurrence with increasing date of collection.
Error	49					

**Table 6.** Results of two-way ANOVA for alien species richness in response to *S. secundatum* invasion (two treatment levels: invaded vs. non-invaded habitats) and sample type (two treatment levels: standing vegetation vs. seed bank). Bold *P*-values denote significant effects.

<b>Source of variation</b>	<b>DF</b>	<b>SS</b>	<b><i>F</i></b>	<b><i>P</i></b>	<b><i>r</i><sup>2</sup></b>
Model	3	232.0334	13.8818	< <b>0.0001</b>	0.29
Invasion category	1	1.6936	0.3040	0.5826	
Sample type	1	230.0001	41.2806	< <b>0.0001</b>	
Invasion category × Sample type	1	0.7548	0.1355	0.7136	
Error	102	568.3063			

**Table 7.** Results of general linear models for richness and density of alien germinants in the (a) litter, (b) soil and (c) total (litter and soil combined) seed banks in coastal swamp forest invaded by the alien turf grass *S. secundatum*. Values in bold indicate significance effects. Models presented provide the ‘best fit’ for each response variable based on the backwards step-wise elimination procedure, where the elimination of predictors at each step was verified using the Akaike Information Criterion (AIC).

Seed bank sample type Response variable <sup>a</sup> Predictor variable	DF	SS	F	P	r <sup>2</sup>	Direction of response
<b>(a) Litter seed bank</b>						
<i>Density</i>						
Model	3	174.940	5.495	<b>0.003</b>	0.252	
Alien community richness	1	71.809	6.766	<b>0.012</b>		Positive relationship between alien germinant density in litter and alien richness of standing vegetation in surrounding community across all sites.
Ground cover (%)	1	55.324	5.213	<b>0.027</b>		Positive relationship between alien germinant density in litter and cover of ground layer vegetation in surrounding community.
Collection date	1	69.266	6.526	<b>0.014</b>		Negative relationship between alien germinant density in litter and collection date.
Error	48	520.041				
<i>Richness</i>						
Model	2	11.110	6.116	<b>0.004</b>	0.197	
Invasion category	1	6.870	7.563	<b>0.008</b>		Invaded > Non-invaded; Fig. 4.
Collection date	1	4.364	4.804	<b>0.033</b>		Negative relationship between alien germinant richness in litter and collection date.
Error	49					
<b>(b) Soil seed bank</b>						
<i>Density</i>						
Model	3	21169.65	2.854	<b>0.047</b>	0.149	
Invasion category	1	6048.534	2.447	0.124		
Matrix vegetation cover (%)	1	8019.159	3.244	0.078		
Invasion category × Matrix vegetation cover (%)	1	10699.879	4.328	<b>0.043</b>		Positive relationship between alien germinant density in soil and matrix vegetation cover across invaded sites only.
Error	48	121139.14				

<i>Richness</i>					
Model	6	201.707	8.333	< <b>0.0001</b>	0.521
Invasion category	1	0.244	0.060	0.807	
Alien community richness	1	60.577	15.016	<b>0.0003</b>	Positive relationship between alien germinant richness in soil and alien richness of standing vegetation in surrounding community across all sites.
Ground cover (%)	1	1.339	0.332	0.567	
Upper canopy cover (%)	1	29.093	7.212	<b>0.010</b>	Positive relationship between alien germinant richness in soil and cover of upper canopy in surrounding community across all sites.
Invasion category × Ground cover (%)	1	40.772	10.106	<b>0.003</b>	Positive association between alien germinant richness in soil and cover of ground layer vegetation in surrounding community across non-invaded sites only.
Collection date	1	21.451	5.317	<b>0.026</b>	Negative relationship between alien germinant richness in soil and collection date.
Error	45	185.576			
<b>(c) Total seed bank (litter + soil)</b>					
<i>Density</i>					
Model non-significant	3	21095.79	2.700	0.056	0.142
<i>Richness</i>					
Model	3	167.592	9.315	< <b>0.0001</b>	0.363
Alien community richness	1	72.096	12.021	<b>0.001</b>	Positive relationship between total alien germinant richness and alien richness of standing vegetation in surrounding community across all sites.
Upper canopy cover (%)	1	32.971	5.498	<b>0.023</b>	Positive relationship between total alien germinant richness and cover of upper canopy in surrounding community across all sites.
Collection date	1	33.470	5.581	<b>0.022</b>	Negative relationship between total alien germinant richness and collection date.
Error	48	293.879			

<sup>a</sup> Density = number of germinants/site; Richness = number of species/sample/site.



**Appendix.** Native and alien species detected in surveys of *Stenotaphrum secundatum*-invaded and non-invaded coastal swamp forest seed banks and standing vegetation along the south coast of NSW, Australia. Dispersal strategies are assigned to native species detected within the seed bank only, whilst growth forms are assigned to both native and alien species detected within both the seed bank and standing vegetation. Values for the seed bank are total number of germinants per species summed across either invaded or native sites, as well as percentage of sites within which each species was detected. Values for the standing vegetation are percentage of sites within which each species was detected (we do not present information on the abundance of each species within the standing vegetation).

Species origin  Family Species	Functional group <sup>a</sup>		Seed bank				Standing vegetation	
	Growth form <sup>b</sup>	Dispersal <sup>c</sup>	Invaded sites ( <i>n</i> = 26)		Native sites ( <i>n</i> = 26)		Invaded sites ( <i>n</i> = 26)	Native sites ( <i>n</i> = 26)
			No. germinants	% sites occupied	No. germinants	% sites occupied	% sites occupied	% sites occupied
<b>Native</b>								
Acanthaceae								
<i>Pseuderanthemum variabile</i> (R.Br.) Radlk.	H		0	0	0	0	0	4
Aizoaceae								
<i>Tetragonia tetragonioides</i> (Pall.) Kuntze	H	Wa	20	19	11	22	12	19
Amaranthaceae								
<i>Alternanthera denticulata</i> R.Br.	H	V (exo)	3	8	20	11	0	0
Apiaceae								
<i>Apium prostratum</i> Labill. ex Vent.	H	Wa	231	8	107	30	8	15
<i>Centella asiatica</i> (L.) Urb.	H	N	6	8	98	33	8	0
<i>Hydrocotyle peduncularis</i> R.Br. ex A.Rich.	H	Wa	22	12	16	11	0	7
<i>Hydrocotyle tripartita</i> R.Br. ex A.Rich.	H	Wa	2	8	113	11	0	0*
<i>Trachymene incisa</i> Rudge	H		0	0	0	0	0	4
Apocynaceae								
<i>Parsonsia straminea</i> var. <i>glabrata</i> Pichon	C		0	0	0	0	19	37
<i>Tylophora barbata</i> R.Br.	C		0	0	0	0	8	0
Asteraceae								
Asteraceae sp. 1			0	0	2	4	0	0
Asteraceae sp. 2			0	0	1	4	0	0

Asteraceae sp. 3			2	4	0	0	0	0
<i>Centipeda minima</i> (L.) A.Braun & Asch.	H	Wa	3	4	3	7	0	0
<i>Eclipta platyglossa</i> F.Muell.	H	Wa	0	0	2	4	0	0*
<i>Epaltes australis</i> Less.	H	N	1	4	0	0	0	0
<i>Euchiton gymnocephalus</i> (DC.) Holub	H	Wi	1	4	0	0	0	0
<i>Lagenophora gracilis</i> Steetz	H		0	0	0	0	0	11
<i>Leptinella longipes</i> Hook.f.	H	Wi	12	8	41	11	0	4
<i>Ozothamnus diosmifolius</i> (Vent.) DC.	W	Wi	2	8	1	4	0	0
<i>Pseudognaphalium luteoalbum</i> (L.) Hilliard & B.L.Burtt	H	Wi	0	0	1	4	0	0
<i>Senecio diaschides</i> D.G.Drury	H	Wi	0	0	6	7	0	0
<i>Senecio pinnatifolius</i> A.Rich.	W	Wi	2	8	1	4	0	0
<i>Senecio linearifolius</i> A.Rich.	W	Wi	3	8	4	15	0	0
Brassicaceae								
<i>Cardamine microthrix</i> I.Thomps.	H		0	0	0	0	0	4
Campanulaceae								
<i>Wahlenbergia gracilis</i> (G.Forst.) A.DC.	H	Wi	0	0	5	7	0	0
Caryophyllaceae								
<i>Stellaria flaccida</i> Hook.	H	N	1	4	0	0	0	7
Casuarinaceae								
<i>Casuarina glauca</i> Sieber ex Spreng.	W	Wi	150	88	200	89	8	11
Chenopodiaceae								
<i>Atriplex australasica</i> Moq.	H	Wa	23	4	0	0	0	0
Chenopodiaceae sp. 1			1	4	16	11	0	0
<i>Chenopodium glaucum</i> L.	H	V (endo)	112	15	64	30	0	0
<i>Einadia trigonos</i> (Schult.) Paul G.Wilson	H	Wi	27	8	3	4	0	0*
<i>Enchylaena tomentosa</i> R.Br.	W		0	0	0	0	0	4
<i>Rhagodia candolleana</i> subsp. <i>candolleana</i> Moq.	W		0	0	0	0	0	4
<i>Sarcocornia quinqueflora</i> (Bunge ex Ung.-Sternb.) A.J.Scott	H	Wa	0	0	73	7	0	7

Commelinaceae								
<i>Commelina cyanea</i> R.Br.	H	N	14	15	4	11	23	15
Convolvulaceae								
<i>Calystegia marginata</i> R.Br.	C		0	0	0	0	0	7
<i>Dichondra repens</i> J.R.Forst. & G.Forst.	H	N	0	0	12	19	0	22
Cyperaceae								
<i>Baumea juncea</i> (R.Br.) Palla	G	V (endo)	29	15	80	41	12	26
<i>Bolboschoenus</i> sp.	G	Wa	6	8	0	0	0	0*
<i>Carex appressa</i> R.Br.	G	Wa	2	8	48	15	0	11
<i>Carex longibrachiata</i> Boeck.	G	Wa	0	0	3	4	0	7
<i>Carex</i> sp.	G	Wa	3	4	0	0	0	0
<i>Cyperus laevigatus</i> L.	G	Wa	0	0	2	4	0*	0*
<i>Cyperus lhotskyanus</i> Boeck.	G	Wa	2	8	0	0	0	0
<i>Cyperus polystachyos</i> Rottb.	G	N	372	27	477	26	0*	0*
<i>Cyperus sanguinolentus</i> Vahl	G	Wa	5	4	91	4	0	0
<i>Cyperus</i> sp. 1	G	Wa	1	4	0	0	0	0
<i>Cyperus</i> sp. 2	G	Wa	9	4	0	0	0	0
<i>Ficinia nodosa</i> (Rottb.) Goetgh. et al.	G	Wi	0	0	3	4	0	4
<i>Gahnia clarkei</i> Benl	G	N	37	15	2	4	0	7
<i>Gahnia melanocarpa</i> R.Br.	G		0	0	0	0	0	4
<i>Isolepis habra</i> (Edgar) Sojak	G	Wa	27	23	640	26	0*	0
<i>Isolepis hookeriana</i> Boeck.	G	Wa	0	0	14	19	0	0
<i>Isolepis inundata</i> R.Br.	G	Wa	0	0	20	19	0	0
<i>Isolepis platycarpa</i> (S.T.Blake) Sojak	G	Wa	3	12	22	15	0	0
<i>Isolepis prolifera</i> (Rottb.) R.Br.	G	Wa	80	8	15	4	0	0
<i>Isolepis</i> sp.	G	Wa	0	0	31	7	0	0
<i>Lepidosperma laterale</i> R.Br.	G		0	0	0	0	0	4
<i>Schoenoplectus pungens</i> (Vahl) Palla	G	V (endo)	1	4	3	4	0	0
<i>Schoenoplectus</i> sp.	G	V (endo)	0	0	38	4	0	0
<i>Schoenoplectus validus</i> (Vahl) A.Löve &	G	V (endo)	23	4	88	11	0	4

D.Löve									
<i>Schoenus apogon</i> Roem. & Schult.	G	Wa	1	4	21	7	0	0	
<i>Schoenus maschalinus</i> Roem. & Schult.	G	Wa	18	8	0	0	0	0	
Euphorbiaceae									
<i>Chamaesyce dallachyana</i> (Baill.) D.C.Hassall	H	A	2	8	1	4	0	4	
<i>Chamaesyce drummondii</i> (Boiss.) D.C.Hassall	H	A	2	4	0	0	0	0	
Fabaceae									
<i>Acacia binervata</i> DC.	W	A	0	0	2	4	0	0	
<i>Acacia longifolia</i> subsp. <i>sophorae</i> (Labill.) Court	W	A	0	0	1	4	0	0	
<i>Desmodium gunnii</i> Benth. ex Hook.f.	C		0	0	0	0	0	7	
<i>Desmodium varians</i> (Labill.) G.Don	C		0	0	0	0	0	4	
<i>Glycine clandestina</i> J.C.Wendl.	C		0	0	0	0	0	4	
<i>Glycine microphylla</i> (Benth.) Tindale	C	N	0	0	8	4	0	4	
<i>Glycine tabacina</i> (Labill.) Benth.	C	N	0	0	4	4	0	0	
<i>Kennedia rubicunda</i> Vent.	C	A	0	0	1	4	0	0	
Geraniaceae									
<i>Geranium homeanum</i> Turcz.	H	N	1	4	7	7	0	7	
Goodeniaceae									
<i>Goodenia ovata</i> Sm.	W	A	10	4	0	0	0	0*	
<i>Scaevola albida</i> (Sm.) Druce	H	V (endo)	0	0	4	4	0	0	
<i>Selliera radicans</i> Cav.	H	V (exo)	13	8	28	15	12	19	
Haloragaceae									
<i>Gonocarpus teucrioides</i> DC.	H	N	0	0	3	4	0	4	
<i>Haloragis</i> sp.	W	N	0	0	3	4	0	0	
Juncaceae									
<i>Juncus gregiflorus</i> L.A.S.Johnson	G	Wa	0	0	12	4	0	0	
<i>Juncus kraussii</i> subsp. <i>australiensis</i> (Buchenau) Snogerup	G	Wa	221	58	787	52	27	22	
<i>Juncus planifolius</i> R.Br.	G	Wa	2	4	1	4	0	0	

<i>Juncus prismatocarpus</i> R.Br.	G	Wa	5	4	34	7	0	0
<i>Juncus</i> sp.	G	Wa	0	0	8	4	0	0
<i>Juncus usitatus</i> L.A.S.Johnson	G	Wa	380	42	656	48	0	4
<i>Luzula</i> sp.	G	V (exo)	0	0	1	4	0	0
Juncaginaceae								
<i>Triglochin microtuberosa</i> Aston	G		0	0	0	0	0	4
<i>Triglochin procera</i> R.Br.	G		0	0	0	0	0	4
<i>Triglochin striata</i> Ruiz & Pav.	G	Wa	8	12	24	4	0	7
Lamiaceae								
<i>Clerodendrum tomentosum</i> R.Br.	W		0	0	0	0	0	4
<i>Mentha laxiflora</i> Benth.	H	N	0	0	4	4	0	0*
<i>Plectranthus parviflorus</i> Willd.	H	V (endo)	2	4	0	0	8	0
Lobeliaceae								
<i>Lobelia anceps</i> L.f.	H	V (endo)	339	46	573	59	0	7
<i>Pratia purpurascens</i> (R.Br.) E.Wimm.			0	0	0	0	0	22
Lomandraceae								
<i>Lomandra longifolia</i> Labill.	G	A	0	0	4	11	0	11
Luzuriagaceae								
<i>Eustrephus latifolius</i> R.Br. ex Ker Gawl.	C		0	0	0	0	0	4
<i>Geitonoplesium cymosum</i> (R.Br.) A.Cunn. ex Hook.	C		0	0	0	0	0	4
Menispermaceae								
<i>Stephania japonica</i> var. <i>discolor</i> (Blume) Forman	C	V (endo)	0	0	1	4	0	4
Moraceae								
<i>Ficus coronata</i> Spin	W	V (endo)	0	0	1	4	0	0
Myoporaceae								
<i>Myoporum acuminatum</i> R.Br.	W		2	4	2	4	0	0
Myrtaceae								
<i>Melaleuca ericifolia</i> Sm.	W	Wi	1	4	0	0	0	7

Oleaceae								
<i>Notelaea longifolia</i> Vent.	W		0	0	0	0	0	4
Oxalidaceae								
<i>Oxalis exilis</i> A.Cunn.	H	B	38	12	22	19	0	0
<i>Oxalis perennans</i> Haw.	H	B	158	65	248	70	0	4
<i>Oxalis rubens</i> Haw.	H	B	16	12	1	4	0	7
<i>Oxalis</i> sp.	H	B	42	8	60	48	0	0
Phyllanthaceae								
<i>Breynia oblongifolia</i> Muell.Arg.	W		0	0	0	0	0	4
Pittosporaceae								
<i>Pittosporum undulatum</i> Vent.	W	Vert (end)	2	4	0	0	0	4
Plantaginaceae								
<i>Veronica plebeia</i> R.Br.	H	V (exo)	0	0	5	7	0	0
Poaceae								
<i>Cynodon dactylon</i> (L.) Pers.	G	Wa	6	4	18	7	23	52
<i>Digitaria aequiglumis</i> (Hack. & Arechav.) Parodi	G	Wi	3	4	0	0	0	0
<i>Echinopogon ovatus</i> (G.Forst.) P.Beauv.	G		0	0	0	0	0	4
<i>Entolasia marginata</i> (R.Br.) Hughes	G	N	17	4	18	19	0	19
<i>Entolasia stricta</i> (R.Br.) Hughes	G	N	0	0	1	4	0	4
<i>Eragrostis</i> sp.	G	N	0	0	11	4	0	0
<i>Imperata cylindrica</i> P.Beauv.	G		0	0	0	0	0	4
<i>Lachnagrostis filiformis</i> (G.Forst.) Trin.	G	V (exo)	0	0	9	7	0	0
<i>Microlaena stipoides</i> (Labill.) R.Br.	G	N	0	0	3	11	0	22
<i>Oplismenus aemulus</i> (R.Br.) Roem. & Schult.	G	V (exo)	17	15	67	41	8	30
<i>Oplismenus imbecillis</i> (R.Br.) Roem. & Schult.	G	V (exo)	1	4	0	0	0	15
<i>Paspalidium distans</i> (Trin.) Hughes	G	N	0	0	3	4	0	0
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	G		0	0	0	0	27	15
<i>Poa labillardierei</i> Steud.	G	Wa	1	4	7	22	0	4
<i>Poaceae</i> sp.	G	Wa	23	15	3	11	0	0

<i>Sporobolus virginicus</i> (L.) Kunth	G	Wa	0	0	4	7	0	0
Polygonaceae								
<i>Rumex brownii</i> Campd.	H	Wa	3	4	0	0	0	0
Ranunculaceae								
<i>Clematis aristata</i> Ker Gawl.	C		0	0	0	0	0	7
<i>Ranunculus plebeius</i> R.Br. ex DC.	H	N	0	0	2	4	0	4
Rhamnaceae								
<i>Alphitonia excelsa</i> (A.Cunn. ex Fenzl) Benth.	W	V (endo)	0	0	6	4	0	0
Rosaceae								
<i>Rubus parvifolius</i> L.	W		0	0	0	0	0	7
Rubiaceae								
<i>Galium pripinquinum</i> A. Cunn.	H	V (exo)	0	0	1	4	0	11
<i>Morinda jasminoides</i> A.Cunn.	C		0	0	0	0	0	4
Scrophulariaceae								
<i>Bacopa monnieri</i> (L.) Pennell	H	V (endo)	24	15	45	19	0	0
<i>Mimulus repens</i> R.Br.	H	Wa	15	12	17	30	0	0
Solanaceae								
<i>Solanum americanum</i> Mill.	H	V (endo)	1	4	0	0	0	0
<i>Solanum prinophyllum</i> Dunal	H	V (endo)	0	0	1	4	0	4
<i>Solanum stelligerum</i> Sm.	H		0	0	0	0	0	7
Theophrastaceae								
<i>Samolus repens</i> (J.R.Forst. & G.Forst.) Pers.	H	Wa	37	19	104	30	15	22
Typhaceae								
<i>Typha orientalis</i> C.Presl	G	Wa/Wi	11	27	27	22	0	0*
Ulmaceae								
<i>Trema tomentosa</i> var. <i>aspera</i> (Brongn.) Hewson	W	V (endo)	4	8	3	7	0	0
Violaceae								
<i>Viola hederacea</i> Labill.	H	A	9	12	12	22	0	33
<b>Alien</b>								

Asparagaceae							
<i>Asparagus aethiopicus</i> L.	H	2	4	0	0	23	26
<i>Asparagus asparagoides</i> (L.) Druce	C	0	0	0	0	15	15
Crassulaceae							
<i>Crassula multicava</i> Lem.	H	0	0	0	0	0	4
<i>Crassula sarmentosa</i> var. <i>sarmentosa</i> Harv.	H	0	0	0	0	4	4
Apiaceae							
<i>Cyclospermum leptophyllum</i> (Pers.) Sprague	H	0	0	2	7	0	0
<i>Hydrocotyle bonariensis</i> Lam.	H	20	19	12	7	12	7
Asteraceae							
<i>Ageratina adenophora</i> (Spreng.) R.M.King & H.Rob.	H/W	20	8	11	11	0	0
<i>Aster subulatus</i> Michx.	H/W	10	15	4	7	0	4
<i>Baccharis halimifolia</i> L.	W	0	0	1	4	0	0
<i>Bidens pilosa</i> L.	H	0	0	1	4	4	4
<i>Cirsium vulgare</i> (Savi) Ten.	H	11	15	6	19	0	7
<i>Conyza bonariensis</i> (L.) Cronquist	H	41	58	33	63	0	0
<i>Delairea odorata</i> Lem.	C	0	0	0	0	8	0
<i>Gamochaeta purpurea</i> (L.) Cabrera	H	14	23	13	15	0	0
<i>Senecio madagascariensis</i> Poir.	H	17	35	13	33	0	0
<i>Sonchus asper</i> (L.) Hill	H	0	0	1	4	0	0
<i>Sonchus oleraceus</i> L.	H	15	15	8	30	0	0
<i>Taraxacum officinale</i> Weber	H	2	4	0	0	0	0
Commelinaceae							
<i>Tradescantia fluminensis</i> Vell.	H	0	0	0	0	19	0
Convolvulaceae							
<i>Ipomoea indica</i> (Burm.f.) Merr.	C	0	0	0	0	8	4
Cyperaceae							
<i>Cyperus brevifolius</i> (Rottb.) Hassk.	G	5	4	10	11	0	0
<i>Cyperus eragrostis</i> Lam.	G	2	4	21	7	0	0



<i>Isolepis marginata</i> (Thunb.) A.Dietr.	G	0	0	5	4	0	0
Euphorbiaceae							
<i>Euphorbia peplus</i> L.	H	1	4	0	0	0	0
Fabaceae							
<i>Medicago lupulina</i> L.	H	29	8	1	4	0	0
<i>Medicago polymorpha</i> L.	H	0	0	1	4	0	0
Gentianaceae							
<i>Centaurium erythraea</i> Rafn	H	16	15	7	15	0	0
Iridaceae							
<i>Watsonia meriana</i> (L.) Mill.	H	0	0	0	0	4	0
Juncaceae							
<i>Juncus acutus</i> L.	G	459	15	6	7	4	4
<i>Juncus bulbosus</i> L.	G	0	0	34	11	0	0
<i>Juncus capillaceus</i> Lam.	G	1	4	75	4	0	0
Myrsinaceae							
<i>Anagallis arvensis</i> L.	H	5	12	51	26	0	4
Phytolaccaceae							
<i>Phytolacca octandra</i> L.	H	2	8	1	4	0	0
Plantaginaceae							
<i>Plantago major</i> L.	H	2	8	5	7	0	0
Poaceae							
<i>Axonopus</i> sp.	G	3	4	2	4	0	0
<i>Bromus catharticus</i> Vahl	G	0	0	1	4	0	0
<i>Ehrharta erecta</i> Lam.	G	82	15	14	15	12	15
<i>Paspalum</i> sp.	G	5	12	1	4	0	0
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	G	0	0	4	4	8	7
<i>Stenotaphrum secundatum</i> (Walter) Kuntze	G	24	31	0	0	n/a	n/a
Polygalaceae							
<i>Polygala myrtifolia</i> L.	W	4	4	0	0	0	0
Rosaceae							

<i>Rubus fruticosus</i> L. aggregate	W	1	4	4	7	4	0
Rubiaceae							
<i>Coprosma repens</i> A.Rich.	W	0	0	0	0	0	4
Scrophulariaceae							
<i>Verbascum virgatum</i> Stokes	H	1	4	0	0	0	0
Solanaceae							
<i>Physalis peruviana</i> L.	H	1	4	0	0	0	0
<i>Solanum chenopodioides</i> Lam.	H/W	2	8	11	7	0	0
<i>Solanum nigrum</i> L.	H/W	59	69	34	37	0	7
Verbenaceae							
<i>Lantana camara</i> L.	W	0	0	0	0	4	4
<i>Verbena bonariensis</i> L.	H/W	9	8	2	7	0	0

<sup>a</sup> Functional group information is provided only for native species present in the seed bank.

<sup>b</sup> Growth form: C = Climber, G = Graminoid, H = Herb, W = Woody species.

<sup>c</sup> Dispersal mechanism; Short distance: A = Ant, B = Ballistic, N = None; Long distance: V (endo) = Vertebrate endochory, V (exo) = Vertebrate exochory, Wa = Water, Wi = Wind.

\* Species unique to seed bank during initial site surveys but which emerged in the standing vegetation during subsequent site inspections.