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

Ben Gooden
University of Wollongong, bgooden@uow.edu.au

Kris French
University of Wollongong, kris@uow.edu.au

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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.

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

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3   dispersal strategies

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5   **Authors:**

6   Ben Gooden* and Kris French

7   **Institutional details:** Institute for Conservation Biology and Environmental Management,

8   School of Biological Sciences, University of Wollongong.

9   **Address:** University of Wollongong, Northfields Avenue, Wollongong, NSW, 2522,

10   Australia.

11   * Author for correspondence: Ben Gooden; phone: +61242528993; email:

12   bengooden@gmail.com, bg662@uowmail.edu.au

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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.

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1. Introduction

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

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

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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_4, 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^2,

152   with a foliage cover abundance of $\geq$ 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)] × 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^2 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 (± SE) native

285   species richness pooled across all sites ($n = 52$) was significantly higher in the seed bank

286   (10.75 ± 0.67 species) than the standing vegetation (4.3 ± 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 ± 0.58 species) and non-invaded (9.8 ± 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 (± SE) Sørensen's quotient of similarity (SQ)

298   between the seed bank and standing vegetation was 17.7 (± 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 (± SE) SQ

301   values of 9.9 (± 2.8) % and 25.2 (± 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

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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 andnon-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 (± SE) of 1.23 (± 0.20) and

378   4.17 (± 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 × 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.

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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 (± 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 (± 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 (± 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.
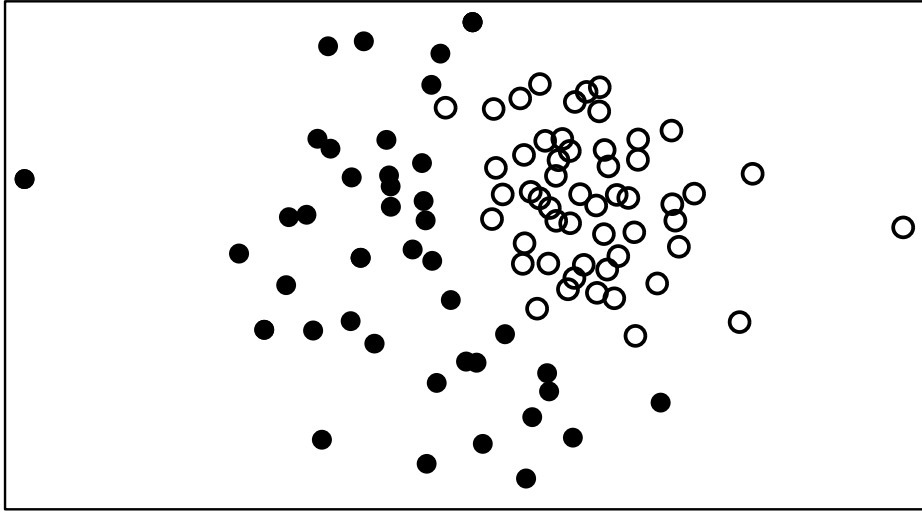
736

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738   *Fig. 2.*
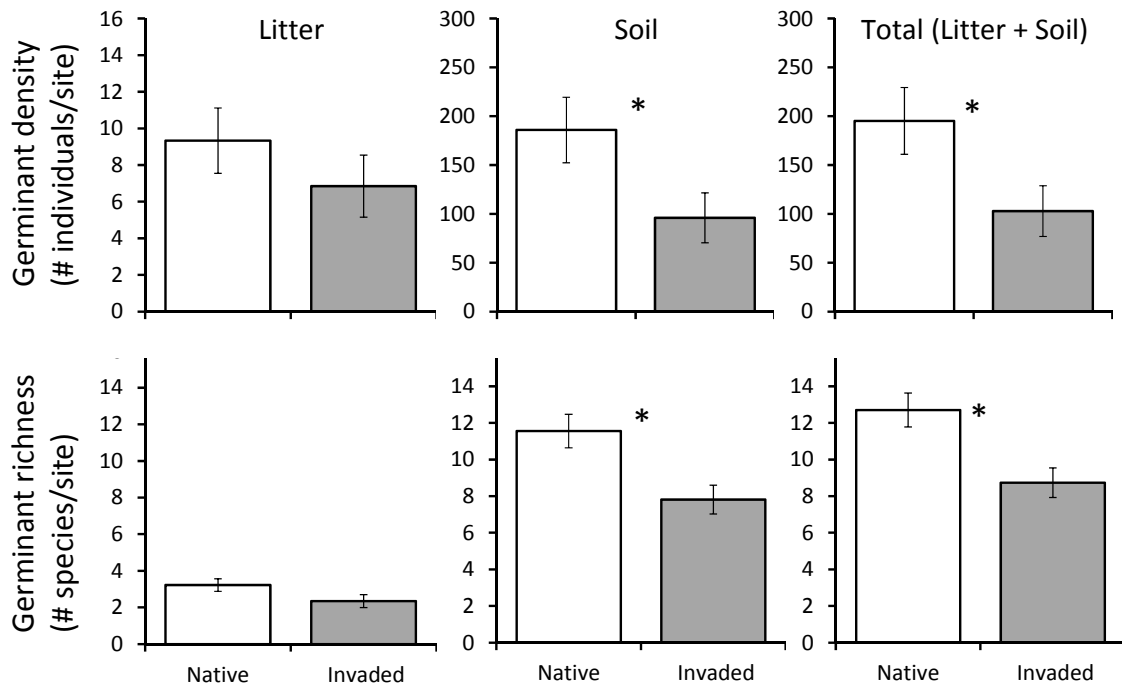
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741   *Fig. 3.*

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743
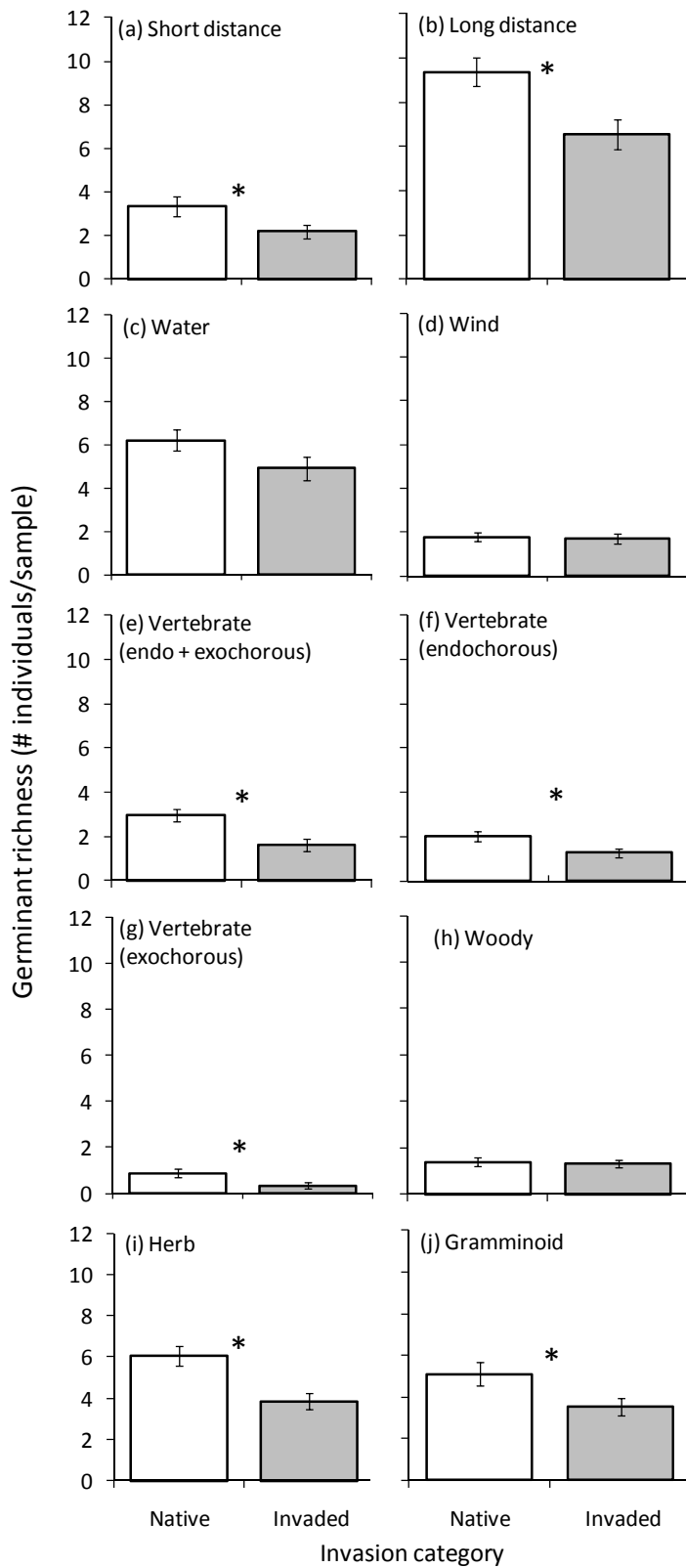
744   *Fig. 4.*
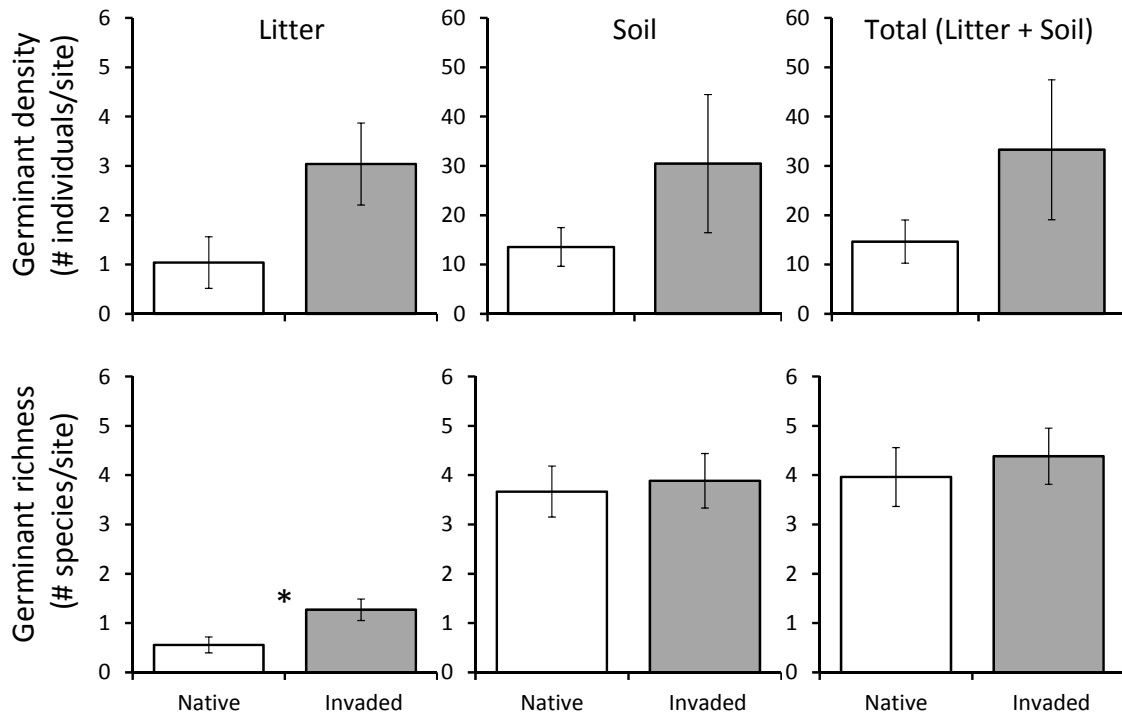
748 *Tables*

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.

Source of variation	DF	SS	*F*	*P*	r^2
Model	3	1691.4721	32.4376	**< 0.0001**	0.49
Invasion category	1	575.4977	33.1092	**< 0.0001**	
Sample type	1	1107.4838	63.7152	**< 0.0001**	
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.

Species	Growth form	Dispersal	Sites occupied (%)		Average dissimilarity (%)	Diss/SD	Contribution to dissimilarity (%)
			Seed bank (*n* = 52)	Standing vegetation (*n* = 46)			
Casuarina glauca	Woody	Wind	89	9	6.17	1.43	6.7
Oxalis perennans	Herb	Ballistic	68	2	4.85	1.11	5.27
Juncus kraussii	Graminoid	Water	55	26	3.89	0.85	4.22
Lobelia anceps	Herb	Vertebrate	53	4	3.6	0.94	3.91
Cynodon dactylon	Graminoid	Water	6	41	3.14	0.73	3.41
Juncus usitatus	Graminoid	Water	45	2	2.97	0.8	3.23
Samolus repens	Herb	Water	25	20	2.61	0.64	2.83
Baumea juncea	Graminoid	Vertebrate	28	20	2.53	0.68	2.74
Oxalis sp.	Herb	Ballistic	36	0	2.47	0.68	2.68
Tetragonia tetragonioides	Herb	Water	21	15	2.24	0.56	2.43
Oplismenus aemulus	Graminoid	Vertebrate	28	20	2.16	0.68	2.34
Parsonsia straminea	Climber	Wind	0	30	2.04	0.59	2.22
Commelina cyanea	Herb	None	13	20	1.99	0.54	2.16
Typha orientalis	Graminoid	Water/Wind	25	0	1.82	0.49	1.98
Phragmites australis	Graminoid	Water/Wind	0	22	1.78	0.46	1.93
Apium prostratum	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*[a] Predictor variable	DF	SS	*F*	*P*	*r²*	Direction of response
(a) Litter seed bank						
Density						
Model non-significant	1	81.936	1.019	0.318	0.020	
Richness						
Model non-significant	1	10.166	3.151	0.082	0.058	
(b) Soil seed bank						
Density						
Model	3	297354.8	4.737	**0.006**	0.225	
Invasion category	1	159676.37	7.631	**0.008**		Non-invaded > Invaded; Fig. 2.
Ground cover (%)	1	76142.64	3.639	0.062		
Latitude	1	142490.77	6.810	**0.012**		Decreasing native germinant density in soil with increasing latitude across all sites.
Error	48	1025271.0				
Richness						
Model	3	500.772	12.100	**<0.0001**	0.426	
Invasion category	1	71.848	5.208	**0.027**		Non-invaded > Invaded; Fig. 2.
Native community richness	1	124.838	9.049	**0.004**		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				
(c) Total seed bank (litter + soil)						
Density						
Model	2	228833.8	4.994	**0.011**	0.167	
Invasion category	1	129224.67	5.640	**0.021**		Non-invaded > Invaded; Fig. 2.

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

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

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

[a] 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).

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

Model	2	15.071	7.977		**0.001**	0.242	
Ground cover (%)	1	7.985	8.453		**0.005**		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		**0.026**		Negative relationship between richness of wind dispersed species and latitude.
Error	49						
Vertebrate (total)							
Model	1	24.053	12.132		**0.001**	0.192	
Invasion category	1	24.053	12.132		**0.001**		Non-invaded > Invaded; Fig. 3e.
Error	50	101.117					
Vertebrate (endozoochory)							
Model	1	7.808	6.629		**0.013**	0.115	
Invasion category	1	7.808	6.629		**0.013**		Non-invaded > Invaded; Fig. 3f.
Error	50	60.078					
Vertebrate (exozoochory)							
Model	2			11.127	**0.004**		
Invasion category	1			6.607	**0.010**		Non-invaded > Invaded; Fig. 3g.
Collection date	1			4.607	**0.032**		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.

Source of variation	DF	SS	F	P	r^2
Model	3	232.0334	13.8818	**< 0.0001**	0.29
Invasion category	1	1.6936	0.3040	0.5826	
Sample type	1	230.0001	41.2806	**< 0.0001**	
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*[a] Predictor variable	DF	SS	*F*	*P*	r^2	Direction of response
(a) Litter seed bank						
Density						
Model	3	174.940	5.495	**0.003**	0.252	
Alien community richness	1	71.809	6.766	**0.012**		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	**0.027**		Positive relationship between alien germinant density in litter and cover of ground layer vegetation in surrounding community.
Collection date	1	69.266	6.526	**0.014**		Negative relationship between alien germinant density in litter and collection date.
Error	48	520.041				
Richness						
Model	2	11.110	6.116	**0.004**	0.197	
Invasion category	1	6.870	7.563	**0.008**		Invaded > Non-invaded; Fig. 4.
Collection date	1	4.364	4.804	**0.033**		Negative relationship between alien germinant richness in litter and collection date.
Error	49					
(b) Soil seed bank						
Density						
Model	3	21169.65	2.854	**0.047**	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	**0.043**		Positive relationship between alien germinant density in soil and matrix vegetation cover across invaded sites only.
Error	48	121139.14				

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Richness						
Model	6	201.707	8.333	**<0.0001**	0.521	
Invasion category	1	0.244	0.060	0.807		
Alien community richness	1	60.577	15.016	**0.0003**		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	**0.010**		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	**0.003**		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	**0.026**		Negative relationship between alien germinant richness in soil and collection date.
Error	45	185.576				
(c) Total seed bank (litter + soil)						
Density						
Model non-significant	3	21095.79	2.700	0.056	0.142	
Richness						
Model	3	167.592	9.315	**<0.0001**	0.363	
Alien community richness	1	72.096	12.021	**0.001**		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	**0.023**		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	**0.022**		Negative relationship between total alien germinant richness and collection date.
Error	48	293.879				

[a] 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	Functional group[a]		Seed bank				Standing vegetation	
Family *Species*	Growth form[b]	Dispersal[c]	Invaded sites ($n = 26$)		Native sites ($n = 26$)		Invaded sites ($n = 26$)	Native sites ($n = 26$)
			No. germinants	% sites occupied	No. germinants	% sites occupied	% sites occupied	% sites occupied
Native								
Acanthaceae								
Pseuderanthemum variabile (R.Br.) Radlk.	H		0	0	0	0	0	4
Aizoaceae								
Tetragonia tetragonioides (Pall.) Kuntze	H	Wa	20	19	11	22	12	19
Amaranthaceae								
Alternanthera denticulata R.Br.	H	V (exo)	3	8	20	11	0	0
Apiaceae								
Apium prostratum Labill. ex Vent.	H	Wa	231	8	107	30	8	15
Centella asiatica (L.) Urb.	H	N	6	8	98	33	8	0
Hydrocotyle peduncularis R.Br. ex A.Rich.	H	Wa	22	12	16	11	0	7
Hydrocotyle tripartita R.Br. ex A.Rich.	H	Wa	2	8	113	11	0	0*
Trachymene incisa Rudge	H		0	0	0	0	0	4
Apocynaceae								
Parsonsia straminea var. *glabrata* Pichon	C		0	0	0	0	19	37
Tylophora barbata 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
Centipeda minima (L.) A.Braun & Asch.	H	Wa	3	4	3	7		0	0
Eclipta platyglossa F.Muell.	H	Wa	0	0	2	4		0	0*
Epaltes australis Less.	H	N	1	4	0	0		0	0
Euchiton gymnocephalus (DC.) Holub	H	Wi	1	4	0	0		0	0
Lagenophora gracilis Steetz	H		0	0	0	0		0	11
Leptinella longipes Hook.f.	H	Wi	12	8	41	11		0	4
Ozothamnus diosmifolius (Vent.) DC.	W	Wi	2	8	1	4		0	0
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt	H	Wi	0	0	1	4		0	0
Senecio diaschides D.G.Drury	H	Wi	0	0	6	7		0	0
Senecio pinnatifolius A.Rich.	W	Wi	2	8	1	4		0	0
Senecio linearifolius A.Rich.	W	Wi	3	8	4	15		0	0
Brassicaceae									
Cardamine microthrix I.Thomps.	H		0	0	0	0		0	4
Campanulaceae									
Wahlenbergia gracilis (G.Forst.) A.DC.	H	Wi	0	0	5	7		0	0
Caryophyllaceae									
Stellaria flaccida Hook.	H	N	1	4	0	0		0	7
Casuarinaceae									
Casuarina glauca Sieber ex Spreng.	W	Wi	150	88	200	89		8	11
Chenopodiaceae									
Atriplex australasica Moq.	H	Wa	23	4	0	0		0	0
Chenopodiaceae sp. 1			1	4	16	11		0	0
Chenopodium glaucum L.	H	V (endo)	112	15	64	30		0	0
Einadia trigonos (Schult.) Paul G.Wilson	H	Wi	27	8	3	4		0	0*
Enchylaena tomentosa R.Br.	W		0	0	0	0		0	4
Rhagodia candolleana subsp. *candolleana* Moq.	W		0	0	0	0		0	4
Sarcocornia quinqueflora (Bunge ex Ung.-Sternb.) A.J.Scott	H	Wa	0	0	73	7		0	7

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

D.Löve

Schoenus apogon Roem. & Schult.	G	Wa	1	4	21	7	0	0
Schoenus maschalinus Roem. & Schult.	G	Wa	18	8	0	0	0	0

Euphorbiaceae

Chamaesyce dallachyana (Baill.) D.C.Hassall	H	A	2	8	1	4	0	4
Chamaesyce drummondii (Boiss.) D.C.Hassall	H	A	2	4	0	0	0	0

Fabaceae

Acacia binervata DC.	W	A	0	0	2	4	0	0
Acacia longifolia subsp. *sophorae* (Labill.) Court	W	A	0	0	1	4	0	0
Desmodium gunnii Benth. ex Hook.f.	C		0	0	0	0	0	7
Desmodium varians (Labill.) G.Don	C		0	0	0	0	0	4
Glycine clandestina J.C.Wendl.	C		0	0	0	0	0	4
Glycine microphylla (Benth.) Tindale	C	N	0	0	8	4	0	4
Glycine tabacina (Labill.) Benth.	C	N	0	0	4	4	0	0
Kennedia rubicunda Vent.	C	A	0	0	1	4	0	0

Geraniaceae

Geranium homeanum Turcz.	H	N	1	4	7	7	0	7

Goodeniaceae

Goodenia ovata Sm.	W	A	10	4	0	0	0	0*
Scaevola albida (Sm.) Druce	H	V (endo)	0	0	4	4	0	0
Selliera radicans Cav.	H	V (exo)	13	8	28	15	12	19

Haloragaceae

Gonocarpus teucrioides DC.	H	N	0	0	3	4	0	4
Haloragis sp.	W	N	0	0	3	4	0	0

Juncaceae

Juncus gregiflorus L.A.S.Johnson	G	Wa	0	0	12	4	0	0
Juncus kraussii subsp. *australiensis* (Buchenau) Snogerup	G	Wa	221	58	787	52	27	22
Juncus planifolius R.Br.	G	Wa	2	4	1	4	0	0

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

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

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

Alien

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

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

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

[a] Functional group information is provided only for native species present in the seed bank.

[b] Growth form: C = Climber, G = Graminoid, H = Herb, W = Woody species.

[c] 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.