1

2

3

4

5   # Trait values and not invasive status determine competitive outcomes

6   between native and exotic invasive species under varying soil

7   nutrient availability

8

9

10

11   Samiya Tabassum[*]

12

13

14   *Department of Biological Sciences, Macquarie University, NSW 2109, Australia*

15

16   *Corresponding author: Samiya Tabassum

17   E-mail: samiya.tabassum@students.mq.edu.au

18   Phone: +61 2 9850 8160

19

20   Running headline: Competitive interactions between invasive and native species at different

21   soil nutrient levels

This thesis is written in the form of a journal article from the Journal of Ecology (with tables and figures included in text)

Declaration

I wish to acknowledge the following assistance in the research detailed in this report:

Michelle Leishman for guidance during project planning, design and interpretation. Drew Allen for statistical advice. Joshua Griffiths, Claire Laws and Urvashi Lallu for help with experimental set up, harvesting and data entry. Muhammad Masood for providing assistance with the glasshouse operations.

All other research described in this report is my own original work.

SAMIYA TABASSUM

23/04/2015

Word count: 7, 890 (excluding figures, tables and references)

22   **Summary**

23

24   1. Invasion by exotic plants presents a major threat to global biodiversity and is often

25   associated with nutrient enrichment of soils, particularly on soils of naturally low

26   fertility. It is likely that the outcome of competitive interactions between native and

27   exotic invasive plants may be mediated by soil nutrient availability.

28   2. I independently investigated competitive effect and response and the occurrence of

29   asymmetric competition in a glasshouse experiment where seedlings of eight

30   functionally similar pairs of exotic invasive and native species from low fertility

31   Hawkesbury Sandstone derived soil were grown under low and high nutrient

32   availability.

33   3. I tested the hypotheses that native species would be competitively superior in low

34   nutrient environments because they employ a resource conservation strategy and

35   exotic invasive species would be competitively superior in high nutrient

36   environments because they employ a resource acquisition strategy. I also

37   hypothesised that exotic invasive species would be more plastic in their response to

38   increased nutrient availability compared to native species.

39   4. I found that nutrient availability did not mediate competitive interactions between

40   exotic invasive and native species. Instead, two exotic invasive and one native species

41   were competitively superior irrespective of nutrient availability. Competitively

42   superior species displayed a mixture of both nutrient conservation and acquisition

43   strategies in the low and high nutrient treatments. Exotic invasive species were also

44   not found to have higher degrees of trait plasticity compared with native species.

45   5. *Synthesis.* This study provides evidence that the *a priori* classification of exotic

46   invasive and native species does not predict competitive superiority at varying

47   nutrient levels but rather species specific differences in trait values provide a

48   competitive advantage in response to nutrient availability.

49

50 Key words: Competition, functional traits, low resource, nutrients, plant invasion

51

52

53

54

55

56

57

58

59

60

61

62

63

64

65

66

67

68

Introduction

Exotic species invasion constitutes a major threat to native biodiversity and as such there has been much research into identifying traits that confer invasiveness in order to detect potential problem invaders before they are introduced (Pheloung, Williams & Halloy 1999; Daehler & Carino 2000). However, it is difficult to find evidence for a universal invasive syndrome because the traits of successful invaders are often context specific, being dependent on conditions found in the recipient community (Sher & Hyatt 1999; Alpert, Bone & Holzapfel *et al.* 2000; Daehler 2003; Tecco *et al.* 2010; Matzek 2011; Palacio-López & Gianoli 2011). Hypotheses concerning traits of successful invaders based on traits occurring in the recipient community predict different outcomes. For example, hypotheses based on limiting similarity and biotic filtering postulate that exotic invasive species will be successful in a recipient community if they are functionally dissimilar to the resident native species in order to reduce competition for resources and ultimately avoid competitive exclusion (Alpert, Bone & Holzapfel 2000; Fargione, Brown & Tilman 2003; Emery 2007; Funk *et al.* 2008). An example is the successful invasion of nitrogen fixing legumes into communities containing non-leguminous species (Turnbull *et al.* 2005). Alternatively, hypotheses based on habitat filtering suggest that exotic invasive and native species should have similar functional trait values in response to shared environmental conditions of an area such as climate and resource availability (Thompson, Hodgson & Rich 1995; Alpert, Bone & Holzapfel 2000). Empirical studies have shown that exotic invasive and native species converge on similar functional trait syndromes in response to a range of environmental conditions (Leishman, Thomson & Cooke 2010; Tecco *et al.* 2010; Drenovsky, Khasanova & James 2012). Which traits confer success in recipient environments, however, depends on a variety of factors

5

93   including characteristics of the competitive environment, nature of resource limitations and

94   type and frequency of disturbance (Sher & Hyatt 1999; Alpert, Bone & Holzapfel 2000).

95

96   Successful invasion of communities has often been associated with disturbance that

97   increases the availability of a limiting resource (Sher & Hyatt 1999). Nutrient availability is a

98   common limiting resource in communities, with anthropogenic activities increasing nutrient

99   availability in many historically nutrient limited environments worldwide (Vitousek *et al.*

100 1997; Leishman, Hughes & Gore 2004). Numerous studies have found a link between exotic

101 invasive success and high nutrient availability in a variety of different environments (e.g.

102 Claassen & Marler 1998; Ostertag & Verville 2002; Lake & Leishman 2004; Suding, LeJeune &

103 Seastedt 2004; Pfeifer-Meister *et al.* 2008; Abraham, Corbin & D'Antonio 2009). Exotic

104 invasive species are thought to proliferate in these conditions because they possess higher

105 values for traits such as photosynthetic capacity (Pattison, Goldstein & Ares 1998; Baruch &

106 Goldstein 1999; Gulías *et al.* 2003; Funk & Vitousek 2007; Osunkoya *et al.* 2010; Matzek

107 2012), specific leaf area (Baruch & Goldstein 1999; Lake & Leishman 2004; Leishman *et al.*

108 2007; Leishman, Thomson & Cooke 2010; Osunkoya *et al.* 2010; Tecco *et al.* 2010), relative

109 growth rate (Pattison, Goldstein & Ares 1998; Burns 2006; James & Drenovsky 2007), foliar

110 nutrient content (Baruch & Goldstein 1999; Durand & Goldstein 2001; Leishman *et al.* 2007;

111 Leishman, Thomson & Cooke 2010) and lower tissue construction costs (Baruch & Goldstein

112 1999) and leaf dry matter content (Matzek 2011) compared to co-occurring native species.

113 This resource acquisition strategy in high nutrient environments positions exotic invasive

114 species on the higher end of the global leaf economics spectrum, where relatively small

115 investment in tissue longevity yields fast growth returns (Wright *et al.* 2004; Leishman *et al.*

116 2007; Leishman, Thomson & Cooke 2010; Tecco *et al.* 2010; Matzek 2012). Across species,

6

117 exotic invasive species have been shown to have a higher photosynthetic capacity for a given

118 specific leaf area (SLA) or leaf nitrogen content compared with co-occurring native species

119 (Gulías *et al.* 2003; Leishman *et al.* 2007; Leishman, Thomson & Cooke 2010). This allows

120 exotic invasive species to achieve a greater return for a given investment in leaf tissue and

121 hence even faster growth compared with native species (Osunkoya *et al.* 2010). Thus, there

122 is consistent evidence suggesting that exotic invasive species have the capacity for rapid

123 growth, allowing them to capitalise more on additional soil nutrients compared with native

124 species.

125

126 Despite nutrient enriched areas experiencing greater rates of invasion (González *et al.* 2010),

127 exotic invasive species still occur on nutrient poor soils (Funk & Vitousek 2007). However,

128 the mechanisms and traits allowing exotic invasive species to proliferate in low nutrient

129 environments may be different to those needed in high nutrient environments (Funk 2013).

130 Species adapted to low nutrient environments frequently display resource conservation

131 traits such as slow growth, high resource use efficiency, low SLA and long lived, robust

132 tissues (Durand & Goldstein 2001; Gulías *et al.* 2003; Leishman *et al.* 2007). In order to

133 outperform native species adapted to low nutrient environments, invading species must be

134 more proficient at acquiring and utilising limiting resources (Funk & Vitousek 2007). Many

135 studies have found exotic invasive species occurring in low nutrient environments to be

136 more nutrient use efficient than co-occurring native species (e.g. Baruch & Goldstein 1999;

137 Durand & Goldstein 2001; Funk & Vitousek 2007; Drenovsky, Martin & James 2008; Firn,

138 Porber & Buckley 2012; but see Leishman *et al.* 2007; Leishman, Thomson & Cooke 2010). In

139 fact, a recent review by Funk (2013) investigating the physiology of native and exotic

140 invasive species from resource poor environments found more studies reporting greater

nutrient use efficiency in exotic invasive compared with native species when soil nutrient

availability was low. It has also been proposed that exotic invasive organisms can succeed in

low nutrient environments due to lower nutrient requirements to maintain higher growth

and reproduction rates than co-occurring native species (González *et al.* 2010). The ability of

exotic invasive species to construct cheaper less dense tissue may also confer a competitive

advantage in low resource environments by providing an initial increase in growth (James *et al.* 2011; Drenovsky, Khasanova & James 2012). Greater nutrient use efficiency coupled with

lower nutrient requirements and tissue construction costs enable exotic invasive species to

achieve a greater gain in growth per unit resource, which may also confer competitive

advantages in low nutrient environments.

Experiments that have directly manipulated nutrient availability and investigated

competitive interactions between exotic invasive and native species have reported

conflicting results. Some studies have found that nutrient addition has significantly altered

competitive interactions, with native species outcompeting exotic invasive species when

nutrient levels are low but exotic invasive species gaining the upper hand when nutrient

levels are increased (e.g. Huenneke 1990; Witkowski 1991; Claassen & Marler 1998;

Abraham, Corbin & D'Antonio 2009; Littschwager *et al.* 2010). Daehler 2003 suggests that

the success of exotic invasive species is highly context dependent, with exotic invasive

species often taking advantage of increased nutrient availability, especially after disturbance

(Davis, Grime & Thompson 2000). These results suggest that exotic invasive species are

specialised to invade more productive environments and may be able to do so because they

are more phenotypically plastic (Burns & Winn 2006). Phenotypic plasticity, broadly defined

as the change in phenotype or physiology of organisms in response to environmental

165 change, has long been suggested to increase the success of exotic invasive species (e.g.

166 Sexton, McKay & Sala 2002; Richards *et al.* 2006; Funk 2008). Differences in the plasticity of

167 traits between exotic invasive and native species may affect trait values and hence

168 competitive interactions when resource levels vary (Burns 2006; Richards *et al.* 2006; but see

169 Burns & Winn 2006). Evidence suggests that exotic invasive species are more plastic for

170 certain traits in their response to increased resource availability compared with co-occurring

171 native species (Funk 2008; Osunkoya *et al.* 2010; Davidson, Jennions & Nicotra 2011;

172 Drenovsky, Khasanova & James 2012; but see Burns & Winn 2006; Palacio-López & Gianoli

173 2011). This may allow exotic invasive species to take greater advantage of additional

174 resources and explain their success in high nutrient environments (Burns & Winn 2006).

175

176 Although traits and plasticity may vary between native and exotic invasive species under low

177 and high resource availability, previous studies have found that nutrient addition has had no

178 significant effect on competitive interactions between exotic invasive and native species

179 (e.g. Corbin & D'Antonio 2004; Thomsen, Corbin & D'Antonio 2006). Many of these studies

180 have found that exotic invasive species have been superior competitors irrespective of

181 nutrient availability (e.g. Kolb *et al.* 2002; Lowe, Lauenroth & Burke 2003; González *et al.*

182 2010; James *et al.* 2011; French 2012; Vallano, Selmants & Zavaleta 2012). Exotic invasive

183 species may outperform native species irrespective of resource availability because they

184 possess intrinsically higher values for competitively favourable traits (Godoy, Valladares &

185 Castro-Díez 2011; Matzek 2012). A meta-analysis by van Kleunen *et al.* (2010) found that the

186 success of exotic invasive species compared with native species was not dependent on the

187 type of environmental conditions they were grown in, with exotic invasive species having

188 higher values for traits associated with reproduction, physiology, leaf-area allocation, shoot

189 allocation, size and growth rate.

190

191 Studies that have investigated competitive interactions between exotic invasive and native

192 species and the functional traits associated with competitive success have measured traits of

193 plants grown without competition (e.g. Thomsen, Corbin & D'Antonio 2006; Vallano,

194 Selmants & Zavaleta 2012; Gruntman *et al.* 2014, but see Peperkorn, Werner & Beyschlag

195 2005). In fact, the majority of studies investigating plant traits and their plasticity have been

196 conducted in the absence of competition by using biomass as a proxy for competitive

197 success, limiting our ability to assess their functional significance (Hulme 2008; Davidson,

198 Jennions & Nicotra 2011). Understanding which functional traits confer a competitive

199 advantage at varying nutrient availability may provide more insight into invasive success,

200 particularly in low nutrient environments. Furthermore, most studies investigating

201 competition between exotic invasive and native species from low nutrient environments

202 have been conducted on species from nitrogen limited environments. Phosphorus, a highly

203 immobile nutrient leached into the soil from weathering rocks, is another important limiting

204 soil nutrient for plants (Lynch & Brown 2001), particularly in Australian environments

205 (Beadle 1962; Handreck 1997). However, few studies have investigated competition

206 between exotic invasive and native species from historically phosphorus limited

207 environments (González *et al.* 2010).

208

209 Hawkesbury Sandstone vegetation of the Sydney region provides an excellent opportunity to

210 study invasion in low nutrient environments because of the low nutrient content,

211 particularly phosphorus, of Hawkesbury Sandstone derived soil (typically 30-100 mg kg^{-1} at

212   undisturbed hill slope sites, Beadle 1962; Lake & Leishman 2004). Despite the nutrient

213   limitation, Hawkesbury Sandstone derived soil supports a diverse range of native flora. Due

214   to the close proximity of Hawkesbury Sandstone derived vegetation remnants to urban

215   development, many areas have been subject to physical disturbance from tracks and roads

216   and increased water and nutrient availability from stormwater outlets. Lake & Leishman

217   (2004) found sites located on hill slopes below stormwater outlets on Hawkesbury

218   Sandstone derived soil had an almost fivefold increase in total phosphorus levels compared

219   with control hill slope sites (487 ± 76 mg kg^{-1} below stormwater outlets compared with 93 ± 49

220   mg kg^{-1} at hill slope control sites). This increase in phosphorus availability has been shown to

221   facilitate exotic species invasion on Hawkesbury Sandstone derived soil (King & Buckney

222   2002; Lake & Leishman 2004; Leishman, Hughes & Gore 2004).

223

224   Although nutrient addition has been linked to invasive success in Hawkesbury Sandstone

225   derived soil, invasive species have been shown to survive in the low nutrient conditions

226   characteristic of this soil. In a study conducted by Leishman & Thomson (2005), native

227   species survival was not found to be significantly higher than exotic invasive species survival

228   when both plant types were grown on low nutrient Hawkesbury Sandstone derived soil in

229   the glasshouse and in the field. However, the occurrence of exotic invasive species within

230   undisturbed remnants of Hawkesbury Sandstone vegetation is rare (King & Buckney 2002;

231   Lake & Leishman 2004; Leishman, Hughes & Gore 2004). Previous work has also shown that

232   intact natural reserves occurring on Hawkesbury Sandstone derived soil are not limited in

233   terms of invasive species propagule supply (King & Buckney 2001). It may be possible that

234   exotic invasive species are not occurring in low nutrient areas of Hawkesbury Sandstone

235   derived soil because they are competitively excluded by native species and instead are

236   confined to areas of nutrient enrichment where such competitive pressure is alleviated.

237   Functionally similar exotic invasive and native species occurring on Hawkesbury Sandstone

238   derived soil have not been grown together in controlled competition experiments.

239   Understanding the competitive dynamics between co-occurring native and invasive species

240   from low nutrient Hawkesbury Sandstone derived soil and how this varies with increasing

241   nutrient availability may provide insights into the factors affecting community composition

242   and assembly in this system and other low nutrient availability systems.

243

244   In this study I grew functionally similar exotic invasive and native species from low nutrient

245   Hawkesbury Sandstone derived soil in paired competition experiments with varying nutrient

246   supply. The specific questions I investigated were:

247   1. Does nutrient availability mediate competitive interactions between exotic invasive

248   and native species from low nutrient Hawkesbury Sandstone derived soil?

249   I hypothesised that under low nutrient conditions, native species would suppress the growth

250   of exotic invasive species more than they were being suppressed by them (i.e. competitive

251   effect greater than competitive response) while exotic invasive species would be

252   competitively superior under high nutrient conditions.

253   2. Which functional traits are conferring competitive superiority in low and high

254   nutrient environments?

255   I hypothesised that competitively superior species in low nutrient environments would have

256   resource conservation strategies (e.g. low photosynthetic rates, low SLA, low relative growth

257   rates) while competitively superior species in high nutrient environments would have

258   resource acquisition strategies (e.g. high photosynthetic rate, high SLA, high relative growth

259   rates).

260   3.   Do native and exotic invasive species differ in the plasticity of traits in response to

261   nutrient availability?

262 I hypothesised that exotic invasive species would display greater plasticity in response to

263 higher nutrient availability compared to native species.

264

265

266

267

268

269

270

271

272

273

274

275

276

277

278

279

280

281

282

283

284 **Materials and methods**

285

286 STUDY SPECIES

287

288 Eight pairs of native and exotic invasive species that co-occur on Hawkesbury Sandstone

289 derived soil were used in this experiment. Invasive species used in this study were selected

290 based on their status on plantnet.rbgsyd.nsw.gov.au, all being species exotic to Australia and

291 common invaders in Hawkesbury Sandstone vegetation (Leishman & Thomson 2005;

292 Leishman, Thomson & Cooke 2010). All native species used in this study commonly occur on

293 Hawkesbury Sandstone derived soil and are not known to be invasive elsewhere in Australia

294 or around the world. Seeds of the exotic invasive species were collected from the field in

295 August 2014. The exotic invasive species were then matched with commonly occurring

296 native species from Hawkesbury Sandstone derived soil based on the following criteria:

297 species within each pair were of the same growth form (e.g. trees, shrubs, climbers) and had

298 the same life history characteristics (e.g. annuals or perennials). Seeds of the native study

299 species were obtained from a commercial seed supply company (Nindethana Seed Service,

300 Albany, Western Australia). All study species and their traits are described in Table 1.

301

302

303

304

305

306

307

Table 1. Information on the taxonomy, growth form and life history of the species pairs used in this study. Seed mass (mg) was calculated by averaging the mass of 20 oven dried seeds for each species. Species denoted with an asterisk are the exotic invasive species within each pair

Species	Family	Seed mass	Growth form	Life history
Acacia linifolia (Vent.) Willd.	Fabaceae	23.6	Tree	Perennial
*Senna pendula** (Willd.) H.S. Irwin & Barneby	Fabaceae	33.1	Tree	Perennial
Hakea dactyloides (Gaertn.) Cav.	Proteaceae	22.6	Tree	Perennial
*Ligustrum sinense** Lour.	Oleaceae	17.4	Tree	Perennial
Allocasuarina distyla (Vent.) L.A.S. Johnson	Casuarinaceae	2.0	Tree	Perennial
*Cotoneaster glaucophyllus** Franch.	Malaceae	9.3	Tree	Perennial
Banksia oblongifolia Cav.	Proteaceae	17.0	Tree	Perennial
*Ligustrum lucidum** Aiton	Oleaceae	18.1	Tree	Perennial
Hardenbergia violacea (Schneev.) Stearn	Fabaceae	15.9	Vine	Perennial
*Acetosa sagittata** (Thunb.) L.A.S. Johnson & B.G. Briggs	Polygonaceae	1.8	Vine	Perennial
Xerochrysum bracteatum (Vent.) Tzvelev	Asteraceae	0.7	Herb	Annual
*Bidens pilosa** L.	Asteraceae	1.3	Herb	Annual
Einadia nutans subsp. *nutans* (R.Br.) A.J. Scott	Chenopodiaceae	0.5	Herb	Perennial
*Sida rhombifolia** L.	Malvaceae	2.0	Herb	Perennial
Atriplex semibaccata R.Br.	Chenopodiaceae	0.7	Herb	Perennial
*Verbena bonariensis** L.	Verbenaceae	0.3	Herb	Perennial

314

315 EXPERIMENTAL DESIGN

316

317 The seeds for all 16 study species were germinated on moist filter paper in sterile petri

318 dishes. A germination trial was conducted using a subset of the seeds to ascertain the time

319 to germination for all study species. The remaining seeds were then set up in the petri dishes

320 at varying times to ensure all species germinated (cotyledons emerged) within 72 hours of

321 each other.

322

323 Once cotyledons had emerged, seedlings were transplanted into pots (diameter 17 cm,

324 depth 17 cm) containing a mixture of one part Hawkesbury Sandstone derived soil and five

325 parts crushed sandstone. The Hawkesbury Sandstone derived soil was obtained from a

326 bushland reserve adjacent to Macquarie University. As the amount of available Hawkesbury

327 Sandstone derived soil was low, it was mixed with crushed sandstone. Total phosphorus and

328 total nitrogen of the soil-sandstone mix was found to be 36 ± 0.2 mg kg^{-1} and 237 ± 27 mg kg^{-1}

329 respectively. Seedlings of each species were either grown individually or surrounded by

330 three individuals of the complementary species from each native-invasive species pair. Each

331 of the neighbour seedlings was planted approximately 2 cm from the target individual to

332 form a triangle around the target individual. Each pot was randomly assigned to one of two

333 treatments: control (no additional nutrients added) and added nutrients (liquid fertiliser

334 applied on a weekly basis). There were six replicates for each combination of competition,

335 treatment and species pair, resulting in a total of 384 pots (2 nutrient treatments x 4

336 competition treatments x 8 species pairs x 6 replicates).

337

338   Individual seedlings were replaced for up to one week after transplanting if mortality

339   occurred. After two weeks of growth, treatments were applied weekly as follows: control

340   (low) nutrients – 125 mL of water only and added (high) nutrients – 0.3 g of fertiliser

341   (Aquasol, Hortico Nurseries; 23N:3.95P:14K) dissolved in 125 mL of water. The level of

342   fertiliser added was based on a study conducted by Thomson & Leishman (2004) in which

343   they investigated the mortality of native seedlings from Hawkesbury Sandstone derived soil

344   with increasing nutrient availability. I chose this particular concentration because it had a

345   significant negative effect on the survival of the native seedlings but did not cause high levels

346   of mortality, as was the case with the higher nutrient concentrations in Thomson &

347   Leishman's study. Because of the low nitrogen content of the sand/soil mix compared with

348   the levels typically found in Hawkesbury Sandstone derived soil (Table 2), all pots were given

349   an additional half dose of nutrients (0.15 g of fertiliser dissolved in 125 mL of water) on a

350   monthly basis to prevent complete nutrient depletion. The glasshouse temperature was set

351   to a maximum of 25˚C during the day and a maximum of 18˚C during the night. All plants

352   were mist watered for three minutes four times a day. Additional mist watering was

353   conducted during hot days to minimise water limitation. When treatments were applied the

354   mist watering system was turned off for the day to reduce nutrient leaching. Pots were

355   randomly assigned a new position in the glasshouse on a fortnightly basis to reduce the

356   effect of microclimates on growth. After one month of growth, lattices were placed around

357   the perimeter of the pots containing climbing species to help contain their spread.

358

359

360

361

362 **Table 2.** Concentrations (mg kg^{-1}) of total soil phosphorus (P) and total soil nitrogen (N) of

363 natural and nutrient enriched Hawkesbury Sandstone derived soil from the field and the soil

364 used in my experiment. Ranges from the field were compiled using various studies (Hannon

365 1956; Clements 1983; Leishman 1990; King & Buckney 2002; Lake & Leishman 2004;

366 Leishman, Hughes & Gore 2004; Leishman & Thomson 2005; Thomson & Leishman 2005).

367 Nutrient concentrations for the experimental soil are reported as means ± standard error.

368 Nitrogen and phosphorus concentrations for the experimental soil were obtained at the end

369 of the experiment. Nutrients were applied in solution on a weekly basis and as such these

370 measurements of soil nutrients are conservative estimates of what was available to the

371 plants.

372

	Field soil				Experimental soil			
	Control		Nutrient enriched		Control		Nutrient enriched	
	N	P	N	P	N	P	N	P
	180-1100	20-110	1400-2700	110-500	251.7±26.8	53.7±0.8	581±20.6	113.7±1.2

373

374

375 HARVESTING AND MEASUREMENT OF TRAITS

376

377 Plants were harvested after ten weeks of growth and a total of five traits related to growth

378 rates and resource capture were measured (Table 3). All functional traits were measured on

379 target plants grown with competition.

380

381 Photosynthetic rate was measured on a fully expanded outer canopy leaf for each individual

382 target plant using a LI-COR LI-6400 portable photosynthesis system (Lincoln, Nebraska, USA).

383 Plants were moved to a growth chamber set at 28˚C and light levels at 400 μmol m^{-2} s^{-1} and

384 allowed to acclimatise to the conditions for 15-20 minutes prior to measurement.

385 Measurements of photosynthetic rate were taken in the growth chamber to minimise

386 variation caused by weather conditions in the glasshouse. Leaves were patted dry with a

387 paper towel before measurements were taken. Measurements were taken randomly across

388 species and treatments. Reference CO_2 was set at 400 p-p-m, relative humidity between 45-

389 60%, block temperature at 22°C and PAR at 1500 μmol m^{-2} s^{-1} following the method of

390 Leishman, Thomson & Cooke (2010). Photosynthetic measurements were taken after about

391 2-3 minutes when CO_2 concentrations in the chamber stabilised. Three measurements were

392 taken for each leaf. The measured leaves were then collected, scanned to determine area,

393 oven dried and weighed. Maximum photosynthetic rate was then calculated on a mass basis

394 (A_{mass}) by multiplying by the specific leaf area (SLA) of the leaf (Table 3).

395

396 Each target plant was then separated from its neighbours (if present) and divided into three

397 constituent components: (i) 2-3 fully expanded outer canopy leaves (ii) the remaining leaf

398 biomass (iii) stem and branch biomass. Root biomass for species grown with competition

399 was not investigated as the roots of the target species were too intertwined to separate

400 from the neighbour plants. Root biomass of singly grown species was carefully washed

401 before being patted dry with paper towel. Stem length of the target species was measured

402 as the length from the root boundary to the apical meristem. All leaf biomass was weighed

403 to determine leaf fresh mass to be used to calculate leaf dry matter content (LDMC). The 2-3

404 randomly selected outer canopy leaves were scanned to determine leaf area using a LI-COR

405 LI-3100C Area Meter (Lincoln, Nebraska, USA) in order to calculate SLA. All biomass

406 components were then oven dried and weighed to calculate LDMC (dry leaf mass/fresh leaf

407   mass) and SLA (Table 3). The dried weight of the different components of the plants were

408   added together to give total biomass. Relative growth rate (RGR) was calculated as dried

409   aboveground biomass per replicate minus mean seed biomass per species divided by 70

410   days (duration of the experiment). Soil samples were bulked across species and competition

411   level for each nutrient treatment and analysed for total phosphorus by acid digestion and

412   total nitrogen by dry combustion. Soil samples were analysed at the Sydney Environment

413   and Soil Laboratory (Thornleigh, Sydney, NSW) and the Environmental Analysis Laboratory

414   (Southern Cross University, Lismore, NSW).

415

416   **Table 3.** Description of the growth and allocation traits measured in this study

Trait	Description	Units
SLA	Specific leaf area	$cm^2\,g^{-1}$
A_{mass}	Photosynthetic rate per unit mass	$\mu mol\ CO_2\ g^{-2}\ leaf\ s^{-1}$
SL	Stem length	cm
LDMC	Leaf dry matter content	-
RGR	Relative growth rate	$g\ g^{-1}\ day^{-1}$

417

418

419   MEASURING COMPETITION

420

421   When investigating resource competition, it is important to distinguish between the two

422   types of competition; competitive effect and competitive response (Goldberg & Landa

423   1991). The competitive effect of a species is the degree to which neighbour plants suppress

424   the performance of a target plant while competitive response is the degree to which a target

425   plant resists suppression by neighbours (Goldberg 1996). Thus for a species to be considered

426   competitively superior, its competitive effect should be greater than its competitive

427 response, meaning that it should suppress the performance of its neighbour more than it is

428 being suppressed by them (Gruntman *et al.* 2014).

429

430 Competitive effect and response were calculated for each species pair using the Relative

431 Interaction Index (RII) (Armas *et al.* 2004):

432

433 RII = $(B_w - B_o)/(B_w + B_o)$

434

435 where B_w is the total biomass of the target plant grown with competition and B_o is the total

436 biomass of the target plant grown without competition. The root biomass of the target

437 plants grown in competition was too difficult to separate from neighbour plants, therefore

438 only aboveground biomass for target species grown singly and in competition was used to

439 calculate RII values.

440

441 Values for the RII range from -1 to 1. Negative values indicate a suppressive effect of the

442 target by the neighbours while positive values indicate a facilitative effect of the target by

443 the neighbours. The RII can be used to estimate both competitive effect and response

444 depending on whether it is viewed in terms of the target or neighbour species. When viewed

445 in terms of the target species the RII gives an estimate of competitive response, the degree

446 to which a species resists suppression by its neighbours (Goldberg 1996). However when

447 viewed in terms of the neighbour species the RII gives an estimate of competitive effect, the

448 degree to which they suppress the growth of the target plant (Goldberg 1996). Reciprocal

449 competition experiments (where each species within a species pair is both the target and

450 neighbour) provide an independent calculation for the two components of competitive

451 ability (Thomsen, Corbin & D'Antonio 2006; Gruntman *et al.* 2014).

452

453 Relative interaction index values were calculated by randomly pairing pots with the target

454 species grown alone and in competition resulting in each pot only being used once.

455 However, due to mortality, some species had an unequal number of replicates for pairing. In

456 such cases average biomass of target species grown singly or target species grown with

457 competition were used to achieve a balanced dataset. This was done on 12 occasions.

458

459 DATA ANALYSIS

460

461 To investigate whether nutrient addition affected competitive interactions between exotic

462 invasive and native species I conducted a mixed model three factor ANOVA. The factors used

463 in the model were nutrient treatment (low or high nutrient), origin (exotic invasive or native)

464 and species pair. Nutrient treatment and origin were designated as fixed factors while

465 species pair was designated as a random factor. The RII values were used as the response

466 variable. If a significant three way interaction between nutrient treatment, origin and

467 species pair was present, then separate two factor ANOVAs were conducted for each of the

468 species pairs, with origin and nutrient treatment set as fixed factors. If a significant

469 interaction was found then a Tukey's post hoc comparison of means was conducted to

470 determine which native and exotic invasive species pairs competed asymmetrically (i.e. one

471 reduced the growth of the other more than it was reduced by it) at each nutrient level.

472

473   To investigate which functional traits contributed to competitive success in high and low

474   nutrient environments, separate two factor ANOVAs for each trait were conducted for

475   species pairs that competed asymmetrically at each nutrient level. A significant origin effect

476   indicated that either the exotic invasive or native species in each pair had a higher trait value

477   irrespective of nutrient treatment. A significant origin x treatment interaction indicated that

478   the trait values of exotic invasive and native species within each pair were contingent on

479   nutrient availability. Plasticity of each of the traits in response to nutrient availability was

480   determined by a significant nutrient treatment effect. Differences in plasticity between

481   exotic invasive and native species were determined by a significant nutrient treatment x

482   origin interaction. Tukey's post hoc comparison of means was used to ascertain which

483   species had higher trait means within each nutrient treatment and showed a plastic

484   response to nutrient availability. The magnitude of plasticity was also determined by

485   calculating the difference between the minimum and maximum trait means divided by the

486   maximum trait mean and multiplying this by 100 (Valladares, Sanchez-Gomez & Zavala 2006;

487   Lamarque *et al.* 2015). All variables were log transformed prior to analysis to fulfil the

488   assumptions of normality and homogeneity of variances. The significance level for all

489   statistical tests was 0.05. All analysis was conducted using the statistical software package

490   Minitab 17.1 (Minitab 2015). Trait means and standard errors presented are from back

491   transformed values.

492

493

494

495

496

Results

COMPETITIVE ABILITY

There was a significant three way interaction between treatment, origin and species pairs, indicating that natives and exotic invasives from each species pair competed differently across the nutrient treatments (Table 4). Separate two factor ANOVAs for each of the eight species pairs revealed that for three of the species pairs (*X. bracteatum*/*B. pilosa*, *E. nutans* subsp. *nutans*/*S. rhombifolia* and *H. dactyloides*/*L. sinense*) there was a significant origin effect, indicating that natives or exotic invasives within those pairs were competitively superior irrespective of nutrient treatment (Table 5). For the *H. violacea*/*A. sagittata* pair there was a significant nutrient treatment x origin interaction, indicating that competitive interactions between the exotic invasive and native species were mediated by nutrient availability (Table 5). Tukey's post hoc comparison revealed that in two of the species pairs (*X. bracteatum*/*B. pilosa* and *E. nutans* subsp. *nutans*/*S. rhombifolia*) the exotic invasive species was competitively superior in both nutrient treatments (Table 6, Fig. 1b,c) and in the remaining species pair (*H. dactyloides*/*L. sinense*) the native species was competitively superior in both nutrient treatments (Table 6, Fig. 1a). Tukey's post hoc comparison for the *H. violacea*/*A. sagittata* pair revealed the native species to be competitively superior in the low nutrient treatment while there was no significant difference in competitive ability between the exotic invasive and native species in the high nutrient treatment (Table 6, Fig. 1d).

521   **Table 4.** Results of the three factor ANOVA testing the effects of origin (exotic invasive or

522   native status), nutrient treatment (low control treatment or high added nutrient treatment)

523   and species pair on relative interaction index (RII) values of 16 co-occurring exotic invasive

524   and native species from low nutrient Hawkesbury Sandstone vegetation. Significant results

525   are in bold

526

Source	df	SS	MS	F	P
Treatment	1	1.3895	1.3895	4.34	0.076
Origin	1	1.2747	1.2747	0.87	0.383
Species pair	7	5.6861	0.8123	0.65	0.709
Treatment x Origin	1	0.4822	0.4822	0.88	0.379
Treatment x Species pair	7	2.2406	0.3201	0.59	0.752
Origin x Species pair	7	10.3194	1.4742	2.7	0.107
Treatment x Origin x Species pair	7	3.827	0.5467	2.77	**0.01**
Error	159	31.3679	0.1973		
Total	190				

527

528

529

530

531

532

533

534

535

536

537   **Table 5.** Results of separate two factor ANOVAs testing the effects of origin (exotic invasive

538   or native status) and nutrient treatment (low control treatment or high added nutrient

539   treatment) on Relative Interaction Index for each of the eight exotic invasive/native species

540   pairs. Significant results are in bold

541

	Source								
	Treatment			Origin			Treatment x Origin		
Species pair	df	F	P	df	F	P	df	F	P
A. linifolia / S. pendula	1,23	6.11	**0.023**	1,23	2.05	0.167	1,23	0.11	0.745
H. dactyloides / L. sinense	1,23	0.02	0.901	1,23	5.81	**0.026**	1,23	2.02	0.171
A. distyla / C. glaucophyllus	1,23	0.25	0.625	1,23	3.08	0.095	1,23	0.43	0.52
B. oblongifolia / L. lucidum	1,23	1.09	0.308	1,23	2.47	0.132	1,23	2.16	0.157
H. violacea / A. sagittata	1,23	2.65	0.119	1,23	2.42	0.135	1,23	11.65	**0.003**
X. bracteatum / B. pilosa	1,21	0.76	0.394	1,21	34.41	**<0.001**	1,21	0.78	0.388
E. nutans subsp. nutans / S. rhombifolia	1,20	0.84	0.374	1,20	12.66	**0.002**	1,20	1.98	0.178
A. semibaccata / V. bonariensis	1,24	5.15	**0.034**	1,24	0.43	0.517	1,24	3.61	0.071

542
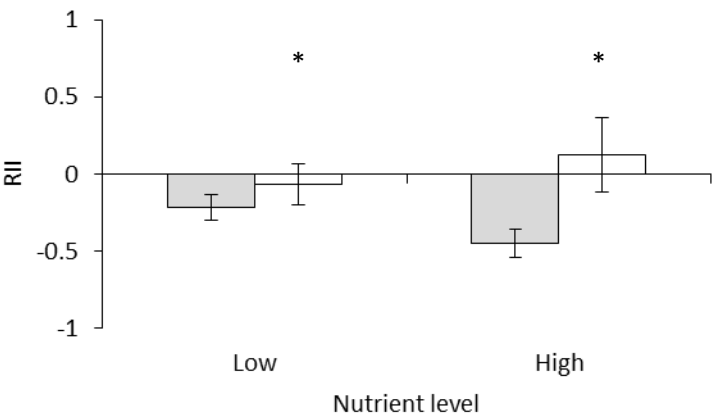
543

544

545

546

547

548

549

550　**Table 6.** Mean RII values for each native and exotic invasive species under low (control) and

551　high (added) nutrient treatments. Mean RII values that were significantly different within

552　each species pair under each nutrient treatment are indicated in bold. Negative RII values

553　indicate that competition has a negative effect on the target plant while positive RII values

554　indicate the opposite. Although species within a pair may both be negatively affected by

555　competition, one species may be competitively superior because it is being less suppressed
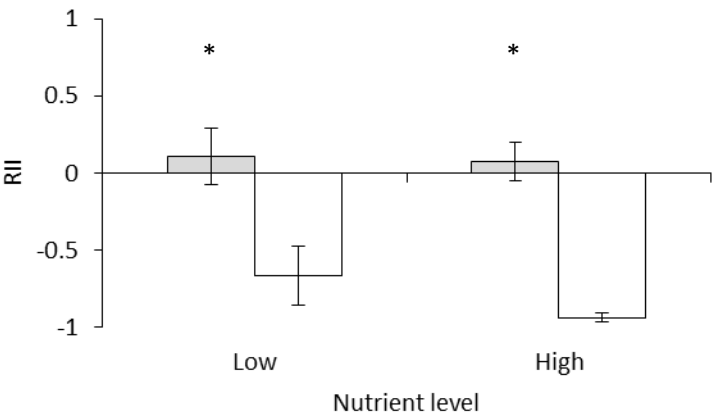
556　than its counterpart

557

Species pair		Low nutrient		High nutrient	
		Native	Invasive	Native	Invasive
A. linifolia / S. pendula	Mean	0.018	-0.194	-0.319	-0.451
	SE	0.095	0.083	0.181	0.095
H. dactyloides / L. sinense	Mean	**-0.067**	-0.216	**0.128**	-0.449
	SE	0.085	0.130	0.093	0.241
A. distyla / C. glaucophyllus	Mean	-0.358	-0.166	-0.560	-0.138
	SE	0.175	0.211	0.105	0.191
B. oblongifolia / L. lucidum	Mean	0.266	-0.225	0.197	0.181
	SE	0.127	0.174	0.142	0.193
H. violacea / A. sagittata	Mean	**-0.086**	-0.663	-0.672	-0.456
	SE	0.177	0.054	0.116	0.079
X. bracteatum / B. pilosa	Mean	-0.664	**0.105**	-0.935	**0.073**
	SE	0.189	0.184	0.027	0.122
E. nutans subsp. *nutans / S. rhombifolia*	Mean	-0.911	**0.548**	-0.781	**-0.349**
	SE	0.046	0.338	0.109	0.321
A. semibaccata / V. bonariensis	Mean	0.420	0.080	-0.707	-0.021
	SE	0.333	0.344	0.145	0.276

558

559

560

561   (a) *H. dactyloides / L. sinense* pair
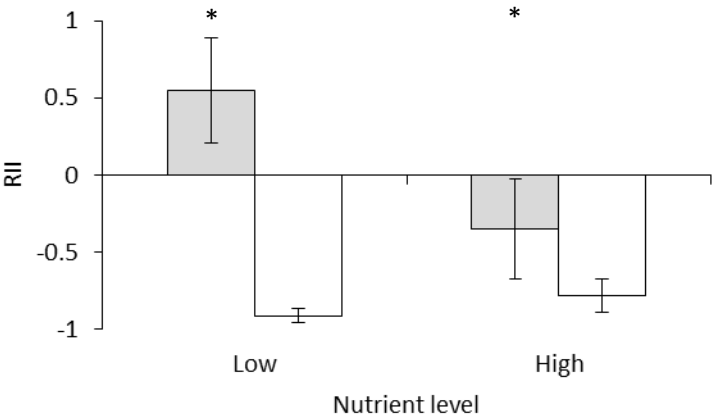

562

563   (b) *X. bracteatum / B. pilosa* pair

564

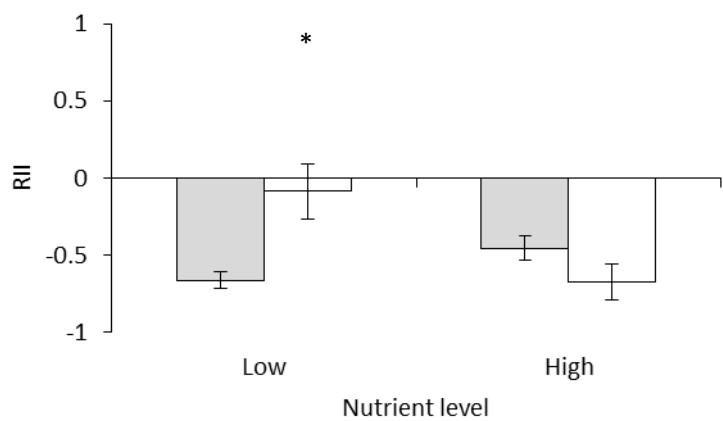565   (c) *E. nutans* subsp. *nutans / S. rhombifolia* pair

566

567

568

569   (d) *H. violacea / A. sagittata* pair

570

571   **Fig. 1.** Mean relative interaction index (RII) of the four species pairs in which there was

572   asymmetric competition (one species reduced the growth of the other more than it was

573   reduced by it) in one or both nutrient treatments. Exotic invasive species are denoted by the

574   grey bars while native species are denoted by the white bars. Species with a significantly

575   greater RII value (i.e. competitively superior species) within each nutrient treatment are

576   indicated by an asterisk.

577

578   TRAIT VALUES

579

580   In the low nutrient treatment two native species (*H. dactyloides* and *H. violacea*) and two

581   exotic invasive species (*B. pilosa* and *S. rhombifolia*) were found to be competitively superior

582   compared to their respective exotic invasive and native counterparts. In terms of the

583   competitively superior native species, *H. dactyloides* was found to have significantly lower

584   SLA and significantly greater stem length and RGR when compared with its exotic invasive

585   counterpart *L. sinense* (Tables 7a and 8). Differences in A_{mass} could not be examined because

586   the leaves of *L. sinense* were too small for photosynthetic measurements. *H. violacea* was

587   found to have a significantly higher LDMC compared with its exotic invasive counterpart *A.*

29

588   *sagittata* however there was no significant difference in SLA, A_{mass}, stem length or RGR

589   values (Tables 7d and 8). In terms of the competitively superior exotic invasive species, *B.*

590   *pilosa* was found to have significantly lower SLA and significantly higher A_{mass}, stem length

591   and LDMC than its native counterpart *X. bracteatum* (Tables 7b and 8). *S. rhombifolia* was

592   found to have significantly lower SLA and significantly greater stem length and LDMC than its

593   native counterpart *E. nutans* subsp. *nutans* (Tables 7c and 8). Differences in A_{mass} could not

594   be examined because the leaves of *E. nutans* subsp. *nutans* were too small for

595   photosynthetic measurements.

596

597   In the high nutrient treatment, one native species (*H. dactyloides*) and two exotic invasive

598   species (*B. pilosa* and *S. rhombifolia*) were found to be competitively superior compared to

599   their respective exotic invasive and native counterparts. In terms of the competitively

600   superior native species, *H. dactyloides* had significantly lower SLA and significantly higher

601   A_{mass}, stem length, and RGR compared to its exotic invasive counterpart *L. sinense* (Tables 7a

602   and 8). In terms of the competitively superior exotic invasive species, *B. pilosa* had

603   significantly lower SLA and significantly higher A_{mass}, stem length, LDMC and RGR compared

604   to its native counterpart *X. bracteatum* (Tables 7b and 8). *S. rhombifolia* was found to have

605   significantly lower SLA and significantly higher A_{mass} than its native counterpart *E. nutans*

606   subsp. *nutans* (Tables 7c and 8).

607

608   PLASTICITY OF TRAITS

609

610   In general, native and exotic invasive species did not differ in the amount of plasticity

611   displayed in response to nutrient addition. Both native and exotic invasive species showed

612 high levels of plasticity, with exotic invasive and native species showing an average increase

613 in trait values of 96% and 81% respectively in response to nutrient addition across all traits.

614

615 For the *H. dactyloides / L. sinense* pair in which the native *H. dactyloides* was found to be

616 competitively superior in both the nutrient treatments, there was a significant plastic

617 response for stem length for both species (Table 7a). *H. dactyloides* increased stem length by

618 83.4% and *L. sinense* increased stem length by 86.4% in response to increased nutrient

619 availability (Table 8). There was also a difference in the magnitude of plasticity in RGR

620 between *H. dactyloides* and *L. sinense* (Table 7a), with *H. dactyloides* showing a 69.8%

621 increase in RGR in response to increased nutrient availability while *L. sinense* did not show a

622 significant plastic response (Table 8). Plasticity in A_{mass} could not be explored because the

623 leaves of *L. sinense* grown in the low nutrient treatment were too small for photosynthetic

624 measurements.

625

626 For the *X. bracteatum /B. pilosa* pair in which the exotic invasive *B. pilosa* was competitively

627 superior in both the nutrient treatments, there was a significant plastic response to nutrient

628 availability for stem length (Table 7b). Both *X. bracteatum* and *B. pilosa* increased stem

629 length in response to increased nutrient availability, showing an 88.5% increase and 78.6%

630 increase respectively (Table 8). There was also a difference in the magnitude of plasticity in

631 RGR (Table 7b); with *B. pilosa* showing a 92.9% increase in RGR in response to increased

632 nutrient availability while *X. bracteatum* did not show a significant plastic response (Table 8).

633

634 For the *E. nutans* subsp. *nutans /S. rhombifolia* pair in which the exotic invasive *S.*

635 *rhombifolia* was competitively superior in both nutrient treatments, there was a significant

plastic response for RGR in response to nutrient availability (Table 7c). Both *E. nutans* subsp.

nutans and *S. rhombifolia* increased RGR in response to increased nutrient availability,

showing a 99.6% and 92.1% increase respectively (Table 8). There was also a difference in

the magnitude of plasticity between the two species for stem length and LDMC (Table 7c). *E.*

nutans subsp. *nutans* showed a 28.6% increase in LDMC in response to increased nutrient

availability while *S. rhombifolia* did not show a significant plastic response (Tables 8). In

terms of stem length, *E. nutans* subsp. *nutans* showed a 94.7% increase in response to

increased nutrient availability while *S. rhombifolia* increased by 75.6% in response to

increased nutrient availability (Table 8). Plasticity in A_{mass} could not be explored because the

leaves of *E. nutans* subsp. *nutans* grown in the low nutrient treatment were too small for

photosynthetic measurements.

For the *H. violacea* /*A. sagittata* pair in which the native *H. violacea* was competitively

superior in the low nutrient treatment while there was no difference in competitive ability

between the two species in the high nutrient treatment, there was a difference in the

magnitude of plasticity between the two species for stem length and RGR (Table 7d). *S.*

sagittata showed an 82.4% and 94.3% increase in stem length and RGR respectively in

response to increased nutrient availability while *H. violacea* did not show a significant plastic

response for either trait (Table 8).

Table 7. Results of separate two factor ANOVAs conducted for each trait for species pairs that showed asymmetric competition in one or both nutrient treatments. Significant results are indicated in bold. A significant treatment x origin interaction indicates that exotic invasives and natives differed in the magnitude of plasticity. A_{mass} of the *H. dactyloides / L. sinense* pair and *E. nutans* subsp. *nutans /S. rhombifolia* pair could not be compared using a two factor ANOVA as the leaves of some of the species grown in the low nutrient treatment were too small for photosynthetic measurements. Instead a one factor ANOVA comparing natives and exotic invasives grown in the high nutrient treatment was conducted

(a) *H. dactyloides / L. sinense* pair

	Source								
	Treatment			Origin			Treatment x Origin		
Trait	df	F	P	df	F	P	df	F	P
SLA	1,23	0.04	0.852	1,23	20.64	**<0.001**	1,23	0.42	0.524
A_{mass}				1,16	24.81	**<0.001**			
Stem length	1,23	10.59	**0.004**	1,23	118.39	**<0.001**	1,23	0.04	0.844
LDMC	1,23	0.62	0.439	1,23	0.26	0.619	1,23	0.09	0.762
RGR	1,23	23.22	**<0.001**	1,23	79.43	**<0.001**	1,23	21.4	**<0.001**

(b) *X. bracteatum /B. pilosa* pair

	Source								
	Treatment			Origin			Treatment x Origin		
Trait	df	F	P	df	F	P	df	F	P
SLA	1,20	2.01	0.174	1,20	26.36	**<0.001**	1,20	0.49	0.492
A_{mass}	1,18	1.05	0.321	1,18	16.01	**0.001**	1,18	1.22	0.286
Stem length	1,21	32.42	**<0.001**	1,21	104.77	**<0.001**	1,21	0.16	0.691
LDMC	1,21	1.18	0.292	1,21	4.73	**0.043**	1,21	0.71	0.411
RGR	1,21	50.23	**<0.001**	1,21	65.99	**<0.001**	1,21	47.4	**<0.001**

672 (c) *E. nutans* subsp. *nutans* /*S. rhombifolia* pair

	Source								
	Treatment			Origin			Treatment x Origin		
Trait	df	F	P	df	F	P	df	F	P
SLA	1,19	3.46	0.082	1,19	9.7	**0.007**	1,19	3.88	0.067
A_{mass}				1,11	15.81	**0.001**			
Stem length	1,19	47.7	**<0.001**	1,19	11	**0.004**	1,19	5.14	**0.038**
LDMC	1,19	5.44	**0.033**	1,19	21.08	**<0.001**	1,19	5.54	**0.032**
RGR	1,19	6.6	**0.021**	1,19	3	0.102	1,19	1.88	0.189

673

674 (d) *H. violacea* /*A. sagittata* pair

	Source								
	Treatment			Origin			Treatment x Origin		
Trait	df	F	P	df	F	P	df	F	P
SLA	1,23	0.12	0.736	1,23	2.46	0.133	1,23	1.1	0.307
A_{mass}	1,23	4.23	0.053	1,23	0.5	0.488	1,23	0.62	0.441
Stem length	1,23	9.83	**0.005**	1,23	0.1	0.754	1,23	7.27	**0.014**
LDMC	1,23	2.28	0.146	1,23	359.62	**<0.001**	1,23	0.54	0.47
RGR	1,23	25.36	**<0.001**	1,23	5.09	**0.035**	1,23	10.8	**0.004**

675

676

677

678

679

680

681

682   **Table 8.** Mean trait values for species pairs that showed asymmetric competition in one or

683   both nutrient treatments. Within each species pair the native species is listed first. The

684   competitively superior species (in one or both nutrient treatments) is indicated in bold.

685   Mean trait values that are significantly greater within each species pair under each nutrient

686   treatment are indicated in bold. Plastic responses for exotic invasive and native species in

687   response to nutrient availability are indicated by asterisks

688

Species pair	Trait		Low nutrient		High nutrient	
			Invasive	Native	Invasive	Native
H. dactyloides / *L. sinense*	SLA	Mean	**122.50**	27.32	**73.80**	30.11
		SE	56.70	1.04	13.90	1.20
	A_{mass}	Mean			93.9	**591.1**
		SE			57.2	46.8
	Stem length	Mean	4.7*	**10.1***	34.2*	**61.0***
		SE	1.0	3.0	1.8	3.6
	LDMC	Mean	0.391	0.328	0.284	0.296
		SE	0.094	0.006	0.055	0.011
	RGR	Mean	2.75×10^{-4}	**0.031***	0.002	**0.103***
		SE	1.14×10^{-4}	0.002	5.8×10^{-4}	0.015
X. bracteatum /**B. pilosa**	SLA	Mean	50.96	**91.00**	55.50	**121.50**
		SE	2.72	17.30	2.24	19.30
	A_{mass}	Mean	**601.5**	104.1	**598.7**	288
		SE	55.4	70.1	85.6	102
	Stem length	Mean	**21.7***	0.7*	**101.3***	6.3*
		SE	6.9	0.3	8.2	2.1
	LDMC	Mean	**0.210**	0.162	**0.217**	0.176
		SE	0.017	0.070	0.007	0.023
	RGR	Mean	0.026*	2.23×10^{-4}	**0.362***	0.004
		SE	0.006	1.02×10^{-4}	0.049	0.002

689

690   **Table 8.** *Continued*

691

Species pair	Trait		Low nutrient		High nutrient	
			Invasive	Native	Invasive	Native
E. nutans subsp. *nutans*						
/*S. rhombifolia*	SLA	Mean	41.23	**273.00**	39.36	**54.81**
		SE	7.74	125.00	2.66	4.08
	A_{mass}	Mean			**612.9**	127.2
		SE			34.3	20.3
	Stem length	Mean	**15.9***	2.3*	65.2*	42.8*
		SE	6.6	1.4	10.9	7.1
	LDMC	Mean	**0.402**	0.136*	0.394	0.190*
		SE	0.031	0.123	0.011	0.017
	RGR	Mean	0.009*	1.04×10^{-4}*	0.108*	0.029*
		SE	0.005	1.09×10^{-4}	0.038	0.015
H. violacea /*A. sagittata*	SLA	Mean	64.25	50.74	57.41	57.50
		SE	2.55	1.41	4.68	10.00
	A_{mass}	Mean	442.8	672.7	298.4	435
		SE	55.5	80.8	16.2	106
	Stem length	Mean	28.2*	59.3	160.5*	92.7
		SE	5.0	10.2	9.5	21.4
	LDMC	Mean	0.103	**0.289**	0.116	**0.300**
		SE	0.005	0.018	0.005	0.016
	RGR	Mean	0.008*	0.023	**0.138***	0.051
		SE	0.001	0.004	0.023	0.022

692

693

694

695

696

697   **Discussion**

698

699   COMPETITIVE INTERACTIONS

700

701   Invasion by exotic species has often been linked to nutrient enrichment of soils but few

702   studies have empirically tested how competitive interactions between native and exotic

703   invasive species differ at varying nutrient levels and the traits associated with competitive

704   superiority (Peperkorn, Werner & Beyschlag 2005). The results of my study did not support

705   my hypothesis that native species are competitively superior in low nutrient conditions and

706   exotic invasive species are competitively superior in the high nutrient conditions. No

707   instances of competitive superiority switching from the exotic invasive to the native species

708   within a pair between nutrient treatments were observed. Instead, one native species (*H.*

709   *dactyloides*) and two exotic invasive species (*B. pilosa* and *S. rhombifolia*) were found to be

710   competitively superior over their exotic invasive and native counterparts irrespective of

711   nutrient availability (Table 4, Figs 1a,b,c). My results from a phosphorus limited environment

712   are concurrent with previous manipulative glasshouse studies from nitrogen limited

713   environments that have found competitive interactions between exotic invasive and native

714   seedlings to be unaffected by nutrient availability (Kolb *et al.* 2002; Lowe, Lauenroth & Burke

715   2003; González *et al.* 2010; James *et al.* 2011; Vallano, Selmants & Zavaleta 2012).

716

717   I found little evidence of exotic invasive species being preferentially outcompeted by native

718   species when grown in low nutrient Hawkesbury Sandstone derived soil. Exotic invasive

719   species, however, are underrepresented in low nutrient Hawkesbury Sandstone derived soils

720   (King & Buckney 2002; Lake & Leishman 2004) despite not being limited in propagule supply

721 (King & Buckney 2001) and having been shown to be able to grow in this low nutrient soil

722 (Leishman & Thomson 2005). Instead, exotic invasive species are largely confined to

723 nutrient enriched areas of Hawkesbury Sandstone derived soil (Leishman, Hughes & Gore

724 2004). These results appear to be contradictory and a discrepancy between laboratory

725 studies and field observations may be due to seedling-seedling competition not being a

726 major determinant of vegetation composition and structure on Hawkesbury Sandstone

727 derived soil. When a species invades an intact vegetation community, competition usually

728 occurs between adult individuals of the resident species and seedlings of the invading

729 species. Competitive interactions can be significantly influenced by the age of the target and

730 neighbour species, with studies showing that many native species outcompeted exotic

731 invasive species when competition was between older natives and exotic invasive seedlings,

732 even at high nutrient availability (Wedin & Tilman 1993; Claassen & Marler 1998; Kolb *et al.*

733 2002; Firn *et al.* 2010; McGlone *et al.* 2012). However, in nutrient enriched areas of

734 Hawkesbury Sandstone derived soil, competition may not contribute significantly to

735 vegetation dynamics as adult native mortality is high in nutrient enriched soils (Thomson &

736 Leishman 2004). This may be because many Australian native species have a low capacity to

737 down-regulate their uptake of phosphorus when soil phosphorus levels are increased, often

738 leading to phosphorus toxicity (Shane, McCully & Lambers 2004; Ryan, Bennett & Tibbett

739 2009). Exotic invasive species may instead be proliferating in nutrient enriched areas not

740 because they are competitively superior *per se* but because they can take advantage of high

741 nutrient availability while the native species cannot (Thomson & Leishman 2004; Leishman &

742 Thomson 2005).

743

744   Areas of Hawkesbury Sandstone derived soil in which competition between seedlings of

745   exotic invasive and native species would occur are on recently disturbed sites such as after

746   burning. Thomson & Leishman (2004) investigated seedling recruitment and survival after

747   fire on control and nutrient enriched areas of Hawkesbury Sandstone derived soil. They

748   found few native species common to low nutrient Hawkesbury Sandstone derived soils were

749   able to survive and establish. These results suggest that it is the direct effect of soil nutrient

750   availability on plant survival and performance rather than the indirect effect of competition

751   that is shaping community composition in nutrient enriched areas. When the total biomass

752   of singly grown plants was analysed, I found a significant increase in biomass in response to

753   nutrient addition for both exotic invasive and native species. However, pots that received

754   the high nutrient treatment had total phosphorus concentrations that were marginally

755   higher than and total nitrogen concentrations that were within the normal range found at

756   undisturbed control sites (Table 2). Because soluble nutrients are highly available to plants it

757   is likely that the concentrations obtained at the end of the experiment may not have

758   reflected the true availability of nitrogen and phosphorus. Thus it is unclear whether these

759   concentrations may have produced a true effect of high nutrient availability.

760

761   The lack of a consistent effect of nutrient availability on competitive interactions between

762   exotic invasive and native species may be suggestive of species-specific differences in

763   nutrient limitation. This is because species have a range of mechanisms for acquiring

764   nutrients such that soil nutrient availability to different species may not reflect soil nutrient

765   concentration. Thus my results may not reflect resource competition between species.

766   Furthermore, it is possible that the competitive superiority of certain species may be the

767   result of multiple competitive mechanisms (French 2012). *B. pilosa* and *S. rhombifolia*, the

768 two exotic invasive species that were competitively superior irrespective of nutrient

769 availability, have been shown to negatively affect growth of neighbouring competitors via

770 allelopathy (Gliessman 1983; Meissner, Nel & Beyers 1986). It may be possible that both

771 interference and resource competition are acting in concert to reduce the growth of

772 competing species in certain species pairs. Additionally, because my species were not

773 phylogenetically paired, nutrient acquisition traits associated with particular families may

774 have affected competitive interactions. For example, the competitive superiority of *H.*

775 *dactyloides* and *H. violacea* in the low nutrient treatment may have been attributed to their

776 possession of cluster roots and nitrogen fixing root nodules, respectively.

777

778 FUNCTIONAL TRAITS

779

780 The results of my study did not strongly support my hypothesis that competitively superior

781 species in the low nutrient treatment would employ a resource conservation strategy and

782 competitively superior species in the high nutrient treatment would employ a resource

783 acquisition strategy. Competitively superior species (irrespective of plant origin) in the low

784 nutrient treatment had both resource conservation (lower SLA and LDMC) and resource

785 acquisition (greater stem length) traits (Table 8). Similarly, competitively superior species in

786 the high nutrient treatment had both resource conservation (lower SLA) and resource

787 acquisition (greater stem length, A_{mass} and RGR) traits (Table 8). Thus *a priori* grouping of

788 exotic invasive and native species did not predict competitive superiority at varying resource

789 levels (Thomson, Corbin & D'Antonio 2006; Matzek 2011; Manea & Leishman 2011). There is

790 not always a consistent relationship between exotic invasive or native status and growth

791 response to nutrient availability. Although many studies have found exotic invasive species

792   to proliferate with increased nutrient availability (Leishman & Thomson 2005), some have

793   not (Padgett & Allen 1999; Lowe, Lauenroth & Burke 2002). These results suggest that

794   species specific differences in trait values in response to nutrient availability are driving

795   competitive outcomes rather than invasive status (Lowe, Lauenroth & Burke 2003; Thomson,

796   Corbin & D'Antonio 2006; Vallano, Selmants & Zavaleta 2012). This finding of functional

797   similarity between exotic invasive and native species in response to nutrient availability

798   supports the idea of plant community assembly based on habitat filtering (Leishman,

799   Thomson & Cooke 2010; Tecco *et al.* 2010; Drenovsky, Khasanova & James 2012).

800

801   Both lower SLA and greater stem length conferred a competitive advantage in both high and

802   low nutrient treatments (Table 8). Specific leaf area (or its inverse leaf mass per area (LMA))

803   is a key trait in the leaf economics spectrum of plants (Wright *et al.* 2004). Species with low

804   SLA tend to have long leaf lifespans and consequently low photosynthetic capacity (Poorter

805   & Evans 1998; Wright, Reich & Westoby 2001; Westoby *et al.* 2002; Leishman *et al.* 2007;

806   Leishman, Thomson & Cooke 2010). However, in the high nutrient treatment we found

807   competitively superior species to have both significantly lower SLA and significantly higher

808   photosynthetic capacity than their counterpart species (Table 8). This contradictory result

809   may be explained by examining the relationship between SLA and its underlying

810   components: leaf density and thickness. Species with low SLA have thick leaf laminas, denser

811   tissues, or both (Witkowski & Lamont 1991; Niinemets 1999). Variation in both leaf density

812   and thickness has been shown to not have a significant effect on SLA (Witkowski & Lamont

813   1991). However, variation in leaf density and thickness can affect photosynthetic rates.

814   Niinemets (1999) found a significant negative correlation between leaf density and A_{mass} but

815   a weak relationship between leaf thickness and A_{mass}. Dense leaves can decrease

816   photosynthetic rates by limiting the diffusion of CO_2 and the penetration of light into the leaf

817   (Niinemets & Sack 2006). If leaf density differed between competitively superior and inferior

818   species in the high nutrient treatment such that competitively superior species had less

819   dense leaves, then this could explain the contrasting relationship observed between A_{mass}

820   and SLA.

821

822   Stem length was also associated with competitive superiority in both the low and high

823   nutrient treatments. Numerous studies have found in high nutrient treatments plants

824   preferentially allocate more resources to aboveground rather than belowground growth

825   (e.g. Leishman & Thomson 2005; Funk 2008; Littschwager *et al.* 2010; Vallano, Selmants &

826   Zavaleta 2012). Thus investment in stem length should confer a competitive advantage in

827   high nutrient environments. However, we also found that competitively superior species in

828   the low nutrient treatment had greater stem length than their counterpart species (Table 8).

829   This may be because the low nutrient treatment was not limiting in terms of growth. It may

830   also be that greater stem length can also provide a competitive advantage for seedlings in

831   low nutrient environments by shading competitors (Peperkorn, Werner & Beyschlag 2005).

832

833   TRAIT PLASTICITY

834

835   The results of my study did not support my hypothesis that the extent of phenotypic

836   plasticity in response to higher nutrient availability was greater for exotic invasive species

837   compared to native species. Many studies have attributed the success of exotic invasive

838   species in nutrient enriched environments to their higher levels of plasticity in response to

839   nutrients compared with native species (e.g. Davidson, Jennions & Nicotra 2011; Firn, Prober

840 & Buckley 2012). However, I found that nutrient enrichment did not preferentially advantage

841 invasive species over native species. Instead I found that two invasive species (*B. pilosa* and

842 *S. rhombifolia*) and one native species (*H. dactyloides*) were competitively superior to their

843 counterpart species irrespective of nutrient availability. This may have been because the

844 control and added nutrient treatments were not limiting nor did they alleviate nutrient

845 limitation, respectively. There was no clear evidence of exotic invasive species being more

846 plastic in response to nutrient availability compared with native species. This result is

847 consistent with previous species level plasticity studies finding no significant difference in

848 plasticity of traits between exotic invasive and native species in response to nutrient as well

849 as light and water availability (Peperkorn, Werner & Beyschlag 2005; Burns & Winn 2006;

850 Palacio-López & Gianoli 2011; Drenovsky, Khasanova & James 2012; Matzek 2012). Both

851 exotic invasive and native species showed similar albeit high levels of plasticity within each

852 species pair, adding further evidence to the notion that trait plasticity is not inhibited in low

853 resource environments (Funk 2008; Godoy, Valladares & Castro-Díez 2011; Drenovsky,

854 Khasanova & James 2012). Traits that showed a consistent plastic response to higher

855 nutrient availability were stem length and RGR (Table 8). However, in most cases

856 competitively superior species within each species pair had greater stem length and RGR

857 irrespective of nutrient availability (Table 8). Differences in mean trait values have been

858 shown to influence growth between species with similar levels of plasticity (Godoy,

859 Valladares & Castro-Díez 2011, 2012; Matzek 2012). In fact, low levels of plasticity may be

860 advantageous to a species that has optimal mean values for traits that confer competitive

861 superiority (Peperkorn, Werner & Beyschlag; van Kleunan & Fischer 2005; Godoy, Valladares

862 & Castro-Díez 2011; Matzek 2012).

863

864   CONCLUSION

865

866   In summary, I found no evidence of nutrient availability mediating competitive interactions

867   between exotic invasive and native seedlings from low nutrient Hawkesbury Sandstone

868   derived soil. Instead I found two exotic invasive and one native species to be competitively

869   superior irrespective of nutrient availability. Irrespective of plant origin, competitively

870   superior species in both low and nutrient enriched conditions displayed a mixture of nutrient

871   conservation and acquisition strategies. I also found exotic invasive and native species to not

872   differ in plasticity in response to greater nutrient availability. These results suggest that

873   exotic invasive and native species show similar functional trait syndromes in response to

874   shared environmental conditions and reinforce the idea that there is no universal invasive

875   archetype (Leishman, Thomson & Cooke 2010; Tecco *et al.* 2010; Matzek 2011).

876

877

878

879

880

881

882

883

884

885

886

887

Acknowledgements

888

889

896

897

898

899

900

901

902

903

904

905

906

907

908

909

910

911

912　**References**

913

914　Abraham, J., Corbin, J. & D'Antonio, C. (2009). California native and exotic perennial grasses

915　　　differ in their response to soil nitrogen, exotic annual grass density, and order of

916　　　emergence. *Plant Ecology*, **201**, 445-456.

917　Alpert, P., Bone, E. & Holzapfel, C. (2000). Invasiveness, invasibility and the role of

918　　　environmental stress in the spread of non-native plants. *Perspectives in Plant*

919　　　*Ecology, Evolution and Systematics*, **3**, 52-66.

920　Armas, C., Ordiales, R. & Pugnaire, F.I. (2004). Measuring plant interactions: a new

921　　　comparative index. *Ecology*, **85**, 2682-2686.

922　Baruch, Z. & Goldstein, G. (1999). Leaf construction cost, nutrient concentration, and net CO_2

923　　　assimilation of native and invasive species in Hawaii. *Oecologia*, **121**, 183-192.

924　Beadle, N.C.W. (1962). Soil phosphate and the delimitation on plant communities in Eastern

925　　　Australia II. *Ecology*, **43**, 281-288.

926　Burns, J.H. (2006). Relatedness and environment affect traits associated with invasive and

927　　　noninvasive introduced Commelinaceae. *Ecological Applications*, **16**, 1367-1376.

928　Burns, J.H. & Winn, A.A. (2006). A comparison of plastic responses to competition by invasive

929　　　and non-invasive congeners in the Commelinaceae. *Biological Invasions*, **8**, 797-807.

930　Claassen, V.P. & Marler, M. (1998). Annual and perennial grass growth on nitrogen-depleted

931　　　decomposed granite. *Restoration Ecology*, **6**, 175-180.

932　Clements, A. (1983). Suburban development and resultant changes in the vegetation of the

933　　　bushland of the northern Sydney region. *Australian Journal of Botany*, **8**, 307-319.

934　Corbin, J.D. & D'Antonio, C.M. (2004). Can carbon addition increase competitiveness of

935　　　native grasses? A case study from California. *Restoration Ecology*, **12**, 36-43.

936   Daehler, C.C. (2003). Performance comparisons of co-occurring native and alien invasive

937   plants: implications for conservation and restoration. *Annual Review of Ecology,*

938   *Evolution and Restoration*, **34**, 183-211.

939   Daehler, C.C. & Carino, D.A. (2000). Predicting invasive plants: prospects for a general

940   screening system based on current regional models. *Biological Invasions*, **2**, 93-102.

941   Davidson, A., Jennions, M. & Nicotra, A.B. (2011). Do invasive species show higher

942   phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis.

943   *Ecology Letters*, **14**, 419-431.

944   Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities:

945   a general theory of invasibility. *Journal of Ecology*, **88**, 528-534.

946   Drenovsky, R.E., Khasanova, A. & James, J.J. (2012). Trait convergence and plasticity among

947   native and invasive species in resource-poor environments. *American Journal of*

948   *Botany*, **99**, 629-639.

949   Drenovsky, R.E., Martin, C.E. & James, J.J. (2008). Variation in resource acquisition and

950   utilisation traits between native and invasive perennial forbs. *American Journal of*

951   *Botany*, **95**, 681-687.

952   Durand, L.Z. & Goldstein, G. (2001). Photosynthesis, photoinhibition, and nitrogen use

953   efficiency in native and invasive tree ferns in Hawaii. *Oecologia*, **126**, 345-354.

954   Emery, S.H. (2007). Limiting similarity between invaders and dominant species in herbaceous

955   plant communities? *Journal of Ecology*, **95**, 1027-1035.

956   Fargoine, J., Brown, C. & Tilman, D. (2003). Community assembly and invasion: an

957   experimental test of neutral vs. niche processes. *Proceedings of the National*

958   *Academy of Sciences of the United States of America*, **100**, 8916-8920.

959   Firn, J., MacDougall, A.S., Schmidt, S. & Buckley, Y.M. (2010). Early emergence and resource

960   availability can competitively favour natives over a functionally similar invader.

961   *Oecologia*, **163**, 775-784.

962   Firn, J., Prober, S.M. & Buckley, Y.M. (2012). Plastic traits of an exotic grass contribute to its

963   abundance but are not always favourable. *PLoS ONE*, **7**, e35870.

964   doi:10.1371/journal.pone.0035870

965   French, K. (2012). Competition strength of two significant invasive species in coastal dunes.

966   *Plant Ecology*, **213**, 1667-1673.

967   Funk, J.L. (2008). Differences in plasticity between invasive and native plants from a low

968   resource environment. *Journal of Ecology*, **96**, 1162-1173.

969   Funk, J.L. (2013). The physiology of invasive plants in low-resource environments.

970   *Conservation Physiology*, **1**, 1-17.

971   Funk, J.L., Cleland, E.E., Suding, K.N. & Zavaleta, E.S. (2008). Restoration through reassembly:

972   plant traits and invasion resistance. *Trends in Ecology and Evolution*, **23**, 695-703.

973   Funk, J.L. & Vitousek, P.M. (2007). Resource-use efficiency and plant invasion in low-

974   resource systems. *Nature*, **446**, 1079-1081.

975   Gliessman, S.R. (1983). Allelopathic interactions in crop-weed mixtures. *Journal of Chemical*

976   *Ecology*, **9**, 991-999.

977   Godoy, O., Valladares, F. & Castro-Díez, P. (2011). Multispecies comparison reveals that

978   invasive and native plants differ in their traits but not in their plasticity. *Functional*

979   *Ecology*, **25**, 1248-1259.

980   Godoy, O., Valladares, F. & Castro-Díez, P. (2012). The relative importance for plant

981   invasiveness of trait means, and their plasticity and integration in a multivariate

982   framework. *New Phytologist*, **195**, 912-922.

983   Goldberg, D.E. (1996). Competitive ability: definitions, contingency and correlated traits.

984   *Philosophical Transactions of the Royal Society of London Biological Sciences*, **351**,

985   1377-1385.

986   Goldberg, D.E. & Landa, K. (1991). Competitive effect and response: hierarchies and

987   correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013-1030.

988   Gonzàlez, A.L., Kominoski, J.S., Danger, M., Ishida, S., Iwai, N. & Rubach, A. (2010). Can

989   ecological stoichiometry help explain patterns of biological invasions? *Oikos*, **119**,

990   779-790.

991   Gruntman, M., Pehl, A.K., Joshi, S. & Tielbörger, K. (2014). Competitive dominance of the

992   invasive plant *Impatiens glandulifera*: using competitive effect and response with a

993   vigorous neighbour. *Biological Invasions*, **16**, 141-151.

994   Gulías, J., Flexas, J., Mus, M., Cifre, J., Lefi, E. & Medrano, H. (2003). Relationship between

995   maximum leaf photosynthesis, nitrogen content and specific leaf area in Balearic

996   endemic and non-endemic Mediterranean species. *Annals of Botany*, **92**, 215-222.

997   Handreck, K.A. (1997). Phosphorus requirements of Australian native plants. *Australian

998   Journal of Soil Research*, **35**, 241-289.

999   Hannon, N. (1956). The status of nitrogen in the Hawkesbury sandstone soils and their plant

1000   communities in the Sydney district. *Proceedings of the Linnean Society of New South

1001   Wales*, **81**, 119-143.

1002   Huenneke, L.F., Hamberg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. (1990). Effects of

1003   soil resources on plant invasion and community structure in Californian serpentine

1004   grassland. *Ecology*, **71**, 478-491.

1005   Hulme, P.E. (2008). Phenotypic plasticity and plant invasions: is it all Jack? *Functional

1006   Ecology*, **22**, 3-7.

1007   James, J.J. & Drenovsky, R.E. (2007). A basis for relative growth rate differences between

1008   native and invasive forb seedlings. *Rangeland Ecology and Management*, **60**, 395-

1009   400.

1010   James, J.J., Drenovsky, R.E., Monaco, T.A. & Rinella, M.J. (2011). Managing soil nitrogen to

1011   restore annual grass-infested plant communities: effective strategy or incomplete

1012   framework? *Ecological Applications*, **21**, 490-502.

1013   King, S.A. & Buckney, R.T. (2001). Exotic plants in the soil stored seed bank of urban

1014   bushland. *Australian Journal of Botany*, **49**, 717-720.

1015   King, S.A. & Buckney, R.T. (2002). Invasion of exotic plants in nutrient enriched urban

1016   bushland. *Austral Ecology*, **27**, 573-583.

1017   Kolb, A., Alpert, P., Enters, D. & Holzapfel, C. (2002). Patterns of invasion within a grassland

1018   community. *Journal of Ecology*, **90**, 871-881.

1019   Lake, J.C. & Leishman, M.R. (2004). Invasion success of exotic plants in natural ecosystems:

1020   the role of disturbance, plant attributes and freedom from herbivores. *Biological*

1021   *Conservation*, **117**, 215-226.

1022   Lamarque, L.J., Lortie, C.J., Porté, A.J. & Delzon, S. (2015). Genetic differentiation and

1023   phenotypic plasticity in life-history traits between native and introduced populations

1024   of invasive maple trees. *Biological Invasions*, **17**, 1109-1122.

1025   Leishman, M.R. (1990). Suburban development and resultant changes in the phosphorus

1026   status of soils in the area of Ku-ring-gai, Sydney. *Proceedings of the Linnean Society of*

1027   *New South Wales*, **112**, 15-25.

1028   Leishman, M.R., Haslehurst, T., Ares, A. & Baruch, Z. (2007). Leaf trait relationships of native

1029   and invasive plants: community- and global-scale comparisons. *New Phytologist*, **176**,

1030   635-643.

1031   Leishman, M.R., Hughes, M.T. & Gore, D.B. (2004). Soil phosphorus enhancement below

1032   stormwater outlets in urban bushland: spatial and temporal changes and the

1033   relationship with invasive plants. *Australian Journal of Soil Research*, **42**, 197-202.

1034   Leishman, M.R. & Thomson, V.P. (2005). Experimental evidence for the effects of additional

1035   water, nutrients and physical disturbance on invasive plants in low fertility

1036   Hawkesbury Sandstone soils, Sydney, Australia. *Journal of Ecology*, **93**, 38-49.

1037   Leishman, M.R., Thomson, V.P. & Cooke, J. (2010). Native and exotic invasive plants have

1038   fundamentally similar carbon capture strategies. *Journal of Ecology*, **98**, 28-42.

1039   Littschwager, J., Lauerer, M., Blagodatskaya, E. & Kuzyakov, Y. (2010). Nitrogen uptake and

1040   utilisation as a competition factor between invasive *Duchesnea indica* and native

1041   *Fragaria vesca*. *Plant and Soil*, **331**, 105-114.

1042   Lowe, P.N., Lauenroth, W.K. & Burke, I.C. (2002). Effects of nitrogen availability on the

1043   growth of native grasses and exotic weeds. *Journal of Range Management*, **55**, 94-98.

1044   Lowe, P.N., Lauenroth, W.K. & Burke, I.C. (2003). Effects of nitrogen availability on

1045   competition between *Bromus tectorum* and *Bouteloua gracilis*. *Plant Ecology*, **167**,

1046   247-254.

1047   Lynch, J.P. & Brown, K.M. (2001). Topsoil foraging – an architectural adaptation of plants to

1048   low phosphorus availability. *Plant and Soil*, **237**, 225-237.

1049   Matzek, V. (2011). Superior performance and nutrient-use efficiency of invasive plants over

1050   non-invasive congeners in a resource-limited environment. *Biological Invasions*, **13**,

1051   3005-3014.

1052   Matzek, V. (2012). Trait values, not trait plasticity, best explain invasive species' performance

1053   in a changing environment. *PLoS ONE*, **7**, e48821. doi:10.1371/journal.pone.0048821

1054   McGlone, C.M., Sieg, C.H., Kolb, T.E. & Nietupsky, T. (2012). Established native perennial

1055   grasses out-compete an invasive annual grass regardless of soil water and nutrient

1056   availability. *Plant Ecology*, **213**, 445-457.

1057   Meissner, R., Nel, P.C. & Beyers, E.A. (1986). Allelopathic influence of *Tagetes* and *Bidens-*

1058   infested soils on seedling growth of certain crop species. *South African Journal of*

1059   *Plant Science*, **3**, 176-180.

1060   Minitab (2015). Minitab 17.1: statistical software. State College, PA, United States.

1061   Niinemets, Ü. (1999). Components of leaf dry mass per area – thickness and density – alter

1062   leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist*,

1063   **144**, 35-47.

1064   Niinemets, Ü. & Sack, L. (2006). Structural determinants of leaf light-harvesting capacity and

1065   photosynthetic potentials. *Progress in Botany*, **67**, 385-419.

1066   Osunkoya, O.O., Bayliss, D., Panetta, F.D. & Vivian-Smith, G. (2010). Variation in

1067   ecophysiology and carbon economy of invasive and native woody vines of riparian

1068   zones in south-eastern Queensland. *Austral Ecology*, **35**, 636-649.

1069   Ostertag, R. & Verville, J.H. (2002). Fertilisation with nitrogen and phosphorus increases

1070   abundance of non-native species in Hawaiian montane forests. *Plant Ecology*, **162**,

1071   77-90.

1072   Padgett, P.E. & Allen, E.B. (1999). Differential responses to nitrogen fertilization in native

1073   shrubs and exotic annuals common to Mediterranean coastal sage scrub of

1074   California. *Plant Ecology*, **144**, 93-101.

1075   Palacio-López, K. & Gianoli, E. (2011). Invasive plants do not display greater phenotypic

1076   plasticity than their native or non-invasive counterparts: a meta-analysis. *Oikos*, **120,**

1077   1393-1401.

1078   Pattison, R.R., Goldstein, G. & Ares, A. (1998). Growth, biomass allocation and

1079   photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia*, **117**,

1080   449-459.

1081   Peperkorn, R., Werner, C. & Beyschlag, W. (2005). Phenotypic plasticity of an invasive acacia

1082   versus two native Mediterranean species. *Functional Plant Biology*, **32**, 933-944.

1083   Pfeifer-Meister, L., Cole, E.M., Roy, B.A. & Bridgham, S.D. (2008). Abiotic constraints on the

1084   competitive ability of exotic and native grasses in a Pacific Northwest prairie.

1085   *Oecologia*, **155**, 357-366.

1086   Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999). A weed risk assessment model for use as

1087   a biosecurity tool evaluating plant introductions. *Journal of Environmental*

1088   *Management*, **57**, 239-251.

1089   Poorter, H. & Evans, J.R. (1998). Photosynthetic nitrogen-use efficiency of species that differ

1090   inherently in specific leaf area. *Oecologia*, **116**, 26-37.

1091   Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. (2006). Jack of all trades,

1092   master of some? On the role of phenotypic plasticity in plant invasion. *Ecology*

1093   *Letters*, **9**, 981-993.

1094   Ryan, M.H., Ehrenberg, S., Bennett, R.G. & Tibbett, M. (2009). Putting the P in *Ptilotus*: a

1095   phosphorus-accumulating herb native to Australia. *Annals of Botany*, **103**, 901-911.

1096   Sexton, J.P., McKay, J.K. & Sala, A. (2002). Plasticity and genetic diversity may allow saltcedar

1097   to invade cold climates in North America. *Ecological Applications*, **12**, 1652-1660.

1098   Shane, M.W., McCully, M.E. & Lambers, H. (2004). Tissue and cellular phosphorus storage

1099   during development of phosphorus toxicity in *Hakea prostrata* (Proteaceae). *Journal*

1100   *of Experimental Botany*, **55**, 1033-1044.

1101   Sher, A.A. & Hyatt, L.A. (1999). The disturbance resource-flux invasion matrix: a new

1102   framework for patterns of plant invasion. *Biological Invasions*, **1**, 107-114.

1103   Suding, K.N., LeJeune, K.D. & Seastedt, T.R. (2004). Competitive impacts and responses of an

1104   invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia*,

1105   **141**, 526-535.

1106   Tecco, P.A., Díaz, S., Cabido, M. & Urcelay, C. (2010). Functional traits of alien plants across

1107   contrasting climatic and land-use regimes: do aliens join the locals or try harder than

1108   them? *Journal of Ecology*, **98**, 17-27.

1109   Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995). Native and alien invasive plants: more of

1110   the same? *Ecography*, **18**, 390-402.

1111   Thomsen, M.A., Corbin, J.D. & D'Antonio, C.M. (2006). The effect of soil nitrogen on

1112   competition between native and exotic perennial grasses from northern coastal

1113   California. *Plant Ecology*, **186**, 23-35.

1114   Thomson, V.P. & Leishman, M.R. (2005). Post-fire vegetation dynamics in nutrient-enriched

1115   and non-enriched sclerophyll woodland. *Austral Ecology*, **30**, 250-260.

1116   Turnbull, L.A., Rahm, S., Baudois, O., Eichenberger-Glinz, S., Wacker, L. & Schmid, B. (2005).

1117   Experimental invasion by legumes reveals non-random assembly in grassland

1118   communities. *Journal of Ecology*, **93**, 1062-1070.

1119   Valladares, F., Sanchez-Gomez, D. & Zavala, M. (2006). Quantitative estimation of

1120   phenotypic plasticity: bridging the gap between the evolutionary concept and its

1121   ecological applications. *Journal of Ecology*, **94**, 1103-1116.

1122   Vallano, D.M., Selmants, P.C. & Zavaleta, E.S. (2012). Simulated nitrogen deposition

1123   enhances the performance of an exotic grass relative to native serpentine grassland

1124   competitors. *Plant Ecology*, **213**, 1015-1026.

1125 van Kleunan, M. & Fischer, M. (2005). Constraints on the evolution of adaptive phenotypic

1126 plasticity in plants. *New Phytologist*, **166**, 49-60.

1127 van Kleunen, M., Weber, E. & Fischer, M. (2010). A meta-analysis of trait differences

1128 between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235-245.

1129 Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schnidler, D.W.,

1130 Schlesinger, W.H. & Tilman, D.G. (1997). Human alteration of the global nitrogen

1131 cycle: sources and consequences. *Ecological Applications*, **7**, 737-750.

1132 Wedin, D. & Tilman, D. (1993). Competition among grasses along a nitrogen gradient: initial

1133 conditions and mechanisms of competition. *Ecological Monographs*, **63**, 199-229.

1134 Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). Ecological strategies:

1135 some leading dimensions of variation between species. *Annual Review of Ecology and*

1136 *Systematics*, **33**, 125-159.

1137 Witkowski, E.T.F. (1991). Growth and competition between seedlings of *Protea repens* (L.) L.

1138 and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient

1139 availability. *Functional Ecology*, **5**, 101-110.

1140 Witkowski, E.T.F. & Lamont, B.B. (1991). Leaf specific mass confounds leaf density and

1141 thickness. *Oecologia*, **88**, 486-493.

1142 Wright, I.J., Reich, P.B. & Westoby, M. (2001). Strategy shifts in leaf physiology, structure and

1143 nutrient content between species of high- and low-rainfall and high- and low-nutrient

1144 habitats. *Functional Ecology*, **15**, 423-434.

1145 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares,

1146 J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K.,

1147 Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas,

1148 M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov,

1149   V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004). The

1150   worldwide leaf economics spectrum. *Nature*, **428**, 821-827.