

Belowground competition drives invasive plant impact on native species regardless of nitrogen availability

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Author contributions: AB and CS conceived the experiment; AB conducted the experiment and data analysis; DP coordinated fieldwork; AB, CS, DP, NO and KO designed experiments and wrote the manuscript.

1 **Abstract**

2 Plant invasions and eutrophication are pervasive drivers of global change that cause
3 biodiversity loss. Yet, how invasive plant impacts on native species, and the mechanisms
4 underpinning these impacts, vary in relation to increasing nitrogen (N) availability remains
5 unclear. Competition is often invoked as a likely mechanism, but the relative importance of
6 the above and belowground components of this is poorly understood, particularly under
7 differing levels of N availability. To help resolve these issues, we quantified the impact of a
8 globally invasive grass species, *Agrostis capillaris*, on two co-occurring native New Zealand
9 grasses, and vice versa. We explicitly separated above and belowground interactions amongst
10 these species experimentally and incorporated an N addition treatment. We found that
11 competition with the invader had large negative impacts on native species growth (biomass
12 decreased by half), resource capture (total N content decreased by up to 75%) and even
13 nutrient stoichiometry (native species tissue C: N ratios increased). Surprisingly, these
14 impacts were driven directly and indirectly by belowground competition, regardless of N
15 availability. Higher root biomass likely enhanced the invasive grass's competitive superiority
16 belowground, indicating that root traits may be useful tools for understanding invasive plant
17 impacts. Our study shows that belowground competition can be more important in driving
18 invasive plant impacts than aboveground competition in both low and high fertility
19 ecosystems, including those experiencing N enrichment due to global change. This can help
20 to improve predictions of how two key drivers of global change, plant species invasions and
21 eutrophication, impact native species diversity.

22

23 **Keywords**

24 Global change, grassland, mechanism, non-native, nutrient availability.

25 **Introduction**

26 The rapid increases in plant species invasions and soil nitrogen (N) availability are major
27 drivers of global change and biodiversity loss (Vitousek et al. 1997; Stevens et al. 2004; Vilà
28 et al. 2011; Seabloom et al. 2015; Van Kleunen et al. 2015). However, how increasing N
29 availability alters invasive species impacts on native species, and the mechanisms underlying
30 those impacts, remains uncertain. A stronger mechanistic understanding of invasive plant
31 impacts under varying edaphic conditions would enable better prediction of where and when
32 impacts on native species are most likely to occur. In turn, this could facilitate pre-emptive
33 management to prevent negative impacts, thereby protecting native species diversity and
34 ultimately, reducing global biodiversity loss.

35 Interspecific competitive interactions are often proposed as the primary pathway for invasive
36 plant impacts, yet few studies experimentally test whether, or which, competitive
37 mechanisms underlie invader impacts (Levine et al. 2003; Seabloom et al. 2003; Tylianakis et
38 al. 2008; Barney et al. 2013, 2015). For example, the relative importance of above and
39 belowground competitive interactions in determining invasive plant species impacts is
40 unclear. Further uncertainty arises from the likely shifts in importance of different impact
41 mechanisms, such as above and belowground competition, following increases in soil
42 nutrient availability. We found only two experiments that explicitly separated above and
43 belowground competitive interactions between native and invasive species and both reported
44 that belowground competition was more important in delivering invader impacts (Dillenburg
45 et al. 1993; Kueffer et al. 2007). However, other lines of evidence suggest aboveground
46 competition may also be a strong driver, particularly following increases in nutrient
47 availability (Tilman 1982; Cahill 1999; Hautier et al. 2009; Borer et al. 2014). Indeed,
48 increased soil fertility can increase the competitive superiority of invasive plants (Daehler
49 2003; Besaw et al. 2011), which tend to have more exploitative traits than co-occurring native

50 species (Leishman et al. 2007; van Kleunen et al. 2010; Ordonez et al. 2010). These traits
51 should be advantageous under high resource conditions and in competing for light, although
52 evidence for this is mixed (Leishman et al. 2010; Ordonez and Olff 2013). Furthermore, the
53 invasive plant species with the most exploitative aboveground traits tend to have the greatest
54 negative impact on native species (Lai et al. 2015). It is therefore likely that both above and
55 belowground competition can underpin invasive species impacts and that it depends on
56 belowground resource availability, yet experiments that test this explicitly remain remarkably
57 rare.

58 Increasing N availability to increase productivity is common practice in grasslands, where
59 invasion rates are among the highest worldwide (Firn et al. 2011). Additionally, co-occurring
60 invasive and native grass species are often closely related and functionally similar.
61 Grasslands thus constitute ideal model systems in which to test the importance of above and
62 belowground competition as mechanisms of invasive plant impacts across varying levels of
63 soil N availability. One such system is low-fertility New Zealand grassland that is designated
64 as valuable conservation habitat (Mark and McLennan 2005; Rose and Frampton 2007).
65 These grasslands are experiencing widespread declines in native species diversity (Duncan et
66 al. 2001) associated with non-native grass invasions (Rose et al. 2004) and increases in
67 nitrogen (N) availability (Scott 2000; Dickie et al. 2014). Invasive grasses in New Zealand,
68 and elsewhere, tend to have more exploitative traits than co-occurring native grasses (Craine
69 and Lee 2003; Wilsey and Polley 2006), suggesting that invasive grasses may be superior
70 aboveground competitors compared to native grasses (Johnson et al. 2008; Lai et al. 2015).
71 Their aboveground competitive superiority is likely to increase following increases in soil N
72 availability, as this would lead to N no longer being a limiting resource, thereby allowing
73 competition to shift aboveground for light (Wilson and Tilman 1991; Aerts 1999), as has
74 been observed in various grasslands worldwide (Tilman 1988; Bobbink 1991; Hautier et al.

75 2009). However, as far as we are aware, there are no experiments that test this idea by
76 explicitly separating above and belowground competition across varying levels of N. To
77 address this, we test the following specific hypotheses:

- 78 1. Competition between invasive and native grass species benefits the invasive species,
79 *Agrostis capillaris* L., and decreases native species, *Poa cita* Edgar and *Poa colensoi*
80 Hook.f., growth and resource capture, compared with intraspecific competition;
- 81 2. *A. capillaris*' competitive impacts on native species, and the relative importance of
82 aboveground competition over belowground competition, both increase with
83 increasing N availability.

84

85 **Methods**

86 EXPERIMENTAL DESIGN AND GREENHOUSE CONDITIONS

87 We determined the effects of above- and belowground competition of a globally invasive
88 grass, *A. capillaris*, on two common perennial C₃ tussock grasses native to New Zealand: *P.*
89 *cita* and *P. colensoi*. *A. capillaris* is a Eurasian rhizomatous perennial C₃ grass species (height
90 = 20-70 cm) that is one of the most widespread invasive grasses in New Zealand (Edgar and
91 Forde 1991; Craine and Lee 2003; CABI 2017) and is also a pervasive weed in North
92 America, Australia and parts of South America (CABI 2017). It is a habitat generalist that
93 occurs across a wide range of climatic and edaphic conditions in its native and introduced
94 ranges (CABI 2017). These include Atlantic and continental climates at low and high
95 altitudes, along with low fertility, usually acidic, soils, as well as nutrient rich meadows (Hill
96 et al. 1999; Olde Venterink and Güsewell 2010; CABI 2017). *P. colensoi* (height = 5-30 cm)
97 and *P. cita* (height = 30-100 cm) are both short tussock grass species, widespread throughout

98 New Zealand, usually on low fertility acidic soils in montane areas (Daly 1964; Edgar and
99 Connor 2000). Our species were con-familiar and from the same functional group, which
100 controlled for confounding effects due to lifeform (Vila and Weiner 2004). Seeds of all
101 species were sourced from NZ populations by Speciality Seeds and Home Creek Nursery.

102 Treatments consisted of a full factorial cross of two native species identities (*P. cita* and *P.*
103 *colensoi*), four competition types (*control or full intraspecific competition, aboveground*
104 *competition, belowground competition and full competition*; Fig. 1) and two N addition
105 treatments (*control or “low N” and N-addition or “high N”*); with five replicates this made a
106 total of 80 pots. For each native - invasive species combination, two individuals of the native
107 species and two individuals of the invasive species were planted into 1 L pots. To minimise
108 lateral escape from competition, pots were surrounded by a 1 mm nylon mesh that was 10 cm
109 high. In order to separate above- and belowground competition, the pots were split using
110 solid PVC dividers within the pot, sealed with PVC glue and silicon, and opaque plastic
111 dividers above the pot. By varying the alignment of these dividers, four competition
112 treatments were created: 1) *control or intraspecific competition*, where plants were competing
113 with conspecifics above- and belowground; 2) *aboveground* and 3) *belowground*, where
114 plants were either competing with heterospecifics aboveground and conspecifics
115 belowground, or vice versa, respectively; and 4) *full competition*, where plants were
116 competing with heterospecifics above- and belowground (Fig. 1). Treatments were placed in
117 a randomised block design and blocks were rotated weekly. Our replacement design thus kept
118 plant density constant both overall and in each component of the pot (Fig. 1). This design
119 compares the effect of intraspecific competition with interspecific competition, which is
120 sometimes criticised due to the lack of a “zero” competition control, where plants are grown
121 without neighbours. However, invaded grassland communities often become relatively space
122 limited in the absence of a disturbance; therefore in field conditions, it is more likely for

123 plants to encounter neighbours. For this reason, our design was arguably more realistic than
124 an additive design, which involves zero competition treatments and inconsistent plant
125 densities.

126 Nitrogen addition treatment consisted of 133 mg NH_4NO_3 pot^{-1} week^{-1} dissolved in 180 mL
127 de-ionised water, applied evenly over the area of each pot thrice weekly in 60 mL doses.
128 Nitrogen was used to increase resource availability as it is commonly used as an agricultural
129 fertiliser in grasslands. Soil N availability also increases in New Zealand grasslands
130 following invasion and removal of exotic woody species such as *Cytisus scoparius* L. and
131 *Pinus contorta* Douglas (Dickie et al. 2014; Broadbent et al. 2017). This is often followed by
132 exotic grass invasions, including *A. capillaris* (Williams 1998; Dickie et al. 2014), and so
133 might be a mechanism driving invasive success. Our rate of N addition is in line with net soil
134 N-mineralisation rates of grasslands in NZ that have been cleared of invasive N-fixing shrubs
135 (Broadbent et al. 2017).

136 Pots were filled with a mixture of field soil and autoclaved sand (3:1 by volume) to improve
137 drainage. Field soil was collected (depth = 10 cm) from 40 random locations of grassland-
138 shrubland habitat in St. James Conservation Area in New Zealand (Lat. Long. = -42.460273,
139 172.830938). Vegetation at the site consisted of a mixture of native and exotic species,
140 including those used in our study. Soil was sieved (4 mm) and homogenised prior to mixing
141 with sand. Mean pot soil pH (1: 2.5, soil: water) was 6.82 ± 0.02 (mean \pm one SE), mean KCl
142 extractable N concentration (NO_3^- -N and NH_4^+ -N) was 2.97 ± 0.15 $\mu\text{g N g soil}^{-1}$ and mean
143 NaCO_3 extractable PO_4^- -P concentration (Olsen-P) was 4.95 ± 0.29 $\mu\text{g P g soil}^{-1}$. The soils in
144 our study had low inorganic N concentrations (2.97 ± 0.15 $\mu\text{g N g soil}^{-1}$) and low N: P ratios
145 (0.6). These concentrations were determined colorimetrically in a segmented flow stream
146 using an AutoAnalyser (Seal-Analytical).

147 Plants were germinated in potting compost under the same standardised climatic conditions
148 that were used throughout the experiment: lighting regime: Light: Dark 16h: 8h, Temp
149 maximum: minimum 22 °C: 16 °C. After germination, seedlings were carefully transferred
150 into plugs, then two weeks later into pots, on the 21st June 2016. The mean mass of seedlings
151 did not differ between species prior to transplanting into pots ($F = 2.1$, $p = 0.13$, one-way
152 ANOVA). This was determined by harvesting, drying (65 °C for 48 hours) and weighing (\pm
153 0.0001 g) the above- and belowground biomass of a random subset of 20 seedlings of each
154 species at the start of the experiment.

155 Plants were watered equally each day with ca. 100 mL of tap water per pot. The experiment
156 lasted 11 weeks, with all biomass harvested on the 6th September 2016. Biomass from each
157 pot was separated by species and dried at 65 °C for 48 hours after all soil had been washed
158 from roots. Roots of individuals that were competing belowground were carefully separated.
159 Due to the difficulty of separating roots between species, this was only done for one side of
160 the division in each pot; the biomass value obtained was doubled to give an estimate per
161 species per pot. Biomass was separated into above and belowground components, with
162 aboveground components further separated into live and dead biomass, before being weighed
163 to 0.0001 g.

164 MEASUREMENTS AND CALCULATIONS

165 After weighing biomass, belowground and aboveground plant C and N concentrations were
166 measured on ground samples using an automated Dumas procedure on a Vario EL analyser
167 (Elementar). This was used to calculate whole plant mean C: N ratio (the mean of above- and
168 belowground C: N ratios). Since plant tissue C: N ratio is the mass of C relative to the mass
169 of N in plant tissue, it provides a similar measure to tissue %N content, with the advantage of
170 being easily compared to other substrates such as soil. To calculate total N content (g), %N

171 content of above- and belowground biomass components was multiplied by the
172 corresponding biomass (g) and then summed. We also calculated % dead aboveground
173 biomass (of total aboveground biomass) and two allocation patterns: root mass fraction
174 (RMF: belowground biomass/ total biomass) and root nitrogen fraction (RNF: belowground
175 N/ total N).

176 STATISTICAL ANALYSIS

177 We determined the effect of competition with invasive species on native species growth and
178 resource capture (hypothesis 1), and whether competition type and N addition modified this
179 effect (hypothesis 2), by using three-way ANOVAs on native species responses. The
180 responses we tested were mean total, aboveground and belowground biomass (g), mean dead
181 aboveground biomass (%), mean total N content (g), mean C: N ratio, mean RMF and mean
182 RNF. Each ANOVA had native species identity (*P. cita* or *P. colensoi*), competition
183 treatment (*control, aboveground, belowground* or *full*), N addition treatment (*low-N* or *high-*
184 *N*) and all interactions as factors. We also determined the effect of native species competition
185 on invasive species growth and resource capture (hypothesis 1), and whether this differed due
186 to the competition and N addition treatments (hypothesis 2), by using three-way ANOVAs on
187 invasive species responses. We used the same responses and factors in these ANOVAs as for
188 those on native species responses, although the factor “native species identity” now referred
189 to the identity of the native competitor.

190 If a three-way interaction occurred, then the analysis was split by native species identity/
191 native competitor identity in order to facilitate interpretation. In this case, two-way ANOVAs
192 were performed on the responses of each native species separately (or the invasive species in
193 competition with each native species separately) with competition treatment, N addition
194 treatment, and their interaction as factors. Tukey HSD pair-wise significant differences ($p <$

195 0.05) were determined between all levels of any significant factors, including any
196 interactions. Models that violated assumptions of normality or homoscedasticity received a
197 $\log_{10}(y)$ transformation. All analyses were performed in R version 3.2.4 (R Core Team 2016).

198

199 **Results**

200 **BIOMASS RESPONSES**

201 Native and invasive species growth was impacted in contrasting ways by the competition
202 treatments (Table 1; Fig. 2). Both native species responded similarly to competition with the
203 invader, expect for their belowground biomass (Fig. 2). Compared to the control treatment,
204 belowground competition with the invader reduced native species mean total biomass by a
205 third, whilst full competition reduced it by half ($F = 24.6$, $p < 0.01$, Table 1, Fig. 2a).
206 Conversely, belowground competition with native species increased invasive species mean
207 total biomass by 41% and full competition increased it by 65% ($F = 66.0$, $p < 0.01$, Table 1,
208 Fig. 2a). Belowground and full competition between the native and invasive species increased
209 the mean percentage of dead aboveground biomass on native species by a factor of 4 ($F =$
210 44.7 , $p < 0.01$, Table 2, Fig. S1), while reducing it on invasive species to almost half ($F =$
211 14.4 , $p < 0.01$, Table 2, Fig. S1). Nitrogen addition decreased belowground biomass of native
212 species from 0.47 ± 0.05 g (mean \pm one SE) to 0.38 ± 0.04 g and invasive species from $2.20 \pm$
213 0.09 g to 1.75 ± 0.08 g. It also increased invader aboveground biomass from 3.14 ± 0.14 g to
214 3.83 ± 0.18 g. Nonetheless, it did not affect total biomass or dead aboveground biomass, and
215 its effects did not change under the different competition treatments (Tables 1 & 2).
216 Aboveground competition on its own had no effect on native or invasive species growth;
217 however, when combined with belowground competition (i.e. in the full competition
218 treatment) it resulted in a ca. 25% greater decline in native species total biomass, and a

219 greater increase in invasive species biomass, than belowground competition on its own (Fig.
220 2a). The increase in invasive species total biomass in the full competition treatment was
221 principally driven by increases in aboveground biomass (Fig. 2b), not belowground biomass
222 (Fig. 2c); whereas the decline in native species total biomass came predominantly from a
223 decrease in belowground biomass (Fig. 2d).

224 RESOURCE CAPTURE AND ALLOCATION RESPONSES

225 *Total N content*

226 Mean total N content (g) of native and invasive species responded in similar but slightly more
227 complex ways to competition than their biomass. The impact of invasive species competition
228 varied by native species identity ($F = 2.8$, $p < 0.05$, Table 2, Fig. S2) and by N addition ($F =$
229 3.5 , $p = 0.02$, Table 2, Fig. 3b). *P. cita*'s mean total N content declined by c. 40 and 50 %
230 when competing belowground and fully with the invader (Fig. S2), whereas the mean total N-
231 content of *P. colensoi* decreased by c. 60 and 75 % (Fig. S2), respectively. The negative
232 effect of belowground competition on native species mean total N was almost twice as large
233 under the low N treatment (-63%) than the high N treatment (-34%; Fig. 3b). Similarly, the
234 full competition treatment resulted in a 76% decrease under low N conditions compared with
235 a 55% decrease under high N conditions (Fig. 3b). Invasive species mean total N content
236 increased by over 50% when the invader competed with native species belowground, and by
237 over 75% when they competed fully ($F = 79.8$, $p < 0.01$, Table 2, Fig 3a), regardless of native
238 species competitor identity and N addition. Aboveground competition had no effect on native
239 or invasive species resource capture on its own; however, when combined with belowground
240 competition (i.e. in the full competition treatment), it resulted in a ~25% greater increase in
241 invasive species mean total N content than just belowground competition on its own (Fig.
242 3a).

243 *Mean C: N ratio and allocation patterns*

244 There was a three-way interaction between native species identity, competition and N
245 addition treatments on mean C: N ratio of native species ($F = 3.3$, $p = 0.03$, Table 2). We
246 therefore split the analysis by native species identity and tested *P. cita* and *P. colensoi*
247 responses separately (Table 3; Figs. 3c-d). The patterns in their responses were relatively
248 similar (Figs. 3c-d). They both showed stable mean C: N ratios across all competition
249 treatments under the high N treatment (Figs. 3c-d). Under the low-N treatment, they both
250 showed increased mean C: N ratios (*P. cita*, +37%; *P. colensoi* +44%) when competing
251 belowground with the invader (Figs. 3c-d). The key difference between the native species
252 was in the control and aboveground competition treatments; where the mean C: N ratio of *P.*
253 *cita* decreased in the high N treatment, compared to the low N treatment, while *P. colensoi*'s
254 mean C: N ratio showed no difference (Figs. 3c-d). The mean C: N ratio of the invasive
255 species, *A. capillaris*, was mostly stable in response to competition treatments, although it
256 was slightly higher in the aboveground than the belowground or full competition treatments
257 ($F = 4.0$, $p = 0.01$, Table 2; Fig 3e).

258 The allocation patterns of the invasive species showed no significant variation in response to
259 competition treatments (Table 4; Fig. 3f & S3). However, compared to the control treatment,
260 the native species showed a lower RMF in the full competition treatment ($F = 4.7$, $p = <0.01$,
261 Table 4; Fig 3f), and a higher RNF in the belowground competition treatment compared to
262 the aboveground competition treatment ($F = 3.2$, $p = 0.03$, Table 4; Fig S3).

263

264 **Discussion**

265 Contrary to our expectations that aboveground competition would be more important than
266 belowground competition under elevated N availability, belowground competition was in fact
267 central to the impact of the invasive grass species regardless of N availability. The
268 belowground competitive superiority of the invasive grass, *A. capillaris*, caused large
269 declines in native species biomass and total N content, along with alterations to tissue
270 nutrient stoichiometry and biomass allocation patterns. The invader's impact was greatest
271 under low N conditions but it also remained a superior competitor under high N conditions.
272 Considering the paucity of invader impact studies explicitly separating above and
273 belowground competition, along with a general perception of invasive plants as exploitative
274 species that are likely to be stronger aboveground competitors, we suggest that belowground
275 competition may be an under-appreciated mechanism for invasive plant impacts. This is
276 particularly true in high fertility ecosystems, such as those experiencing N enrichment due to
277 global change.

278 COMPETITIVE IMPACT

279 We used direct measures of competition including resource capture, alongside indirect
280 measures such as biomass, in order to determine whether competitive interactions
281 underpinned the differences in species growth (Trinder et al. 2013). Since resource capture
282 rates, i.e. total N content, mirrored the changes in species biomass across competition
283 treatments, it is likely that competitive interactions underpinned these changes. In the full
284 competition treatment, native species' growth and resource capture rates were heavily
285 reduced, while the invader's growth and resource capture increased substantially (Figs. 1 and
286 2). This supports our first hypothesis that competition between the invasive, *A. capillaris*, and
287 the native grass species, *P. cita* and *P. colensoi*, benefits the invasive species and decreases
288 native species growth and resource capture, compared with intraspecific competition.
289 Competition is therefore a clear pathway for the negative impacts of *A. capillaris* on two co-

290 occurring native grasses. The invader's competitive advantage suggests that fitness
291 differences between the invader and native species are likely contributing to *A. capillaris*'s
292 invasive success in these systems (MacDougall et al. 2009). Whilst other invasive plants have
293 been shown to out-compete native species, this often depends on increased nutrient
294 availability (Daehler 2003; Besaw et al. 2011; Seabloom et al. 2015). In contrast, the invader
295 in our study, *A. capillaris*, had large impacts on native species across both high and low N
296 availabilities. This is consistent with previous experiments in native grassland communities,
297 which also found no significant change in competition intensity across soil nutrient gradients
298 (Wilson and Shay 1990; DiTommaso and Aarssen 1991), particularly when interspecific
299 competition intensity is calculated relative to intraspecific competition intensity (Grace 1993;
300 Turkington et al. 1993). For the invader in our study, *A. capillaris*, such universal superior
301 performance over co-occurring native species suggests that *A. capillaris* may be a rare
302 "super-invader" (Daehler 2003). This could partly explain its increasing dominance in native
303 New Zealand grasslands since the 1960s (Rose 1995; Rose et al. 2004).

304 ABOVE VS. BELOWGROUND COMPETITION

305 The invasive grass's superior competitive ability, along with its negative impact on native
306 plant species, was driven by better capture of belowground resources. Evidence for this
307 comes from the decreases in total N content and increases in C: N ratios of native species in
308 the belowground competition treatment relative to the control treatment, along with the co-
309 occurring increases in total N content of the invader. This clearly demonstrates that
310 belowground competition allowed the invader to capture key resources required for plant
311 growth, in this case soil nitrogen, which the native species would otherwise have acquired. It
312 is also possible that release from belowground intraspecific competition allowed the invader
313 to grow faster and larger. In contrast, when native species were released from belowground
314 intraspecific competition their biomass decreased (fig. 1). The only two other studies that

315 separated above and belowground competition explicitly between native and invasive species
316 also both reported that belowground competition was more important in mediating invader
317 impacts than aboveground competition (Dillenburg et al. 1993; Kueffer et al. 2007).
318 However, these experiments tested functionally dissimilar plant species, namely lianas and
319 trees (Dillenburg et al. 1993) or adult trees and saplings (Kueffer et al. 2007), which means
320 their results are influenced by differences in lifeform and stage (Vila and Weiner 2004). Our
321 results extend the findings of these previous studies by showing that belowground
322 competition is a key driver of invasive plant impacts within a single plant functional group,
323 life form and growth stage. In the broader literature, belowground competition has been
324 shown to play a crucial role in structuring plant communities (Fargione et al. 2003; Harpole
325 and Tilman 2006; Hillerislambers et al. 2012) and is often more important in determining
326 competitive outcomes than aboveground competition (Wilson 1988). Nevertheless, the two
327 types of competition are likely to interact (Cahill 2002), and in addition to the direct impact
328 of belowground competition in our study, there was also an indirect impact *via* the facilitation
329 of aboveground competitive interactions. There are three lines of evidence for this. Firstly,
330 the aboveground competition treatment had no effect on native or invasive species responses.
331 Secondly, the full competition treatment had a stronger effect on native and invasive species
332 total biomass responses than the belowground competition treatment. Thirdly, this greater
333 impact on native species biomass responses was accompanied by an increase in invader
334 aboveground biomass (Fig. 2b), suggesting the additional impact on native species is likely to
335 have been driven by shading effects. Nonetheless, the impact of aboveground competition in
336 the full competition treatment was still entirely reliant on the invader's superior capture of
337 belowground resources.

338 The invasive grass's capacity to out-compete the native grasses for belowground resources
339 may be related to its greater root biomass relative to the natives (Figs. 2c-d), since

340 belowground competition appears to be size-symmetric (Cahill and Casper 2000). Root
341 biomass, alongside other root traits, may be influential in driving invasive grass species
342 success (Thomsen et al. 2006), which potentially makes it a useful screening tool.
343 Nonetheless, root biomass alone is unlikely to determine belowground competitive outcomes
344 between species (Cahill 2003), but typically interacts with other factors, such as feedbacks
345 with soil biota (van der Putten et al. 2016). For example, belowground enemy release may
346 also have facilitated the invasive grass's superior competitive abilities belowground (Agrawal
347 et al. 2005; Reinhart and Callaway 2006). Likewise, allelopathic effects cannot be excluded;
348 although we found no evidence in the literature that *A. capillaris* has allelopathic effects on
349 co-occurring species. While the exact reason for *A. capillaris*' belowground superiority is
350 difficult to determine, our results clearly demonstrate that belowground competition is central
351 to delivering this invader's impact.

352 NITROGEN AVAILABILITY

353 While higher N-availability increased the aboveground biomass of the invasive grass but not
354 the native species, it did not increase the invader's impact on native species. Nor did it
355 diminish the relative importance of belowground competition. This contradicts our second
356 hypothesis that *A. capillaris*' competitive impacts on native species, and the relative
357 importance of aboveground competition over belowground competition, both increase with
358 increasing N availability. In fact, native species showed significantly greater reductions in
359 total N content, in response to belowground competition with the invader, under low N
360 conditions than high N conditions. Furthermore, it was only under low N conditions that
361 belowground competition with the invader altered native species tissue nutrient stoichiometry
362 (i.e. increased their C: N ratios). Nitrogen was therefore likely a limiting resource in our
363 experiment, as supported by various lines of evidence. Firstly, the exceptionally low N:P ratio
364 (0.6) of the soil was lower than the critical N:P ratio in aboveground vegetation (ca. 15);

365 below which growth is limited by N (Olde Venterink et al. 2003; Olde Venterink and
366 Güsewell 2010). Secondly, nitrogen addition, in the high N treatment, alleviated the negative
367 impact of belowground competition on native species N capture rates but not their biomass.
368 This suggests the invader out-competed the natives for other belowground resources in the
369 high N treatment, which are essential for growth and either became limiting following N
370 addition, or were co-limiting (Harpole et al. 2011). It is surprising that N addition did not
371 enhance invader impact as non-native grass invasions in New Zealand, and elsewhere, are
372 often associated with increased N availability (Dickie et al. 2014; Seabloom et al. 2015).
373 Furthermore, native grasses that are adapted to low fertility soils, such as those in our study,
374 may not respond to added nutrients, or in some cases may even respond negatively; unlike
375 exotic invasive grasses which often respond positively (Thompson and Leishman 2004;
376 Leishman and Thomson 2005; Radford et al. 2007; Seabloom et al. 2015). However, in its
377 native range, *A. capillaris* is not considered a high-N species (Hill et al. 1999) and invasive
378 plants can also succeed in low fertility environments (Funk and Vitousek 2007; Heberling
379 and Fridley 2016), despite some efforts to restore native species by soil fertility reduction
380 (e.g. Blumenthal et al. 2003). Invasive plants that out-compete co-occurring native species
381 across wide gradients of soil fertility, such as *A. capillaris* in New Zealand grasslands, are
382 likely to have the highest net impacts on native plant communities.

383 CONCLUSION

384 The invasive grass *A. capillaris* reduced co-occurring native grass species biomass by half,
385 and their resource capture by up to 75%. These impacts were driven directly and indirectly by
386 belowground, not aboveground, competition - regardless of N availability. The invader's
387 greater root biomass appeared to facilitate its belowground competitive advantage. However,
388 future studies could incorporate other root traits in order to improve our understanding of
389 native – invasive plant root interactions, as this is currently underdeveloped in comparison

390 with our knowledge of aboveground interactions. The overriding influence of belowground
391 competition across wide levels of N availability in our study was unexpected, as the relative
392 importance of aboveground competition often increases with increasing soil N availability
393 (Wilson and Tilman 1991). Nevertheless, recent analyses reveal the prevalence of nutrient co-
394 limitation across ecosystems globally, including grasslands (Harpole et al. 2011; Fay et al.
395 2015), which underlines the significance of belowground competition for multiple soil
396 nutrients (Harpole and Tilman 2007; Harpole et al. 2016). In light of these findings, our
397 results suggest that belowground competition may be under-appreciated as invasive plant
398 impact mechanism, particularly in high fertility ecosystems, such as those experiencing N
399 enrichment due to global change. Our findings could help to improve predictions of the
400 impact on native species diversity of two pervasive, and interacting, drivers of global
401 environmental change.

402

403 **Acknowledgements**

404 We would like to thank Karen Boot, Rowan Buxton and Chris Morse for field and logistical
405 assistance, along with Matthew Clare and Silke Broadbent for help in the greenhouse, and
406 Paul Chambre for experimental advice. AB is funded by a Lancaster University Faculty of
407 Science and Technology studentship.

408 Conflict of Interest: The authors declare that they have no conflict of interest.

409

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587 **Tables**

588 **Table 1** Results of 3-way ANOVAs testing effects of native species identity (NSI),
 589 competition (C), nitrogen addition (N+) and their interactions on biomass responses (total,
 590 aboveground and belowground) of native (*Poa cita* and *Poa colensoi*) and invasive species
 591 (*Agrostis capillaris*). All factors are fixed effects. Biomass data were log-transformed before
 592 analysis.

	Total biomass			Aboveground biomass		Belowground biomass	
	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Native species							
NSI	1	222.5	<0.01	221.1	<0.01	178.2	<0.01
C	3	24.6	<0.01	18.7	<0.01	30.8	<0.01
N+	1	0.5	0.48	0.4	0.54	10.8	<0.01
NSI * C	3	0.8	0.51	0.9	0.47	4.3	<0.01
NSI * N+	1	1.0	0.31	1.2	0.28	1.6	0.21
C * N+	3	0.3	0.80	0.6	0.61	0.6	0.60
NSI * C * N+	3	0.8	0.51	0.7	0.57	1.5	0.21
Invasive species							
NSI	1	2.1	0.15	4.9	0.03	0.03	0.86
C	3	66.0	<0.01	49.1	<0.01	23.0	<0.01
N+	1	1.9	0.18	30.1	<0.01	26.3	<0.01
NSI * C	3	1.4	0.25	1.3	0.28	0.7	0.53
NSI * N+	1	0.7	0.42	0.1	0.82	0.8	0.37
C * N+	3	1.3	0.28	2.3	0.09	0.2	0.93
NSI * C * N+	3	1.3	0.29	0.4	0.77	1.5	0.22

594 **Table 2** Results of 3-way ANOVAs testing effects of native species identity (NSI),
 595 competition (C), nitrogen addition (N+) and their interactions on % dead aboveground (AG)
 596 biomass, total N content and C/N ratio of native (*P. cita* and *P. colensoi*) and invasive species
 597 (*A. capillaris*). All factors are fixed effects. Total N content and CN ratio data were log-
 598 transformed before analysis.

	% Dead AG biomass			Total N content		C/N ratio	
	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Native species							
NSI	1	1.7	0.20	154.0	<0.01	0.2	0.68
C	3	44.7	<0.01	56.6	<0.01	4.5	<0.01
N+	1	0.1	0.74	65.9	<0.01	206.2	<0.01
NSI * C	3	0.2	0.87	2.8	0.05	1.7	0.18
NSI * N+	1	0.4	0.54	13.5	<0.01	28.7	<0.01
C * N+	3	1.4	0.25	3.5	0.02	14.8	<0.01
NSI * C * N+	3	0.7	0.57	1.1	0.36	3.3	0.03
Invasive species							
NSI	1	0.2	0.63	1.7	0.20	<0.1	0.87
C	3	14.4	<0.01	79.8	<0.01	4.0	0.01
N+	1	0.6	0.43	668.2	<0.01	1233.0	<0.01
NSI * C	3	1.1	0.35	0.7	0.53	0.9	0.42
NSI * N+	1	2.3	0.13	0.03	0.86	0.5	0.49
C * N+	3	0.3	0.82	1.1	0.36	1.3	0.27
NSI * C * N+	3	2.6	0.06	1.1	0.35	1.3	0.29

600 **Table 3** Results of 2-way ANOVAs testing effects of competition (C), nitrogen addition
601 (N+) and their interaction on CN ratio of native species (*P. cita* and *P. colensoi*). All factors
602 are fixed effects. *P. cita* data were log-transformed before analysis.

	CN ratio		
	<i>df</i>	<i>F</i>	<i>P</i>
<i>P. cita</i>			
C	3	4.1	0.01
N+	1	218.2	<0.01
C * N+	3	3.1	0.04
<i>P. colensoi</i>			
C	3	4.1	0.01
N+	1	37.0	<0.01
C * N+	3	13.7	<0.01

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613 **Table 4** Results of 3-way ANOVAs testing effects of native species identity (NSI),
614 competition (C), nitrogen addition (N+) and their interactions on root mass fraction (RMF)
615 and root nitrogen fraction (RNF) of native (*P. cita* and *P. colensoi*) and invasive species (*A.*
616 *capillaris*). All factors are fixed effects. Invasive species data were log-transformed before
617 analysis.

	RMF			RNF	
	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Native species					
NSI	1	<0.1	0.82	5.9	0.02
C	3	4.7	<0.01	3.2	0.03
N+	1	20.5	<0.01	22.7	<0.01
NSI * C	3	0.3	0.84	2.4	0.07
NSI * N+	1	0.1	0.82	0.3	0.58
C * N+	3	0.7	0.57	0.4	0.77
NSI * C * N+	3	1.8	0.16	0.9	0.44
Invasive species					
NSI	1	2.4	0.12	0.2	0.69
C	3	0.7	0.53	1.9	0.14
N+	1	69.2	<0.01	74.6	<0.01
NSI * C	3	0.7	0.56	0.2	0.87
NSI * N+	1	0.3	0.61	0.5	0.50
C * N+	3	1.3	0.30	0.7	0.56
NSI * C * N+	3	0.5	0.66	1.3	0.28

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621 **Figure legends**

622 **Fig. 1** Schematic diagram showing experimental setup for invasive (I) and native (N) species
623 planted in pots with above and belowground partitions to create four competition treatments:
624 a) Control - full intraspecific competition between a pair of invasive and a pair native
625 individuals, but no interspecific competition; b) Aboveground - aboveground interspecific
626 competition between invasive and native individuals, and belowground intraspecific
627 competition; c) Belowground - belowground interspecific competition between invasive and
628 native individuals and aboveground intraspecific competition and d) Full - above and
629 belowground interspecific competition between invasive and native individuals but no
630 intraspecific competition. In a) and d) the above and belowground partitions were flush; they
631 are depicted lightly apart for clarity.

632 **Fig. 2** Biomass responses of native and invasive species to four competition treatments (See
633 Fig. 1 legend for full description). a) Total biomass; b) aboveground biomass for native and
634 invasive species; c) below-ground biomass for invasive species; d) below-ground responses
635 of two native species, *P. cita* and *P. colensoi* to these treatments. Box-and-whisker plots
636 show individual data points, means, one standard error and range of data. Means with the
637 same letter are not significantly different ($p > 0.05$, Tukey HSD post hoc tests); in a) and b)
638 upper case letters are for ANOVAs comparing invader responses; lower case for native
639 species responses

640 **Fig. 3** Resource capture and allocation responses of native and invasive species to four
641 competition treatments (See Fig. 1 legend for full description). a) Total N content for invasive
642 species; b) total N content for native species in high or low N treatments; c) C/N ratio for *P.*
643 *cita* in different N treatments; d) C/N ratio for *P. colensoi* in different N treatments; e) C/N
644 ratio for invasive species; f) root mass fraction (RMF) for native and invasive species. Box-

645 and-whisker plots show individual data points, means, one standard error and range of data.
646 Means with the same letter are not significantly different ($p > 0.05$, Tukey HSD post hoc
647 tests); in f) upper case letters are for ANOVAs comparing invader responses; lower case for
648 native species responses

Fig. 1





