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1 **Species interactions modulate the response of saltmarsh plants to flooding**

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14 **Running head:** Trait responses to chronic flooding and composition

15 **ABSTRACT**

16 **Background and aims:** The vegetation that grows on coastal wetlands is important for ecosystem
17 functioning, a role mediated by plant traits. These traits can be affected by environmental stressors
18 and by the competitive environment the plant experiences. The relative importance of these influences
19 on different traits is poorly understood and, despite theoretical expectations for how factors may
20 interact, empirical data are conflicting. Our aims are to determine the effect of flooding, species
21 composition and their interaction on plant functional traits, and assess the role of biodiversity and
22 species composition in driving community-level responses to flooding.

23 **Methods:** We conducted a factorial glasshouse experiment assessing the effects of species
24 composition (all combinations of three saltmarsh species, *Aster tripolium*, *Plantago maritima* and
25 *Triglochin maritima*) and flooding (immersion of roots) on a suite of functional traits. We also related
26 biomass in mixed species pots to that expected from monocultures to assess how species interactions
27 affect community-level biomass.

28 **Key results:** Species composition frequently interacted with flooding to influence functional traits
29 and community level properties. However, there was also considerable intraspecific variability in
30 traits within each treatment. Generally, effects of flooding were more pronounced for belowground
31 than aboveground biomass, while composition affected aboveground biomass more than belowground
32 biomass. We found both negative and positive interactions between species (indicated by differences
33 in above and belowground biomass from expectations under monoculture), meaning that composition
34 was an important determinate of community function.

35 **Conclusions:** While the effect of flooding alone on traits was relatively weak, it interacted with
36 species composition to modify the response of both individual plants and communities. Our results
37 suggest that responses to increased flooding will be complex and depend on neighbourhood species
38 interactions. Furthermore, intraspecific trait variability is a potential resource that may dampen the
39 effects of changes in flooding regime.

40 **Keywords:** Competition, Coastal, Functional trait, Inundation, Facilitative interaction, Ecosystem
41 function.

42 INTRODUCTION

43 Saltmarshes provide important ecosystem services, such as coastal protection, carbon sequestration
44 and water purification (Barbier et al., 2011). However, the provision of these ecosystem services by
45 saltmarshes is likely to be affected by sea-level rise (Craft et al., 2009). This may increase the
46 provision of some ecosystem services, such as carbon sequestration, due to higher rates of
47 sedimentation (Rogers et al., 2019). However, the provision of ecosystem services may be affected by
48 shifts in plant community composition towards species tolerant of more frequent tidal inundation
49 (Donnelly and Bertness, 2001). Predicting the consequences of these changes for ecosystem service
50 provision is challenging, as it requires knowledge of how plant community diversity and composition
51 affect ecosystem functioning and service delivery. Although this has been widely investigated in other
52 systems (Tilman et al., 2014), evidence from saltmarshes is limited. Existing studies do support a
53 positive relationship between plant diversity and ecosystem functioning (Rupprecht et al., 2017,
54 Möller et al., 2014, Ford et al., 2016, Sullivan et al., 2007), but effects may relate to the impact of a
55 few functionally important species that are more likely to be present in diverse communities (Sullivan
56 et al., 2007).

57 The effect of plants on ecosystem service delivery is influenced by their traits (Díaz et al.,
58 2013), which vary both between species and within species. Intraspecific trait-variation can be
59 substantial, especially across environmental stress gradients, and is due to both turnover in genotypes
60 across gradients and phenotypic plasticity within a single genotype (Eller and Brix, 2012, Richards et
61 al., 2010). Environmental changes can therefore affect ecosystem functioning by changing the
62 distribution of traits within a species as well as by changing species composition, and these intra-
63 specific changes are likely to be especially important in species poor habitats such as saltmarshes.
64 Phenotypic plasticity can also be exhibited in response to competition (Venterink and Güsewell, 2010,
65 Weiner et al., 1990). Plastic changes in response to competition include changes to root architecture to
66 avoid competitors and increased height to overtop competitors (Callaway et al., 2003). These changes
67 to plant traits could influence ecosystem function. For example, root biomass has been shown to
68 positively influence sediment stability in saltmarshes (Ford et al., 2016), while root architecture
69 (density, length, depth) influences soil carbon cycling (De Deyn et al., 2008). Plant height and shoot

70 stiffness can determine the effectiveness of wave attenuation and hence influence coastal protection
71 (Möller et al., 2014, Bouma et al., 2005). Species interactions can be positive as well as negative
72 (Bertness and Shumway, 1993), and these facilitative interactions may cause phenotypic plasticity
73 (Callaway et al., 2003), but the effects of this are poorly understood.

74 Currently, there is limited understanding of the relative importance and interactions of
75 environmental stress and neighbourhood species competition in influencing trait plasticity and
76 ecosystem functioning. Saltmarsh plant communities provide a model system for studying these
77 responses, as there are marked environmental gradients driven by tidal inundation (Chapman, 1939),
78 many species have broad niches potentially allowing phenotypic plasticity across these gradients
79 (Sullivan et al., 2018), competitive and facilitative interactions are important for shaping plant
80 community structure (Bertness and Shumway, 1993) and species richness is low (median species
81 richness in a 0.5 by 0.5 m quadrat = three species, based on data from UK saltmarshes from Mossman
82 et al., 2012) meaning that species interactions can be more easily understood. Previous work in
83 saltmarshes has found that traits relating to plant height and biomass allocation do vary along an
84 environmental stress gradient due to changes in species composition (Minden and Kleyer, 2011,
85 Minden et al., 2012), but the effect of species interactions and interspecific trait variability on trait
86 responses to these tidal inundation stress gradients are not known.

87 Understanding how plant traits vary with differential tidal inundation is important as future
88 chronic sea-level rise will increase the duration and frequency of tidal inundation plant communities
89 at a given elevation will be exposed to, while increases in storm frequency will increase the risk of
90 acute flooding in the upper marsh and areas not normally exposed to tidal inundation. The responses
91 of plants to environmental change vary depending on whether changes are short-term pulses or long-
92 term presses (Smith et al., 2009, Sullivan et al., 2016). It is therefore important to have studies
93 spanning the continuum of responses from acute flooding (e.g. Hanley et al., 2017), to chronic change
94 (e.g. Ury et al., 2019), to variation across spatial gradients in inundation (Minden et al., 2012) to
95 capture this range of responses.

96 In this study we investigated how flooding, and resultant waterlogging, which are the
97 dominant controls on the distribution of saltmarsh plants (Davy et al., 2011), effects saltmarsh plant

98 functional traits. We exposed plants to a five month long flooding treatment, simulating chronic
99 changes in a plant's environment as may occur under sea-level rise. As well as examining the effect of
100 flooding alone, we also test whether plant species composition and diversity affect responses to
101 flooding. We measured a suite of functional traits potentially related to ecosystem functioning and
102 service provision. These are plant height and width (the latter a component of overall vegetation
103 density, and both have been linked to wave attenuation potential (Anderson and Smith, 2014,
104 Rupprecht et al., 2017)), number of leaves and specific leaf area (linked to resource acquisition
105 (Cornelissen et al., 2003)), aboveground biomass (a proxy for productivity as measurements were
106 over one growing season and also related to wave attenuation potential (Paul et al., 2016)) and
107 belowground biomass (linked to productivity and to sediment stability (Gyssels et al., 2005, De
108 Battisti et al., 2019)). We also measured community level metrics: above and belowground biomass,
109 canopy cover and side-on density (both related to habitat provision for invertebrates (Ford et al.,
110 2017), the latter also related to wave attenuation (Möller, 2006)). Using this experiment, we examined
111 (1) the role of flooding and species composition in affecting plant functional traits, (2) whether
112 neighbourhood species composition modified responses to flooding and (3) the role of biodiversity
113 and species composition in driving community-level responses to flooding.

114

115 **METHODS**

116 *Study species*

117 We investigated responses of three study species, sea aster *Aster tripolium*, sea plantain *Plantago*
118 *maritima* and sea arrowgrass *Triglochin maritima* (hereafter *Aster*, *Plantago*, *Triglochin*), to
119 experimental flooding. *Aster* is a pauciennial forb; *Plantago* and *Triglochin* are perennial forbs. Study
120 species were selected as they overlap in their niches, and so co-occur, but differ in niche centroid,
121 both where niche is defined by relating occurrence in the natural saltmarshes to elevation alone (Fig.
122 S1) and in relation to elevation and redox potential (Sullivan et al., 2018). *Aster* grows across a wide
123 range of elevations and flooding frequencies (Gray, 1971). *Plantago* and *Triglochin* have narrower
124 niches in the higher elevations of *Aster*'s niche (Gray, 1971; Fig. S1). *Triglochin* is more tolerant of
125 waterlogged soils than *Plantago* (Sullivan et al., 2018) and *Triglochin* is commonly found in

126 waterlogged areas at the edges of pannes (Fogel et al., 2004). Previous studies have indicated that
127 there may be competitive interactions between these species, but it is not clear which species are
128 competitively dominant and in what circumstances (Davy and Bishop, 1991).

129

130 *Experimental design*

131 The experiment was designed to alter environmental conditions whilst remaining within the study
132 species' fundamental niche, equivalent to moving from a well drained or infrequently flooded part of
133 the saltmarsh (unflooded treatment) to more frequently inundated or poorly drained area (flooded
134 treatment).

135 The plants used in the experiment were plugs grown by British Wildflowers (North
136 Burlingham, Norfolk) from seeds we obtained from three sites across the UK (Southport 53.6785, -
137 2.9873; Freiston 52.9643, 0.09200; Steart 51.2006, -3.0314) and from across the range of elevations at
138 each site. This was to maximise the genetic variation within species. Seed was thoroughly mixed prior
139 to planting.

140 In December 2017, pots (diameter 23 cm, volume 5 l) were filled with a ratio of 1:3 of sand
141 and loam (Boughton Kettering Loam, Amenity Land Solutions UK). Each pot was planted with six
142 nursery-grown plugs in the seven possible planting combinations (i.e. three single species
143 combinations, three two-species combinations and one three-species composition). Each species
144 combination was replicated 16 times in a fully factorial glasshouse experiment. Eight replicates were
145 assigned to the flooded treatment and eight to the unflooded treatment. The experiment totalled 112
146 pots and 672 individual plants. Composition treatments are referred to subsequently by the first letter
147 of each species name, e.g. PA is *Plantago* and *Aster*.

148 Pots in the flooded treatment were placed in 10 cm deep trays that were filled to a depth of 7
149 cm with saline water (at 50% seawater strength, 17.5 g l⁻¹ of Instant Ocean®, Blacksburg, VA, USA)
150 for the duration of the experiment; water was regularly topped up to 7 cm depth with fresh water. See
151 Hanley et al. (2019) for a comparison of effects on plants with natural seawater. Plants in the
152 unflooded treatment were watered to saturation every three days and allowed to drain freely. Pots

153 were randomly distributed throughout the greenhouse. A 12 hour dark light cycle was provided and
154 minimum temperature was kept at above 10 °C throughout the experiment.

155

156 *Trait measurements*

157 In May 2018, after a five month growth period, we measured seven traits of each individual and five
158 community (whole pot) measures. Plant height and width was measured from the base of each plant to
159 the maximum height and widest part of the individual. The number of reproductive structures (flower
160 and seed heads) was recorded on each individual. The six individuals in each pot were then carefully
161 separated by washing soil from the roots over three graduating sieves (minimum 20 µm). The number
162 of live leaves on each individual were counted and three average leaves were selected to calculate
163 specific leaf area (Perez-Harguindeguy et al., 2013). Each of these leaves were placed on a flatbed
164 scanner and scanned at 300 dpi with a resolution of 4961 x 3508 and leaf area calculated using the
165 image processing software ImageJ. Leaves were dried at 70°C for 24 hours and then weighed. The
166 remainder of the aboveground plant material was harvested and dried at 70°C for 48 hours to calculate
167 aboveground biomass; the mass of the three leaves harvested for specific leaf area was added to the
168 total and aboveground plant mass. The remainder of the soil was washed from roots of each individual
169 through the three graduating sieves, and belowground material collected and dried at 70°C for 48
170 hours to quantify belowground biomass. Above and belowground biomass were summed for each
171 individual to calculate total biomass, and the ratio of above to belowground biomass was calculated.

172 To assess community performance, aboveground and belowground biomass, and total
173 biomass in each pot were quantified by summing the measurements for the six individuals. In
174 addition, we quantified the cover of vegetation in the pot when viewed from directly above (top-down
175 vegetation cover, cm²) and vegetation density, quantified as the area covered by plants when viewed
176 from the side (side-on surface area, cm²). Side-on surface area and top-down vegetation cover were
177 quantified by taking standardised photographs. Images for side-on surface area were taken by placing
178 pots against a white background mounted 5 cm from the back of the pot. A photograph was taken
179 focused on the centre of the pot on a tripod-mounted SLR camera perpendicular to the pot from a
180 distance of 1 m. Dispersed room lighting was used to avoid over-exposure. To measure top-down

181 vegetation cover, the pot was then placed onto a dark background and an image taken from 1 m
182 directly above the pot. The areas covered by vegetation in the photographs were calculated using
183 ImageJ.

184

185 *Data analysis*

186 Samples sizes varied due to accidental sample destruction in a laboratory flood (all sample sizes by
187 treatment are given in the Table S1a and b). Due to processing constraints, sample harvesting
188 occurred over a two week period, so to reduce bias in additional growth, care was taken to ensure
189 samples selected for processing on a given day were distributed across treatments. This resulted in
190 missing data being randomly distributed among pots and so does not bias statistical analysis
191 (Ellington et al., 2015).

192 All analysis was conducted in R (R Development Core Team, 2018). The effect of flooding
193 on the proportion of individuals of a species surviving was assessed with a binomial test. A chi-
194 squared test was performed for each species to assess the difference in number of reproductive
195 structure between the flooded and unflooded treatments. Trait variability was quantified as the
196 interquartile range divided by the median, which provides a non-parametric analogue to the
197 coefficient of variation. This was calculated at three levels, across species, within species and within
198 species and treatments. The effect of flooding and composition, and their interaction, on each of the
199 traits was assessed with general linear models, with separate models for each species. To meet
200 assumptions of normality and homogeneity of variances, total biomass, above:belowground ratio and
201 specific leaf area were log transformed, and width was square-root transformed. The number of leaves
202 was modelled in an equivalent way but using a generalised linear model and a Poisson-error
203 distribution as the response variables were count data.

204 To investigate whether species composition and diversity affected biomass we compared
205 observed pot-level values of aboveground, belowground and total biomass with expected values based
206 on the constituent species' performance in the monoculture treatment of this experiment (Loreau and
207 Hector, 2001). To do this whilst accounting for intra-specific variation, we randomly selected n plants
208 from the pool of individuals of the species from monoculture pots in the appropriate flooding

209 treatment, where n is the number of that species in the target pot. Dead individuals were not counted
210 for this calculation of n . We repeated this sampling 1000 times to obtain a distribution of expected
211 values for each pot. We then calculated the standardised effect size of biomass in each pot as observed
212 biomass minus the mean of expected biomass, divided by the standard deviation of expected values
213 (Gotelli et al., 2011). Positive values indicate that biomass is greater than expected given species'
214 performance in monoculture (overyielding), while negative values indicate that biomass is less than
215 expected (underyielding). To test whether composition affected over/underyielding, we used one
216 sample t-tests to assess if the mean biomass standardised effect size in a treatment differed from zero.

217

218 RESULTS

219 *Effects of flooding on individual plants*

220 Nineteen individuals died (17 *Aster*, 2 *Plantago*, no *Triglochin*) during the experiment, with no
221 statistically significant difference between the flooded and unflooded treatments (*Aster*: 11 out of 17
222 died in the flooding treatment, binomial test $P = 0.33$; insufficient sample size for other species).
223 Thirty two individuals across all species (<5% of plants) had reproductive structure (25 *Plantago*, five
224 *Triglochin*, two *Aster*). More individuals had reproductive structures in the unflooded treatment,
225 although this difference was not statistically significant (15 % of all *Plantago* had reproductive
226 structures in the unflooded treatment compared to 7 % in the flooded treatment, binomial test $P =$
227 0.11; note limited statistical power for *Plantago* and insufficient sample size for statistical analysis
228 with other species).

229 There was substantial intra-specific variability in all traits of all species (Fig. S2, Table S2),
230 with intraspecific variation amounting to 71.5 % (± 18.7 % SD) of the total variation in a trait. Trait
231 variability, quantified as the ratio of the interquartile range to the median, was similar when calculated
232 at cross-species, within species, and within species and treatment levels (Fig. S2).

233 Flooding affected the traits of all study species when grown in monoculture, but the traits
234 affected varied among species. Flooding reduced the number of leaves and specific leaf area, but
235 increased the ratio aboveground to belowground biomass for *Aster* ($\ln(\text{Leaves})$: -0.103 ± 0.045 , $z = -$
236 2.29 , $df = 93$, $P = 0.022$; $\ln(\text{SLA})$: -0.462 ± 0.130 SE, $t = 3.54$, $df = 82$, $P < 0.001$; $\ln(\text{AGB:BGB})$:

237 0.956 ± 0.302 SE, $t = 3.17$, $df = 86$, $P = 0.002$). For *Plantago*, flooding increased height and width but
238 reduced the ratio of aboveground to belowground biomass (Height: 92.9 ± 10.6 SE, $t = 8.60$, $df =$
239 92 , $P < 0.001$; sqrt(Width): 2.4 ± 0.5 SE, $t = 4.52$, $df = 92$, $P < 0.001$, ln (AGB:BGB): -0.546 ± 0.252
240 SE, $t = 2.17$, $df = 86$, $P = 0.033$). For *Triglochin*, flooding reduced the number of leaves (ln (Leaves):
241 -0.103 ± 0.048 , $z = -2.16$, $df = 93$, $P = 0.031$). All other species-trait combinations did not differ
242 statistically significantly between flooded and unflooded treatments.

243

244 *How does composition effect trait responses to flooding?*

245 For 14 out of the 18 trait-species combinations examined, the response to flooding was statistically
246 significantly different from that in monoculture in at least one composition treatment (Fig. 1, Table
247 S3). Reversal of flooding effects in monoculture (including where effects in monoculture were not
248 statistically significant) occurred in nine trait-species combinations, strengthening of effects occurred
249 in five and weakening occurred in two. The type of interaction did not closely relate to either the trait
250 investigated or the focal species, except for all weakening interaction effects being for *Plantago* (Fig.
251 1). For *Aster*, the effect of flooding reversed to increase total biomass in the TA composition
252 treatment, reduce relative allocation to aboveground biomass in the TA and PA treatments, reduce
253 height in the PA treatment, and increase SLA in the PA and to a lesser extent TA treatments. The
254 effect of flooding on the number of leaves strengthened from a non-significant negative effect to a
255 strong negative effect in the PTA treatment. For *Plantago*, the change in height and width in response
256 to flooding seen in monocultures was not evident in the PT, PTA and (height only) PA treatments.
257 Flooding increased the number of leaves and specific leaf area in the PA treatment, but this effect on
258 the number of leaves was reversed in the PTA treatment. For *Triglochin*, the response to flooding
259 changed from being weakly positive/ negative to strongly positive in the PTA treatment for height,
260 width, number of leaves and AGB: BGB ratio. For the former three traits, this effect was also seen in
261 the PA treatment. For AGB: BGB ratio, this also increased with flooding for the PT treatment, while
262 the response of specific leaf area to flooding switched from being weakly positive to negative in the
263 PT treatment.

264 Species composition also affected traits independently of flooding (Fig. 1, Table S3). *Aster*
265 biomass was lower in the PTA treatment, while the number of leaves was lower in the PA treatment.
266 *Plantago* had higher biomass in the PT treatment. *Triglochin* had lower biomass in the TA treatment,
267 lower AGB: BGB ratio in the PTA treatment, lower height in the PA treatment, more leaves in the PT
268 treatment and greater specific leaf area in the PA treatment.

269

270 *Effect of flooding and composition on pot level metrics*

271 The effect of flooding and species composition on vegetation cover and density, measured
272 respectively as top-down area and side-on area, was limited. Neither flooding nor composition
273 consistently affected top-down area, but there was a statistically significant interaction between
274 flooding and composition, with greater top-down area in the flooded treatment for the PA and PT
275 compositions (Fig. 2, Table S4). Side-on area was not related to flooding, composition nor their
276 interactions (Table S4). Aboveground biomass was related to composition, with higher biomass in the
277 P and PT composition treatments, but was not related to flooding except for in the PA treatment,
278 where aboveground biomass was lower when flooded (Fig. 2). Flooding reduced belowground
279 biomass, except for in the P and TA treatments, where this effect was reversed. There were also some
280 effects of composition, with lower belowground biomass in the TA treatment than the PT treatment
281 (Fig. 2).

282 Species composition treatments showed both over and underyielding of biomass relative to
283 expectations based on species' performance when grown in monoculture. The PA treatment showed
284 underyielding (i.e. lower biomass than expected) but only when flooded, while the TA treatment
285 showed underyielding in both flooded and unflooded treatments (Fig. 3). In contrast, the PT treatment
286 showed overyielding (i.e. higher biomass than expected), significantly so when flooded (Fig. 3).
287 These compositional effects largely cancelled each other out in the PTA treatment, where total
288 biomass did not differ significantly from expected values, although aboveground biomass was lower
289 than expected in the unflooded treatment. Over and underyielding were primarily through changes to
290 aboveground biomass, with the only deviation in belowground biomass from expected values being
291 underyielding in the unflooded TA treatment.

292 These differences from expected values can be further investigated by looking at species-level
293 departures from expected biomass in monoculture. The lower pot-level total biomass in the flooded
294 PA treatment is reflected in the lower than expected biomass of both *Aster* and *Plantago*, while the
295 lower pot-level total biomass in the TA treatment and higher biomass in the PT treatment mostly
296 relates to the response of just *Triglochin* and *Plantago* respectively (Fig. S3).

297

298 **DISCUSSION**

299 Flooding, species composition and their interaction affected both species traits and total pot-level
300 biomass. However, these effects were generally weak, and were against a backdrop of marked
301 intraspecific trait variability within each treatment. This implies that changes in plant traits, and hence
302 potentially in ecosystem service provision, in response to flooding will be variable and depend on the
303 intra- and interspecific composition of communities. Overall, flooding affected belowground biomass
304 more than aboveground biomass, while composition affected aboveground more than belowground
305 biomass, but there was variation amongst species in their response to flooding and composition. In
306 line with expectations based on species' niches, *Triglochin* responded least to flooding when in
307 monoculture, although this response was affected by species composition. Compositional affects and
308 interactions with flooding were dependent on the identity of interacting species. Depending on the
309 species pair, inter-specific interactions led to underyielding (in pot-level biomass relative to
310 expectations from monoculture) that was independent of flooding treatment, underyielding but only in
311 the flooding treatment, or overyielding enhanced by flooding. This diversity of responses meant that
312 compositional effects on pot-level biomass were largely cancelled out in the three species treatment,
313 or that there were interactions that only manifested when there were three species.

314 *Triglochin* was little affected by the chronic flooding and its resultant waterlogging when
315 grown in monoculture with only one trait, a reduction in the number of leaves, altered by the flooded
316 treatment. This supports the expectations we had based on its niche, as it is known to be relatively
317 tolerant of waterlogged soils (Fogel et al., 2004, Sullivan et al., 2018), particularly in saline conditions
318 (Davy and Bishop, 1991). Furthermore, in waterlogged soils *Triglochin* increases the production of
319 surface roots, which raises the surface of the marsh, ameliorating the conditions and allowing other

320 species to colonise (Fogel et al., 2004). While we found no difference in the above to belowground
321 biomass ratio, there may have been a switch from the production of deeper roots to surface roots in
322 the flooded conditions that we did not capture, as we measured total belowground biomass rather than
323 root architecture. In addition to the total root biomass, root porosity and rooting depth are among a
324 range of adaptations that halophytes have to flooding (Colmer and Flowers, 2008). We found that
325 *Plantago* and *Aster* had contrasting responses of belowground biomass to flooding, with significant
326 reductions in *Aster* and significant increases in *Plantago*. These species differ in their root porosity
327 response to flooding (Justin and Armstrong, 1987), while it is unclear how this relates to belowground
328 biomass, as increased porosity may reduce root mass, the presence of aerenchyma increases tolerance
329 to anoxic, waterlogged soils (Colmer and Flowers, 2008). Whilst we do not know the full suite of
330 adaptations for each of these species, the diversity of potential mechanisms could explain the
331 differential responses we observe here. As changes in root biomass is likely to influence sediment
332 stability, the variable responses of species to chronic flooding means that changes in the provision of
333 erosion protection services are likely to be complex.

334 Very few individuals died during the experiment (<3%) indicating that, in line with our aim,
335 the flooding treatment was insufficiently harsh to result in substantial deaths over the five month
336 experimental period. While we did find some effects of flooding, there was, for example, no effect on
337 total biomass and so it is possible that the flooding treatment was not stressful enough to elicit
338 sufficiently strong responses to quantify. Previous studies with similar treatments have found
339 responses (e.g. Huckle et al., 2000, Wang et al., 2006) even after just two months (Cooper, 1982).
340 While our results of plant performance under chronic flooding were broadly consistent with our
341 expectations based on their realised niches, the sensitivity to flooding was low. We would expect the
342 sensitivity to increase if the study was repeated with transplanted seedlings or at germination, as
343 responses to flooding has previously been related to ontogeny (Baumberger et al., 2012, Lum and
344 Barton, 2020).

345 There was substantial intra-specific variability in all traits of all species. This variation was
346 independent of the environment (i.e. flooding and composition treatments) and at the level of
347 individual, and so is likely to be driven by the genetic diversity of individuals, particularly since we

348 collected seed from a number of geographically distinct locations. High levels of intraspecific trait
349 variation, such as we observed here, can affect plant responses to flooding (White et al., 2014) and
350 this variability in responses can confer resilience of ecosystem functions to future environmental
351 changes, such as increases in flooding with sea level-rise (Oliver et al., 2015).

352 Although genotypic variation is likely to contribute to the observed intraspecific trait
353 variation (Hughes et al., 2008), treatment effects will largely reflect plasticity within a genotype as
354 plants were randomly allocated to treatments from diverse seed sources. The low mortality observed
355 in this experiment indicates that the effect of flooding and composition treatments were not strong
356 enough to pose a filter restricting which genotypes could survive. However, over longer time-scales
357 flooding could alter the relative fitness of different genotypes, leading to a non-random distribution of
358 genotypes across flooding gradients. This could mean that stronger effects of flooding on traits than
359 found here would be observed by looking at spatial variation in traits across inundation gradients, as
360 that would also capture intraspecific trait variation due to turnover in genotypes.

361 Our results indicate that species composition frequently modified the response of plants to
362 flooding, including reversing effects observed in monoculture. This supports previous observations
363 that interspecific interactions can modify how aboveground growth of saltmarsh plants varies with
364 environmental conditions (Huckle et al., 2000, Wang et al., 2006). Composition also affected plant
365 traits independently of flooding treatment, with the greatest number of composition effects on traits
366 observed for *Triglochin*. Compositional effects could be through competitive interactions. These
367 interactions can alter the ratio of aboveground and belowground biomass, with greater belowground
368 allocation if competition is primarily for soil resources (Tilman and Wedin, 1991), and greater
369 aboveground allocation if competition is primarily for light (DeMalach et al., 2016). There is some
370 evidence from saltmarshes that competition can increase biomass allocation to root mass (Dormann et
371 al., 2000, Redelstein et al., 2018), but other studies find composition to mostly affect aboveground
372 rather than belowground biomass (Huckle et al., 2002). Our results are consistent with the latter, with
373 aboveground biomass deviating from expected monoculture values for nine species-treatment pairs,
374 compared to three for belowground biomass. Some changes in plant traits were consistent with
375 competition for light. For example, *Plantago* and *Aster* both had lower than expected aboveground

376 biomass when grown together in the flooded treatment, meaning that interspecific competition was
377 stronger than intraspecific competition. In this treatment both species had higher specific leaf area,
378 which is likely to be due to plants investing in wide but thin leaves to maximise light gathering ability.

379 Species interactions between our study species, assessed by looking at over and underyielding
380 by different species in different treatments, do not follow a linear hierarchy of competitive
381 dominance. *Aster* reduced *Triglochin* biomass, *Aster* and *Plantago* had a negative effect on each
382 other's biomass, while *Plantago* and *Triglochin* had higher than expected biomass, significantly so for
383 *Plantago*. Intransitive competition loops, where competitive hierarchies are non-linear, have
384 previously been documented in saltmarsh plant communities and are considered to be important in
385 promoting species coexistence (Ulrich et al., 2018). Our results show that competition hierarchies can
386 also be broken by positive species interactions. Positive interactions identified by overyielding could
387 arise from niche differences reducing competition for resources (Adler et al., 2007) or through
388 facilitation, where a species makes the environment more favourable for another (Bertness and
389 Shumway, 1993). The former explanation is perhaps unlikely to explain our results as the positively
390 interacting species (*Plantago* and *Triglochin*) had more similar aboveground growth forms (which
391 could influence light interception) to each other than they did to *Aster*, although it is possible that their
392 narrow leaves could pack more densely to intercept light. Although some species interactions were
393 independent of the flooding treatment (the negative effect of *Aster* on *Triglochin*), other species
394 interactions differed between the flooded and unflooded treatment. The Stress Gradient Hypothesis
395 predicts that these positive species interactions will be more frequent when environmental conditions
396 are more stressful (Bertness and Callaway, 1994), as in the flooded treatment. Consistent with this
397 expectation, the positive interaction between *Plantago* and *Triglochin* was only statistically
398 significant in the flooded treatment. Flooding also affected competition, as the competitive interaction
399 between *Plantago* and *Aster* was only evident in the flooded treatment. This is not expected to change
400 with flooding under the Stress Gradient Hypothesis (Conti et al., 2017), but could instead result from
401 environmental stress reducing the ability of plants to tolerate inter-specific competition (Hart and
402 Marshall, 2013). Interestingly, the two negatively interacting species pairs (*Plantago-Aster* and
403 *Triglochin-Aster*) frequently co-occur within the same quadrat (Sullivan et al., 2018), so have some

404 ability to coexist. It may be that interactions are not sufficiently asymmetrical for one species to be
405 competitively excluded (Chesson, 2000), or that underyielding reflects changes in plant growth form
406 that does not necessarily alter plant fitness.

407 As a result of the opposing nature of interactions between pairs of species, or potentially due
408 to new interactions that only emerge when all three species are grown together, total biomass in the
409 three species treatment did not differ significantly from expected values. This does not mean that
410 diversity has no effect on biomass in field conditions as our species composition treatments do not
411 cover the higher diversity levels found on saltmarshes; in > 1000 0.5 by 0.5 m quadrats in UK
412 saltmarshes surveyed by Mossman et al. (2012) there was a median species richness of three, but a
413 maximum species richness of ten. However, by being able to investigate all possible species pairings
414 in a well replicated experiment, we found an important role of species composition in influencing
415 total and aboveground biomass. This is consistent with an earlier study on saltmarshes in the USA,
416 which found that diversity effects were primarily due to the presence of particular species rather than
417 niche complementarity (Sullivan et al., 2007). While we found that species composition primarily
418 affected aboveground biomass rather than belowground biomass, Ford et al. (2016) report that species
419 richness increases sediment stability to erosion. This difference may be because some of the effect of
420 diversity is only seen at higher species richness levels than used in our experiment, although this is
421 unlikely as some effect of diversity is evident in Ford et al. (2016) even with three species.

422 Alternatively, it may be that the complementary nature of different species' root architecture is more
423 important for influencing sediment stability than root biomass alone. The difference in over and
424 underyielding of aboveground biomass due to species composition, and effect of species composition
425 on traits such as plant height, means that composition potentially influences how saltmarsh vegetation
426 attenuates wave energy (Rupprecht et al., 2017). This potential function can itself be influenced by
427 flooding, which we find to alter these species interactions.

428 The variation in functional trait responses to flooding between species and species
429 composition treatments found by our experiment highlights the challenge of predicting how plant
430 communities will respond to chronic flooding and the consequent effects on ecosystem service
431 provision by coastal plants. These differences in responses, combined with trait variability within

432 species, meant that flooding did not shift any trait in a consistent direction across all species and
433 composition treatments. However, it is also this diversity of responses that creates the potential for
434 ecosystem functioning and service provision to be resilient to future increases in coastal flooding
435 (Mori et al., 2013), evidenced by the limited effect of flooding on pot-level metrics of biomass and
436 vegetation density (Fig. 2). The community-level effects of flooding can also be buffered by shifts in
437 species composition towards more flood tolerant species, which can occur even after acute flooding
438 events (Hanley et al., 2017). Such changes did not occur within our experiment, as mortality was low,
439 but are expected to be increasingly important with increasing severity and longer time-scales of
440 environmental change (Smith et al., 2009).

441

442 **CONCLUSION**

443 We find that flooding and species composition interact to affect plant traits, with species composition
444 sometimes altering the direction of flooding effects from that observed in monoculture. Chronic
445 flooding also modified the positive and negative interactions between species pairs, with both positive
446 and negative species interactions more evident in the flooded treatment. Our results suggest that
447 species identity is an important component of community responses to flooding, and will likely
448 mediate effects on ecosystem functioning. Collectively, our results highlight the complexity of
449 predicting how saltmarsh plant functional traits, and hence ecosystem functioning and service
450 provision, will change with the increase in flooding associated with sea level rise. However, it is also
451 this diversity of responses that creates the potential for saltmarshes to be resilient to these future
452 increases in coastal flooding.

453

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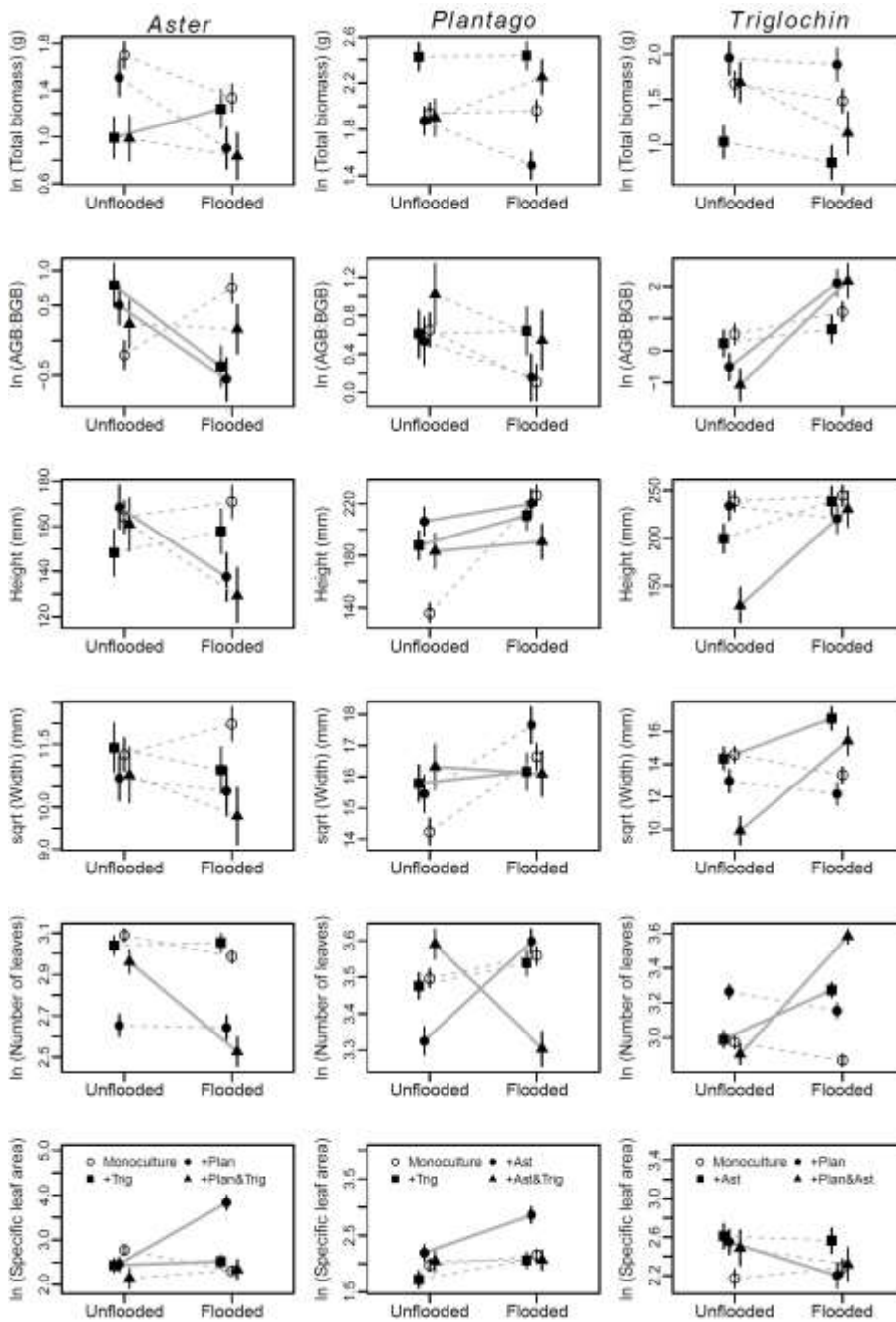
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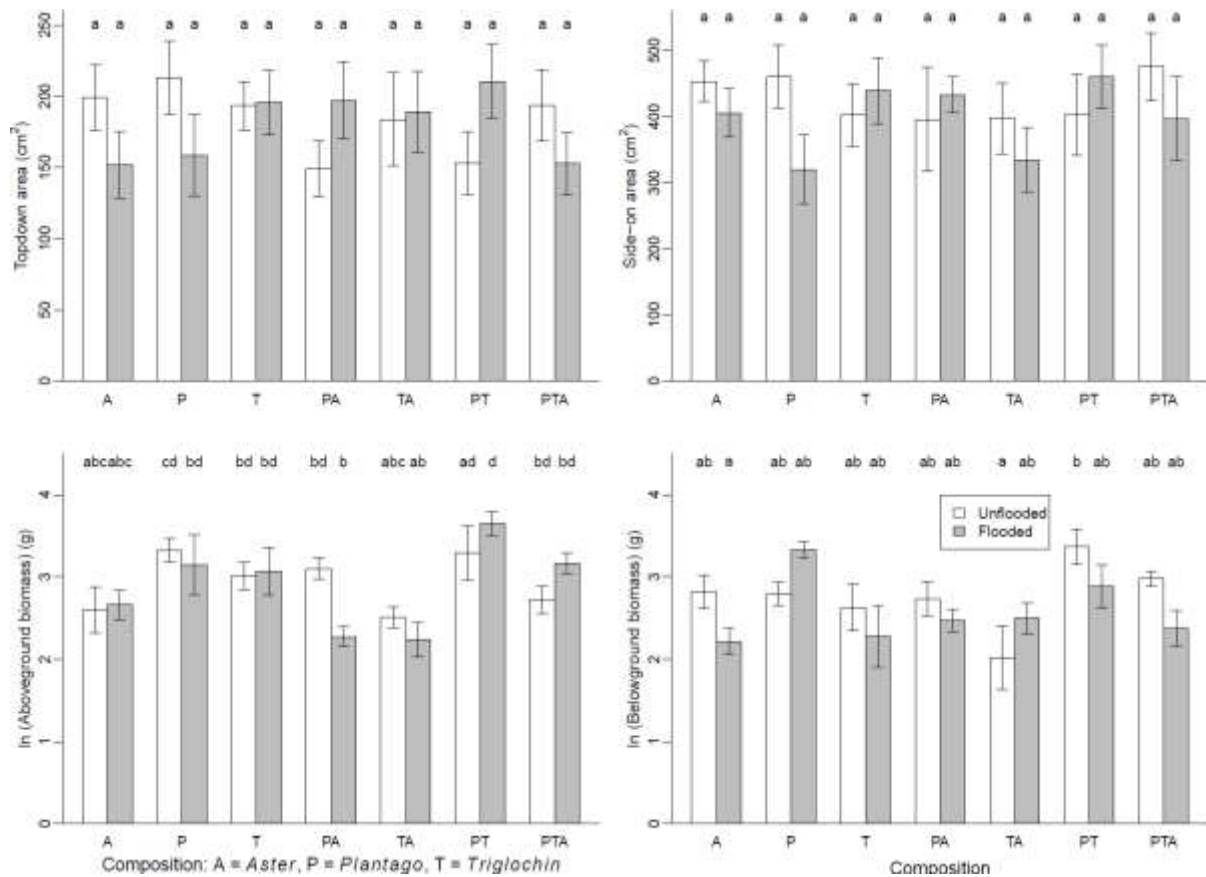
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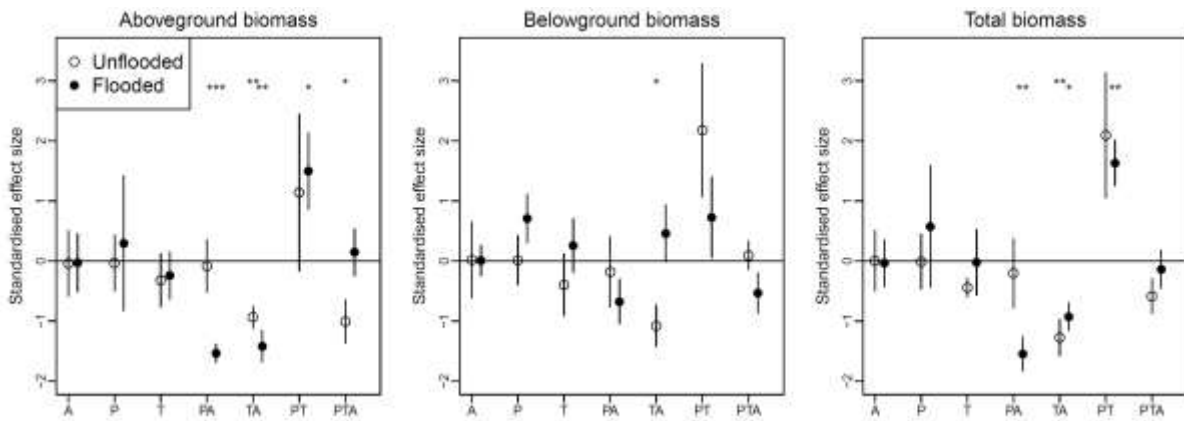
632 **Figure 1.** Effect of flooding and species composition on the traits of individual plants. Symbols show
 633 estimated means \pm SE for each flooding-composition category from linear or generalised linear
 634 models relating values of each trait to flooding treatment, species composition and their interaction.
 635 Statistically significant interactions, indicating that the effect of flooding differs from that in the
 636 monoculture treatment, are shown with solid grey lines.



637

638 **Figure 2.** Effect of species composition and flooding on pot-level metrics. Bars show estimated
 639 means \pm SE from linear models of each variable as a function of flooding treatment, composition and
 640 their interaction. Flooding treatment – composition combinations with different letters are statistically
 641 significantly different from each other ($P < 0.05$) – note that flooding, composition and their
 642 interactions can have statistically significant effects even if treatment – composition combinations do
 643 not differ significantly from other combinations, as they are different contrasts to the same linear
 644 model.

645



646

647 **Figure 3.** Effect of composition and flooding treatments on aboveground, belowground and total
 648 biomass. Biomass values are expressed as standardised effect sizes relative to expected values based
 649 on each species performance in monoculture. Values greater than zero indicate that observed biomass
 650 is greater than expected (overyielding), while negative values indicate that observed values are less
 651 than expected (underyielding). Points show mean values \pm SE for each treatment combination.
 652 Asterisks indicate significant differences from zero assessed using one-sample t tests, *** $P < 0.001$,
 653 ** $P < 0.01$, * $P < 0.05$). Species composition treatments are labelled as in Fig. 2.

654 **SUPPORTING INFORMATION**

655 Figure S1. Elevation range of study species.

656 Figure S2. Intraspecific variation in traits.

657 Figure S3. Over and underyielding separated by species.

658 Table S1a and b. Sample sizes for individual and pot level analyses.

659 Table S2. Variation (median and confidence intervals) in traits in the unflooded monocultures (UF
660 Mono) and across all individuals in all treatments (All).

661 Table S3. Coefficients of linear models of individual plant traits.

662 Table S4. Coefficients on linear models of pot-level metrics

663

664 Ryan S. Edge, Martin J. P. Sullivan, Scott M. Pedley, Hannah L. Mossman

665 **Species interactions modulate the response of saltmarsh plants to flooding:**

666

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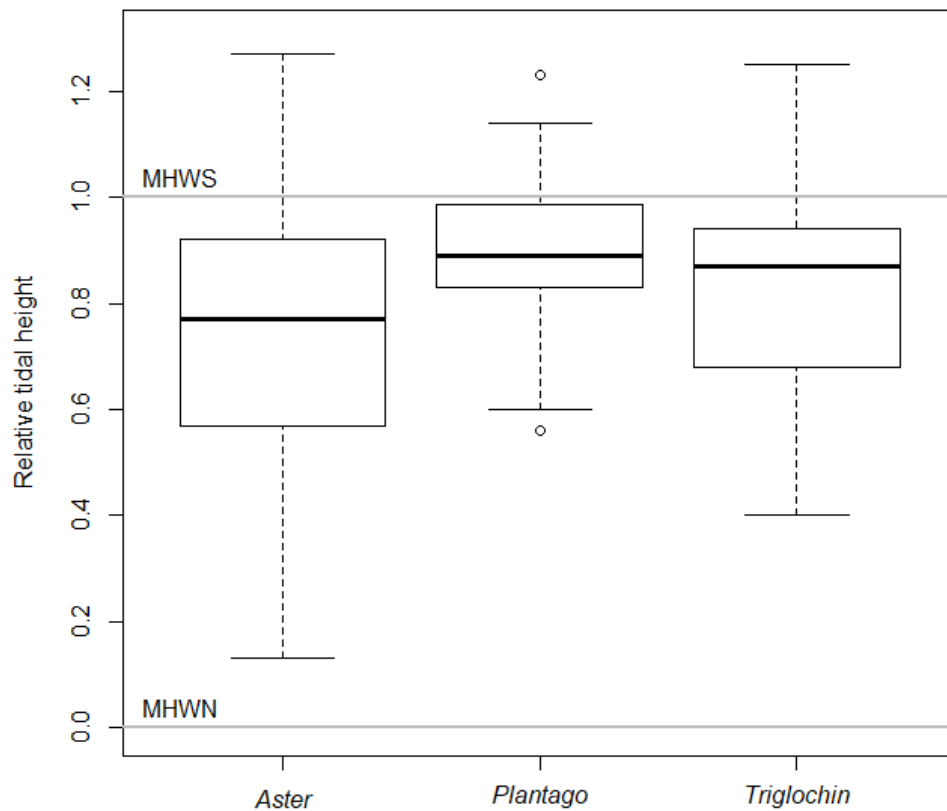
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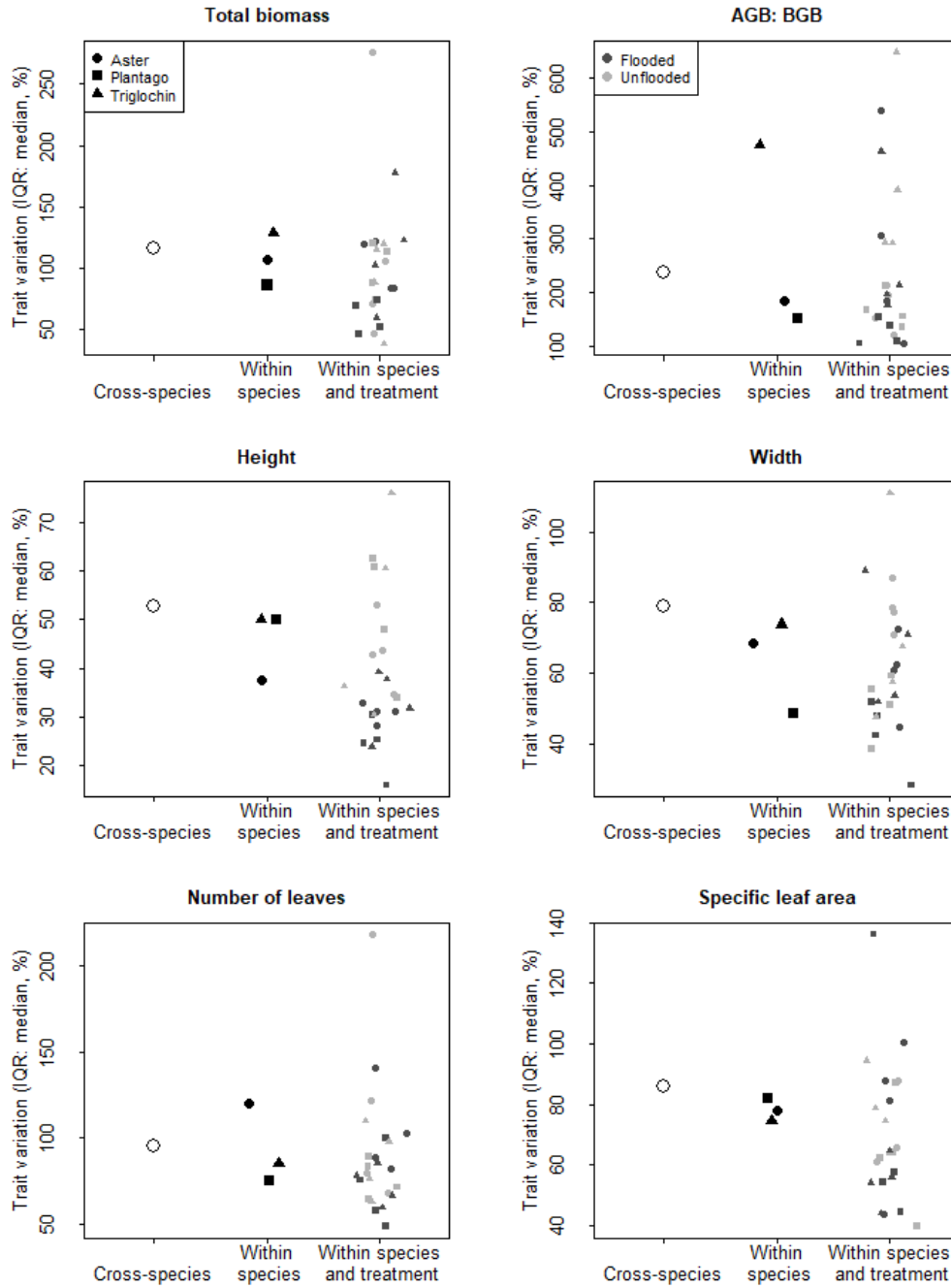
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676



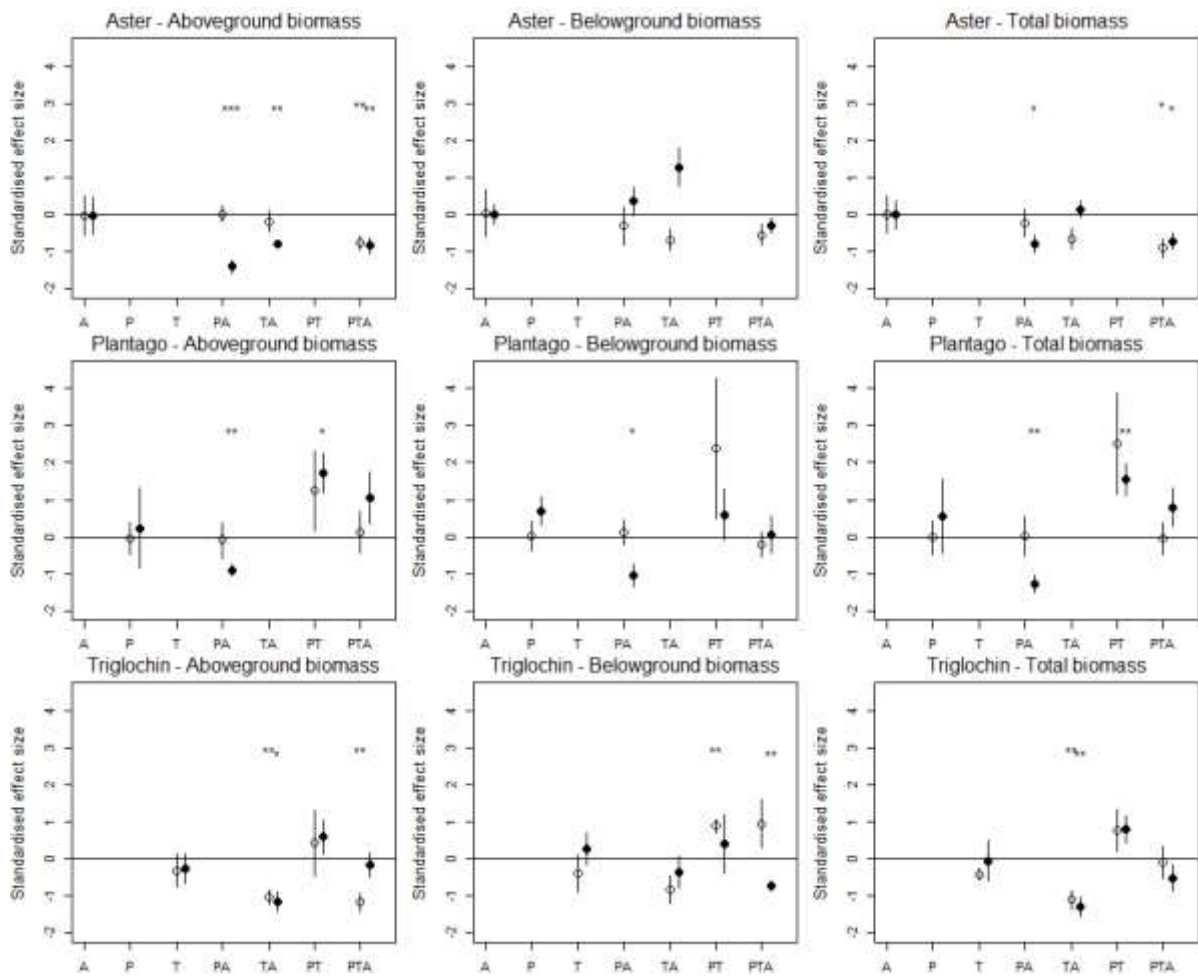
677

678 **Figure S1.** Elevation range of study species. Data are from (Sullivan et al., 2018, Sullivan et al.,
 679 2017). Elevations are expressed as relative tidal height, which are standardised relative to mean high
 680 water spring (MHWS) and mean high water neap (MHWN) to allow comparison amongst sites with
 681 different tidal ranges.



682

683 **Figure S2.** Inter and intra-specific variability in the suite of traits presented in Figure 1. For each trait,
 684 a non-parametric analogue of the coefficient of variation, interquartile range/ median \times 100, was
 685 calculated at three levels (1) cross species, pooling data across species and treatments, (2) within
 686 species, pooling data across treatments, and (3) within each species and treatment combination.



687

688 **Figure S3.** As Fig. 3, but calculating biomass standardised effect sizes for each species separately.

689 Values greater than zero indicate that the species has higher biomass in the treatment than expected

690 based on its performance in monoculture, while negative values indicate that it has lower biomass

691 than expected.

692 **Table S1a.** Sample size for analyses at the individual level. Maximum number of individuals is 224.

	Height	Width	Number of leaves	Total biomass	AGB:BGB	Specific leaf area
<i>Aster</i> ¹	207	207	217	203	202	186
<i>Plantago</i> ²	222	222	222	214	214	197
<i>Triglochin</i>	224	224	219	211	208	196

693 ¹ Not including the 17 individuals that died; ² Not including the 2 individuals that died.

694 **Table S1b.** Sample size for analyses at the pot level per treatment. Maximum number of pots per
695 treatment-composition is eight.

	Composition						
	A	T	P	PA	TA	PT	PTA
Unflooded	8	4	8	8	6	7	7
Flooded	8	7	4	7	5	8	7

696

697 **Table S2.** Variation (median and confidence intervals) in traits in the unflooded monocultures (UF
698 Mono) and across all individuals in all treatments (All)

		<i>Aster</i>		<i>Plantago</i>		<i>Triglochin</i>	
		UF Mono	All	UF Mono	All	UF Mono	All
Height (mm)	25%	138	130	95	140	148	170
	Median	170	170	120	180	240	220
	75%	196	215	170	230	330	270
Width (mm)	25%	88	110	153	100	180	175
	Median	120	175	190	150	210	230
	75%	173	270	265	220	280	310
Number of leaves	25%	12	13	21	11	13	16
	Median	17	23	32	19	19	25
	75%	31	34	43	29	25	38
Total biomass (mg)	25%	3.8956	2.6651	4.9200	2.3157	3.3599	3.9775
	Median	5.3420	5.3618	8.0370	4.5735	5.7979	6.5738
	75%	7.6753	8.4739	10.8025	7.5285	8.4576	10.9913
AGB:BGB ratio	25%	0.3601	0.6032	0.7927	0.4427	0.5787	0.7425
	Median	0.8411	1.5049	2.0640	1.3080	1.2121	1.5899
	75%	2.0028	3.4261	3.9904	5.3719	5.3246	4.1715
Specific leaf area (mm ² mg ⁻¹)	25%	10.99	6.27	5.33	7.98	5.67	6.58
	Median	14.82	10.02	7.68	11.70	7.67	8.71
	75%	23.99	15.42	10.11	17.97	11.71	12.89

699

700 **Table S3.** Coefficients of (generalised) linear models relating traits of individual plants to flooding
701 treatment, composition treatment and their interaction. Separate models were fitted for each species-
702 trait combination.

Species	Trait	Term	Estimate	SE	t*	P
Aster	Total biomass	(Intercept)	1.702	0.115	14.76	<0.001
Aster	Total biomass	Flooded	-0.368	0.165	-2.23	0.027
Aster	Total biomass	Composition - PA	-0.195	0.196	-1	0.321
Aster	Total biomass	Composition - PTA	-0.716	0.225	-3.18	0.002
Aster	Total biomass	Composition - TA	-0.709	0.212	-3.35	0.001
Aster	Total biomass	Flooded:Composition - PA	-0.237	0.289	-0.82	0.415
Aster	Total biomass	Flooded:Composition - PTA	0.217	0.323	0.67	0.503
Aster	Total biomass	Flooded:Composition - TA	0.615	0.293	2.1	0.037
Plantago	Total biomass	(Intercept)	1.938	0.087	22.3	<0.001
Plantago	Total biomass	Flooded	0.023	0.127	0.18	0.856
Plantago	Total biomass	Composition - PA	-0.065	0.149	-0.43	0.665
Plantago	Total biomass	Composition - PT	0.489	0.149	3.27	0.001
Plantago	Total biomass	Composition - PTA	-0.035	0.181	-0.19	0.847
Plantago	Total biomass	Flooded:Composition - PA	-0.406	0.214	-1.9	0.059
Plantago	Total biomass	Flooded:Composition - PT	-0.014	0.214	-0.07	0.948
Plantago	Total biomass	Flooded:Composition - PTA	0.325	0.252	1.29	0.199
Triglochin	Total biomass	(Intercept)	1.672	0.139	12.06	<0.001
Triglochin	Total biomass	Flooded	-0.187	0.19	-0.99	0.325
Triglochin	Total biomass	Composition - PT	0.287	0.231	1.24	0.217
Triglochin	Total biomass	Composition - PTA	0.018	0.262	0.07	0.945
Triglochin	Total biomass	Composition - TA	-0.645	0.228	-2.82	0.005
Triglochin	Total biomass	Flooded:Composition - PT	0.115	0.321	0.36	0.721
Triglochin	Total biomass	Flooded:Composition - PTA	-0.376	0.376	-1	0.319
Triglochin	Total biomass	Flooded:Composition - TA	-0.041	0.324	-0.13	0.9
Aster	AGB: BGB	(Intercept)	-0.207	0.202	-1.03	0.306
Aster	AGB: BGB	Flooded	0.956	0.289	3.31	0.001
Aster	AGB: BGB	Composition - PA	0.708	0.343	2.07	0.04
Aster	AGB: BGB	Composition - PTA	0.439	0.395	1.11	0.267
Aster	AGB: BGB	Composition - TA	0.994	0.371	2.68	0.008
Aster	AGB: BGB	Flooded:Composition - PA	-2.015	0.507	-3.98	<0.001
Aster	AGB: BGB	Flooded:Composition - PTA	-1.028	0.566	-1.81	0.071
Aster	AGB: BGB	Flooded:Composition - TA	-2.117	0.517	-4.09	<0.001
Plantago	AGB: BGB	(Intercept)	0.65	0.176	3.69	<0.001
Plantago	AGB: BGB	Flooded	-0.546	0.258	-2.12	0.036
Plantago	AGB: BGB	Composition - PA	-0.118	0.303	-0.39	0.698
Plantago	AGB: BGB	Composition - PT	-0.04	0.303	-0.13	0.896
Plantago	AGB: BGB	Composition - PTA	0.368	0.368	1	0.318
Plantago	AGB: BGB	Flooded:Composition - PA	0.171	0.434	0.39	0.693
Plantago	AGB: BGB	Flooded:Composition - PT	0.577	0.434	1.33	0.185
Plantago	AGB: BGB	Flooded:Composition - PTA	0.073	0.512	0.14	0.887
Triglochin	AGB: BGB	(Intercept)	0.507	0.313	1.62	0.107
Triglochin	AGB: BGB	Flooded	0.697	0.433	1.61	0.109
Triglochin	AGB: BGB	Composition - PT	-1.017	0.523	-1.95	0.053
Triglochin	AGB: BGB	Composition - PTA	-1.58	0.591	-2.67	0.008

Triglochin	AGB: BGB	Composition - TA	-0.278	0.516	-0.54	0.591
Triglochin	AGB: BGB	Flooded:Composition - PT	1.917	0.733	2.61	0.01
Triglochin	AGB: BGB	Flooded:Composition - PTA	2.545	0.852	2.99	0.003
Triglochin	AGB: BGB	Flooded:Composition - TA	-0.256	0.734	-0.35	0.728
Aster	Height	(Intercept)	164.2	7.1	22.99	<0.001
Aster	Height	Flooded	6.6	10.2	0.65	0.516
Aster	Height	Composition - PA	4.3	12	0.36	0.719
Aster	Height	Composition - PTA	-3.3	13.8	-0.24	0.81
Aster	Height	Composition - TA	-15.9	12.6	-1.26	0.208
Aster	Height	Flooded:Composition - PA	-37.7	17.6	-2.14	0.033
Aster	Height	Flooded:Composition - PTA	-38.2	19.8	-1.92	0.056
Aster	Height	Flooded:Composition - TA	2.9	17.5	0.16	0.87
Plantago	Height	(Intercept)	135.6	7.8	17.38	<0.001
Plantago	Height	Flooded	90.9	11	8.23	<0.001
Plantago	Height	Composition - PA	70.8	13.4	5.28	<0.001
Plantago	Height	Composition - PT	52.3	13.4	3.9	<0.001
Plantago	Height	Composition - PTA	47.8	15.5	3.09	0.002
Plantago	Height	Flooded:Composition - PA	-77.1	19	-4.06	<0.001
Plantago	Height	Flooded:Composition - PT	-67.9	19	-3.58	<0.001
Plantago	Height	Flooded:Composition - PTA	-83.5	21.9	-3.81	<0.001
Triglochin	Height	(Intercept)	239	10.7	22.24	<0.001
Triglochin	Height	Flooded	5.7	15.2	0.38	0.706
Triglochin	Height	Composition - PT	-5	18.6	-0.27	0.788
Triglochin	Height	Composition - PTA	-109.4	21.5	-5.09	<0.001
Triglochin	Height	Composition - TA	-39.4	18.6	-2.12	0.035
Triglochin	Height	Flooded:Composition - PT	-19.5	26.3	-0.74	0.46
Triglochin	Height	Flooded:Composition - PTA	95.2	30.4	3.13	0.002
Triglochin	Height	Flooded:Composition - TA	33.6	26.3	1.28	0.202
Aster	Width	(Intercept)	11.3	0.397	28.36	<0.001
Aster	Width	Flooded	0.7	0.565	1.28	0.2
Aster	Width	Composition - PA	-0.6	0.668	-0.84	0.4
Aster	Width	Composition - PTA	-0.5	0.769	-0.64	0.522
Aster	Width	Composition - TA	0.2	0.699	0.23	0.819
Aster	Width	Flooded:Composition - PA	-1	0.977	-1.06	0.293
Aster	Width	Flooded:Composition - PTA	-1.7	1.102	-1.54	0.124
Aster	Width	Flooded:Composition - TA	-1.3	0.975	-1.29	0.198
Plantago	Width	(Intercept)	14.2	0.42	33.87	<0.001
Plantago	Width	Flooded	2.4	0.595	4.04	<0.001
Plantago	Width	Composition - PA	1.2	0.723	1.67	0.095
Plantago	Width	Composition - PT	1.6	0.723	2.15	0.033
Plantago	Width	Composition - PTA	2.1	0.834	2.49	0.013
Plantago	Width	Flooded:Composition - PA	-0.2	1.023	-0.2	0.841
Plantago	Width	Flooded:Composition - PT	-2	1.023	-1.99	0.048
Plantago	Width	Flooded:Composition - PTA	-2.6	1.18	-2.22	0.027
Triglochin	Width	(Intercept)	14.6	0.496	29.43	<0.001
Triglochin	Width	Flooded	-1.2	0.701	-1.78	0.076
Triglochin	Width	Composition - PT	-1.6	0.858	-1.9	0.059
Triglochin	Width	Composition - PTA	-4.7	0.991	-4.72	<0.001
Triglochin	Width	Composition - TA	-0.2	0.858	-0.27	0.786

Triglochin	Width	Flooded:Composition - PT	0.5	1.214	0.39	0.698
Triglochin	Width	Flooded:Composition - PTA	6.8	1.402	4.83	<0.001
Triglochin	Width	Flooded:Composition - TA	3.7	1.214	3.05	0.003
Aster	Number of leaves (Intercept)		3.089	0.031	100.29	<0.001
Aster	Number of leaves Flooded		-0.103	0.045	-2.29	0.022
Aster	Number of leaves Composition - PA		-0.435	0.062	-6.99	<0.001
Aster	Number of leaves Composition - PTA		-0.128	0.065	-1.98	0.047
Aster	Number of leaves Composition - TA		-0.049	0.055	-0.89	0.375
Aster	Number of leaves Flooded:Composition - PA		0.092	0.092	1	0.32
Aster	Number of leaves Flooded:Composition - PTA		-0.332	0.101	-3.28	0.001
Aster	Number of leaves Flooded:Composition - TA		0.115	0.078	1.47	0.141
Plantago	Number of leaves (Intercept)		3.497	0.025	139.16	<0.001
Plantago	Number of leaves Flooded		0.062	0.035	1.78	0.076
Plantago	Number of leaves Composition - PA		-0.172	0.046	-3.72	<0.001
Plantago	Number of leaves Composition - PT		-0.02	0.044	-0.47	0.641
Plantago	Number of leaves Composition - PTA		0.094	0.049	1.94	0.053
Plantago	Number of leaves Flooded:Composition - PA		0.211	0.062	3.39	0.001
Plantago	Number of leaves Flooded:Composition - PT		0	0.061	0	0.999
Plantago	Number of leaves Flooded:Composition - PTA		-0.35	0.073	-4.83	<0.001
Triglochin	Number of leaves (Intercept)		2.971	0.033	89.97	<0.001
Triglochin	Number of leaves Flooded		-0.103	0.048	-2.16	0.031
Triglochin	Number of leaves Composition - PT		0.292	0.052	5.63	<0.001
Triglochin	Number of leaves Composition - PTA		-0.067	0.067	-0.99	0.32
Triglochin	Number of leaves Composition - TA		0.018	0.058	0.31	0.758
Triglochin	Number of leaves Flooded:Composition - PT		-0.005	0.075	-0.06	0.949
Triglochin	Number of leaves Flooded:Composition - PTA		0.782	0.086	9.07	<0.001
Triglochin	Number of leaves Flooded:Composition - TA		0.388	0.079	4.89	<0.001
Aster	Specific leaf area (Intercept)		9.678	0.108	89.35	<0.001
Aster	Specific leaf area Flooded		-0.462	0.151	-3.05	0.003
Aster	Specific leaf area Composition - PA		-0.319	0.192	-1.66	0.099
Aster	Specific leaf area Composition - PTA		-0.635	0.245	-2.6	0.01
Aster	Specific leaf area Composition - TA		-0.341	0.186	-1.83	0.069
Aster	Specific leaf area Flooded:Composition - PA		1.843	0.271	6.8	<0.001
Aster	Specific leaf area Flooded:Composition - PTA		0.661	0.345	1.91	0.057
Aster	Specific leaf area Flooded:Composition - TA		0.548	0.258	2.12	0.035
Plantago	Specific leaf area (Intercept)		8.882	0.105	84.22	<0.001
Plantago	Specific leaf area Flooded		0.172	0.148	1.16	0.249
Plantago	Specific leaf area Composition - PA		0.216	0.176	1.23	0.221
Plantago	Specific leaf area Composition - PT		-0.255	0.187	-1.36	0.176
Plantago	Specific leaf area Composition - PTA		0.069	0.215	0.32	0.749
Plantago	Specific leaf area Flooded:Composition - PA		0.499	0.25	1.99	0.048
Plantago	Specific leaf area Flooded:Composition - PT		0.168	0.258	0.65	0.516
Plantago	Specific leaf area Flooded:Composition - PTA		-0.152	0.296	-0.51	0.608
Triglochin	Specific leaf area (Intercept)		9.077	0.097	93.39	<0.001
Triglochin	Specific leaf area Flooded		0.113	0.131	0.87	0.387
Triglochin	Specific leaf area Composition - PT		0.38	0.162	2.35	0.02
Triglochin	Specific leaf area Composition - PTA		0.317	0.207	1.53	0.127
Triglochin	Specific leaf area Composition - TA		0.44	0.162	2.72	0.007
Triglochin	Specific leaf area Flooded:Composition - PT		-0.462	0.227	-2.04	0.043

Triglochin Specific leaf area Flooded:Composition - PTA	-0.284	0.285	-1	0.321
Triglochin Specific leaf area Flooded:Composition - TA	-0.159	0.227	-0.7	0.485

703 * Z score for number of leaves.

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705 **Table S4.** Coefficients of linear models relating pot-level metrics to flooding treatment, species
706 composition and their interaction.

Term		Estimate	SE	t	P
Top-down area					
Intercept (Unflooded, A)		199.4	23.4	8.52	<0.001
Treatment	Flooded	-47.7	33.1	-1.44	0.153
Composition	PA	-50.3	32.0	-1.57	0.12
	P	13.9	32.0	0.44	0.665
	PT	-38.0	32.0	-1.19	0.239
	PTA	-4.9	33.1	-0.15	0.883
	TA	-6.7	34.4	-0.20	0.846
	T	-34.8	33.1	-1.05	0.296
Treatment (Flooded): Composition	PA	99.7	46.1	2.16	0.033
	P	-20.3	45.3	-0.45	0.655
	PT	96.8	45.3	2.14	0.035
	PTA	14.2	46.1	0.31	0.759
	TA	50.5	47.8	1.06	0.293
	T	78.7	47.8	1.65	0.103
Side-on area					
Intercept (Unflooded, A)		453.5	44.9	10.09	<0.001
Treatment	Flooded	-48.3	63.5	-0.76	0.449
Composition	PA	-57.5	72.4	-0.79	0.429
	P	6.9	68.6	0.10	0.92
	PT	-52.6	63.5	-0.83	0.41
	PTA	-13.2	63.5	-0.21	0.836
	TA	-50.8	65.8	-0.77	0.442
	T	-48.0	63.5	-0.76	0.452
Treatment (Flooded): Composition	PA	80.6	96.4	0.84	0.405
	P	-89.6	99.8	-0.90	0.372
	PT	107.8	91.4	1.18	0.242
	PTA	4.0	89.9	0.05	0.964
	TA	72.3	91.4	0.79	0.431
	T	61.0	91.4	0.67	0.506
Aboveground biomass					
Intercept (Unflooded, A)		2.6	0.189	13.74	<0.001
Treatment	Flooded	0.061	0.268	0.23	0.82
Composition	PA	0.503	0.268	1.88	0.064
	P	0.725	0.268	2.71	0.008
	PT	0.689	0.277	2.49	0.015
	PTA	0.122	0.277	0.44	0.662
	TA	-0.091	0.289	-0.32	0.753
	T	0.414	0.328	1.26	0.21
Treatment (Flooded): Composition	PA	-0.893	0.385	-2.32	0.023
	P	-0.24	0.423	-0.57	0.572
	PT	0.298	0.385	0.78	0.441
	PTA	0.385	0.392	0.98	0.328

	TA	-0.333	0.42	-0.79	0.43
	T	-0.007	0.429	-0.02	0.988
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Belowground biomass					
	Intercept (Unflooded, A)	2.82	0.211	13.36	<0.001
Treatment	Flooded	-0.604	0.298	-2.03	0.046
Composition	PA	-0.083	0.298	-0.28	0.781
	P	-0.025	0.298	-0.08	0.934
	PT	0.547	0.309	1.77	0.081
	PTA	0.16	0.309	0.52	0.607
	TA	-0.8	0.322	-2.48	0.015
	T	-0.189	0.366	-0.52	0.606
	Treatment (Flooded): Composition	PA	0.34	0.43	0.79
	P	1.137	0.472	2.41	0.018
	PT	0.126	0.43	0.29	0.77
	PTA	-0.004	0.437	-0.01	0.994
	TA	1.082	0.469	2.31	0.024
	T	0.254	0.479	0.53	0.597
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708 **Additional references**

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