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Species interactions modulate the response of saltmarsh plants to flooding

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Running head: Trait responses to chronic flooding and composition

ABSTRACT

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

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

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

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

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

INTRODUCTION

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

The effect of plants on ecosystem service delivery is influenced by their traits (Díaz et al., 2013), which vary both between species and within species. Intraspecific trait-variation can be substantial, especially across environmental stress gradients, and is due to both turnover in genotypes across gradients and phenotypic plasticity within a single genotype (Eller and Brix, 2012, Richards et al., 2010). Environmental changes can therefore affect ecosystem functioning by changing the distribution of traits within a species as well as by changing species composition, and these intra-specific changes are likely to be especially important in species poor habitats such as saltmarshes. Phenotypic plasticity can also be exhibited in response to competition (Venterink and Güsewell, 2010, Weiner et al., 1990). Plastic changes in response to competition include changes to root architecture to avoid competitors and increased height to overtop competitors (Callaway et al., 2003). These changes to plant traits could influence ecosystem function. For example, root biomass has been shown to positively influence sediment stability in saltmarshes (Ford et al., 2016), while root architecture (density, length, depth) influences soil carbon cycling (De Deyn et al., 2008). Plant height and shoot stiffness can determine the effectives of wave attenuation and hence influence coastal protection (Möller et al., 2014, Bouma et al., 2005). Species interactions can be positive as well as negative (Bertness and Shumway, 1993), and these facilitative interactions may cause phenotypic plasticity (Callaway et al., 2003), but the effects of this are poorly understood.

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

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

In this study we investigated how flooding, and resultant waterlogging, which are the dominant controls on the distribution of saltmarsh plants (Davy et al., 2011), effects saltmarsh plant functional traits. We exposed plants to a five month long flooding treatment, simulating chronic changes in a plant's environment as may occur under sea-level rise. As well as examining the effect of flooding alone, we also test whether plant species composition and diversity affect responses to flooding. We measured a suite of functional traits potentially related to ecosystem functioning and service provision. These are plant height and width (the latter a component of overall vegetation density, and both have been linked to wave attenuation potential (Anderson and Smith, 2014, Rupprecht et al., 2017)), number of leaves and specific leaf area (linked to resource acquisition (Cornelissen et al., 2003)), aboveground biomass (a proxy for productivity as measurements were over one growing season and also related to wave attenuation potential (Paul et al., 2016)) and belowground biomass (linked to productivity and to sediment stability (Gyssels et al., 2005, De Battisti et al., 2019)). We also measured community level metrics: above and belowground biomass, canopy cover and side-on density (both related to habitat provision for invertebrates (Ford et al., 2017), the latter also related to wave attenuation (Möller, 2006)). Using this experiment, we examined (1) the role of flooding and species composition in affecting plant functional traits, (2) whether neighbourhood species composition modified responses to flooding and (3) the role of biodiversity and species composition in driving community-level responses to flooding.

METHODS

Study species

We investigated responses of three study species, sea aster Aster tripolium, sea plantain Plantago maritima and sea arrowgrass Triglochin maritima (hereafter Aster, Plantago, Triglochin), to experimental flooding. Aster is a pauciennial forb; Plantago and Triglochin are perennial forbs. Study species were selected as they overlap in their niches, and so co-occur, but differ in niche centroid, both where niche is defined by relating occurrence in the natural saltmarshes to elevation alone (Fig. S1) and in relation to elevation and redox potential (Sullivan et al., 2018). Aster grows across a wide range of elevations and flooding frequencies (Gray, 1971). Plantago and Triglochin have narrower niches in the higher elevations of Aster's niche (Gray, 1971; Fig. S1). Triglochin is more tolerant of waterlogged soils than Plantago (Sullivan et al., 2018) and Triglochin is commonly found in waterlogged areas at the edges of pannes (Fogel et al., 2004). Previous studies have indicated that there may be competitive interactions between these species, but it is not clear which species are competitively dominant and in what circumstances (Davy and Bishop, 1991).

Experimental design

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

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

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

Pots in the flooded treatment were placed in 10 cm deep trays that were filled to a depth of 7 cm with saline water (at 50% seawater strength, 17.5 g l^{-1} of Instant Ocean®, Blacksburg, VA, USA) for the duration of the experiment; water was regularly topped up to 7 cm depth with fresh water. See Hanley et al. (2019) for a comparison of effects on plants with natural seawater. Plants in the unflooded treatment were watered to saturation every three days and allowed to drain freely. Pots were randomly distributed throughout the greenhouse. A 12 hour dark light cycle was provided and minimum temperature was kept at above 10 ˚C throughout the experiment.

Trait measurements

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

To assess community performance, aboveground and belowground biomass, and total biomass in each pot were quantified by summing the measurements for the six individuals. In addition, we quantified the cover of vegetation in the pot when viewed from directly above (top-down vegetation cover, cm^2) and vegetation density, quantified as the area covered by plants when viewed from the side (side-on surface area, cm^2). Side-on surface area and top-down vegetation cover were quantified by taking standardised photographs. Images for side-on surface area were taken by placing pots against a white background mounted 5 cm from the back of the pot. A photograph was taken focused on the centre of the pot on a tripod-mounted SLR camera perpendicular to the pot from a distance of 1 m. Dispersed room lighting was used to avoid over-exposure. To measure top-down vegetation cover, the pot was then placed onto a dark background and an image taken from 1 m directly above the pot. The areas covered by vegetation in the photographs were calculated using ImageJ.

Data analysis

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

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

To investigate whether species composition and diversity affected biomass we compared observed pot-level values of aboveground, belowground and total biomass with expected values based on the constituent species' performance in the monoculture treatment of this experiment (Loreau and Hector, 2001). To do this whilst accounting for intra-specific variation, we randomly selected n plants from the pool of individuals of the species from monoculture pots in the appropriate flooding treatment, where n is the number of that species in the target pot. Dead individuals were not counted for this calculation of n. We repeated this sampling 1000 times to obtain a distribution of expected values for each pot. We then calculated the standardised effect size of biomass in each pot as observed biomass minus the mean of expected biomass, divided by the standard deviation of expected values (Gotelli et al., 2011). Positive values indicate that biomass is greater than expected given species' performance in monoculture (overyielding), while negative values indicate that biomass is less than expected (underyielding). To test whether composition affected over/underyielding, we used one sample t-tests to assess if the mean biomass standardised effect size in a treatment differed from zero.

RESULTS

Effects of flooding on individual plants

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

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

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

0.956 ± 0.302 SE, t = 3.17, df = 86, P = 0.002). For Plantago, flooding increased height and width but reduced the ratio of aboveground to belowground biomass (Height: 92.9 ± 10.6 SE, t = 8.60, df = 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 SE, t = 2.17, df = 86, P = 0.033). For Triglochin, flooding reduced the number of leaves (ln (Leaves): -0.103 ± 0.048, z = -2.16, df = 93, P = 0.031). All other species-trait combinations did not differ statistically significantly between flooded and unflooded treatments.

How does composition effect trait responses to flooding?

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

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

Effect of flooding and composition on pot level metrics

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

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

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

DISCUSSION

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

Triglochin was little affected by the chronic flooding and its resultant waterlogging when grown in monoculture with only one trait, a reduction in the number of leaves, altered by the flooded treatment. This supports the expectations we had based on its niche, as it is known to be relatively tolerant of waterlogged soils (Fogel et al., 2004, Sullivan et al., 2018), particularly in saline conditions (Davy and Bishop, 1991). Furthermore, in waterlogged soils Triglochin increases the production of surface roots, which raises the surface of the marsh, ameliorating the conditions and allowing other species to colonise (Fogel et al., 2004). While we found no difference in the above to belowground biomass ratio, there may have been a switch from the production of deeper roots to surface roots in the flooded conditions that we did not capture, as we measured total belowground biomass rather than root architecture. In addition to the total root biomass, root porosity and rooting depth are among a range of adaptations that halophytes have to flooding (Colmer and Flowers, 2008). We found that Plantago and Aster had contrasting responses of belowground biomass to flooding, with significant reductions in Aster and significant increases in Plantago. These species differ in their root porosity response to flooding (Justin and Armstrong, 1987), while it is unclear how this relates to belowground biomass, as increased porosity may reduce root mass, the presence of aerenchyma increases tolerance to anoxic, waterlogged soils (Colmer and Flowers, 2008). Whilst we do not know the full suite of adaptations for each of these species, the diversity of potential mechanisms could explain the differential responses we observe here. As changes in root biomass is likely to influence sediment stability, the variable responses of species to chronic flooding means that changes in the provision of erosion protection services are likely to be complex.

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

There was substantial intra-specific variability in all traits of all species. This variation was independent of the environment (i.e. flooding and composition treatments) and at the level of individual, and so is likely to be driven by the genetic diversity of individuals, particularly since we collected seed from a number of geographically distinct locations. High levels of intraspecific trait variation, such as we observed here, can affect plant responses to flooding (White et al., 2014) and this variability in responses can confer resilience of ecosystem functions to future environmental changes, such as increases in flooding with sea level-rise (Oliver et al., 2015).

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

Our results indicate that species composition frequently modified the response of plants to flooding, including reversing effects observed in monoculture. This supports previous observations that interspecific interactions can modify how aboveground growth of saltmarsh plants varies with environmental conditions (Huckle et al., 2000, Wang et al., 2006). Composition also affected plant traits independently of flooding treatment, with the greatest number of composition effects on traits observed for Triglochin. Compositional effects could be through competitive interactions. These interactions can alter the ratio of aboveground and belowground biomass, with greater belowground allocation if competition is primarily for soil resources (Tilman and Wedin, 1991), and greater aboveground allocation if competition is primarily for light (DeMalach et al., 2016). There is some evidence from saltmarshes that competition can increase biomass allocation to root mass (Dormann et al., 2000, Redelstein et al., 2018), but other studies find composition to mostly affect aboveground rather than belowground biomass (Huckle et al., 2002). Our results are consistent with the latter, with aboveground biomass deviating from expected monoculture values for nine species-treatment pairs, compared to three for belowground biomass. Some changes in plant traits were consistent with competition for light. For example, Plantago and Aster both had lower than expected aboveground biomass when grown together in the flooded treatment, meaning that interspecific competition was stronger than intraspecific competition. In this treatment both species had higher specific leaf area, which is likely to be due to plants investing in wide but thin leaves to maximise light gathering ability.

Species interactions between our study species, assessed by looking at over and underyielding by different species in different treatments, do not follow a linear hierarchy of competitive dominance. Aster reduced Triglochin biomass, Aster and Plantago had a negative effect on each other's biomass, while Plantago and Triglochin had higher than expected biomass, significantly so for Plantago. Intransitive competition loops, where competitive hierarchies are non-linear, have previously been documented in saltmarsh plant communities and are considered to be important in promoting species coexistence (Ulrich et al., 2018). Our results show that competition hierarchies can also be broken by positive species interactions. Positive interactions identified by overyielding could arise from niche differences reducing competition for resources (Adler et al., 2007) or through facilitation, where a species makes the environment more favourable for another (Bertness and Shumway, 1993). The former explanation is perhaps unlikely to explain our results as the positively interacting species (Plantago and Triglochin) had more similar aboveground growth forms (which could influence light interception) to each other than they did to Aster, although it is possible that their narrow leaves could pack more densely to intercept light. Although some species interactions were independent of the flooding treatment (the negative effect of Aster on Triglochin), other species interactions differed between the flooded and unflooded treatment. The Stress Gradient Hypothesis predicts that these positive species interactions will be more frequent when environmental conditions are more stressful (Bertness and Callaway, 1994), as in the flooded treatment. Consistent with this expectation, the positive interaction between Plantago and Triglochin was only statistically significant in the flooded treatment. Flooding also affected competition, as the competitive interaction between Plantago and Aster was only evident in the flooded treatment. This is not expected to change with flooding under the Stress Gradient Hypothesis (Conti et al., 2017), but could instead result from environmental stress reducing the ability of plants to tolerate inter-specific competition (Hart and Marshall, 2013). Interestingly, the two negatively interacting species pairs (Plantago-Aster and Triglochin-Aster) frequently co-occur within the same quadrat (Sullivan et al., 2018), so have some ability to coexist. It may be that interactions are not sufficiently asymmetrical for one species to be competitively excluded (Chesson, 2000), or that underyielding reflects changes in plant growth form that does not necessarily alter plant fitness.

As a result of the opposing nature of interactions between pairs of species, or potentially due to new interactions that only emerge when all three species are grown together, total biomass in the three species treatment did not differ significantly from expected values. This does not mean that diversity has no effect on biomass in field conditions as our species composition treatments do not cover the higher diversity levels found on saltmarshes; in > 1000 0.5 by 0.5 m quadrats in UK saltmarshes surveyed by Mossman et al. (2012) there was a median species richness of three, but a maximum species richness of ten. However, by being able to investigate all possible species pairings in a well replicated experiment, we found an important role of species composition in influencing total and aboveground biomass. This is consistent with an earlier study on saltmarshes in the USA, which found that diversity effects were primarily due to the presence of particular species rather than niche complementarity (Sullivan et al., 2007). While we found that species composition primarily affected aboveground biomass rather than belowground biomass, Ford et al. (2016) report that species richness increases sediment stability to erosion. This difference may be because some of the effect of diversity is only seen at higher species richness levels than used in our experiment, although this is unlikely as some effect of diversity is evident in Ford et al. (2016) even with three species. Alternatively, it may be that the complementary nature of different species' root architecture is more important for influencing sediment stability than root biomass alone. The difference in over and underyielding of aboveground biomass due to species composition, and effect of species composition on traits such as plant height, means that composition potentially influences how saltmarsh vegetation attenuates wave energy (Rupprecht et al., 2017). This potential function can itself be influenced by flooding, which we find to alter these species interactions.

The variation in functional trait responses to flooding between species and species composition treatments found by our experiment highlights the challenge of predicting how plant communities will respond to chronic flooding and the consequent effects on ecosystem service provision by coastal plants. These differences in responses, combined with trait variability within species, meant that flooding did not shift any trait in a consistent direction across all species and composition treatments. However, it is also this diversity of responses that creates the potential for ecosystem functioning and service provision to be resilient to future increases in coastal flooding (Mori et al., 2013), evidenced by the limited effect of flooding on pot-level metrics of biomass and vegetation density (Fig. 2). The community-level effects of flooding can also be buffered by shifts in species composition towards more flood tolerant species, which can occur even after acute flooding events (Hanley et al., 2017). Such changes did not occur within our experiment, as mortality was low, but are expected to be increasingly important with increasing severity and longer time-scales of environmental change (Smith et al., 2009).

CONCLUSION

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

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FIGURES

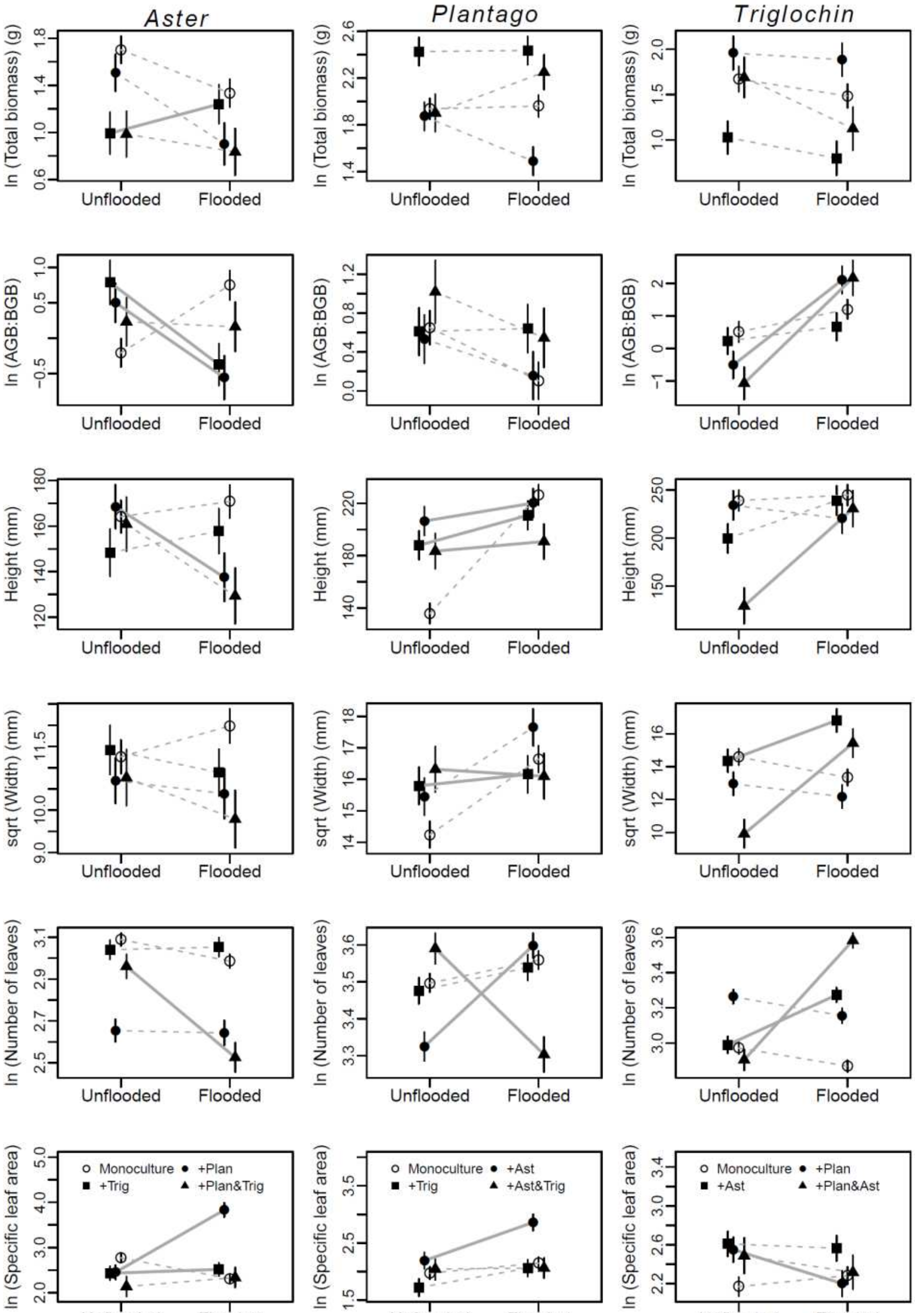

Figure 1. Effect of flooding and species composition on the traits of individual plants. Symbols show estimated means ± SE for each flooding-composition category from linear or generalised linear models relating values of each trait to flooding treatment, species composition and their interaction. Statistically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

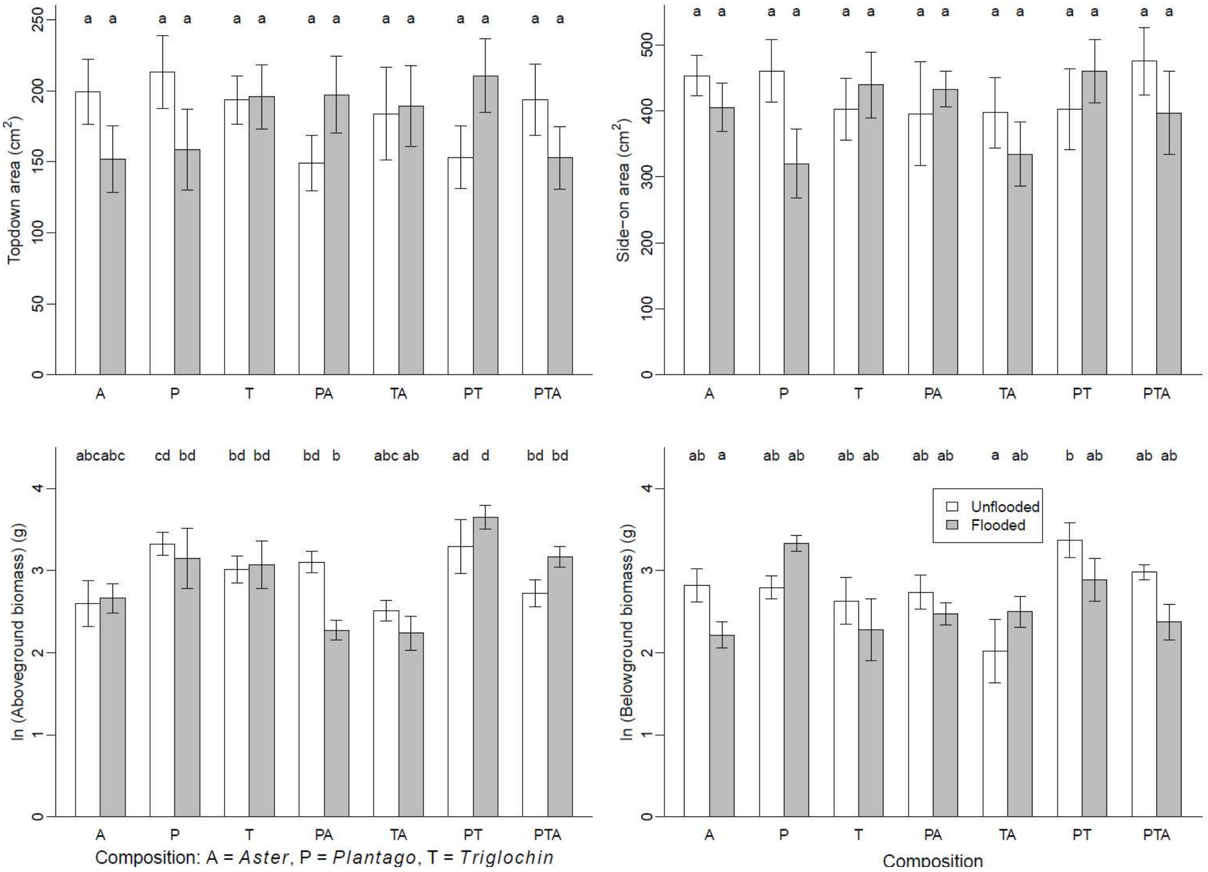

Figure 2. Effect of species composition and flooding on pot-level metrics. Bars show estimated means ± SE from linear models of each variable as a function of flooding treatment, composition and their interaction. Flooding treatment – composition combinations with different letters are statistically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

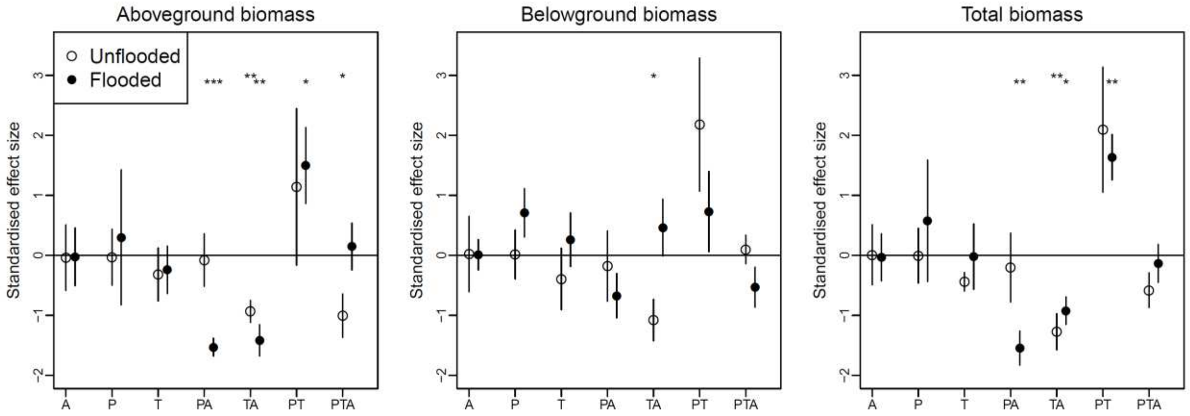

Figure 3. Effect of composition and flooding treatments on aboveground, belowground and total biomass. Biomass values are expressed as standardised effect sizes relative to expected values based on each species performance in monoculture. Values greater than zero indicate that observed biomass is greater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

SUPPORTING INFORMATION

Figure S1. Elevation range of study species.

Figure S2. Intraspecific variation in traits.

Figure S3. Over and underyielding separated by species.

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

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

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

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

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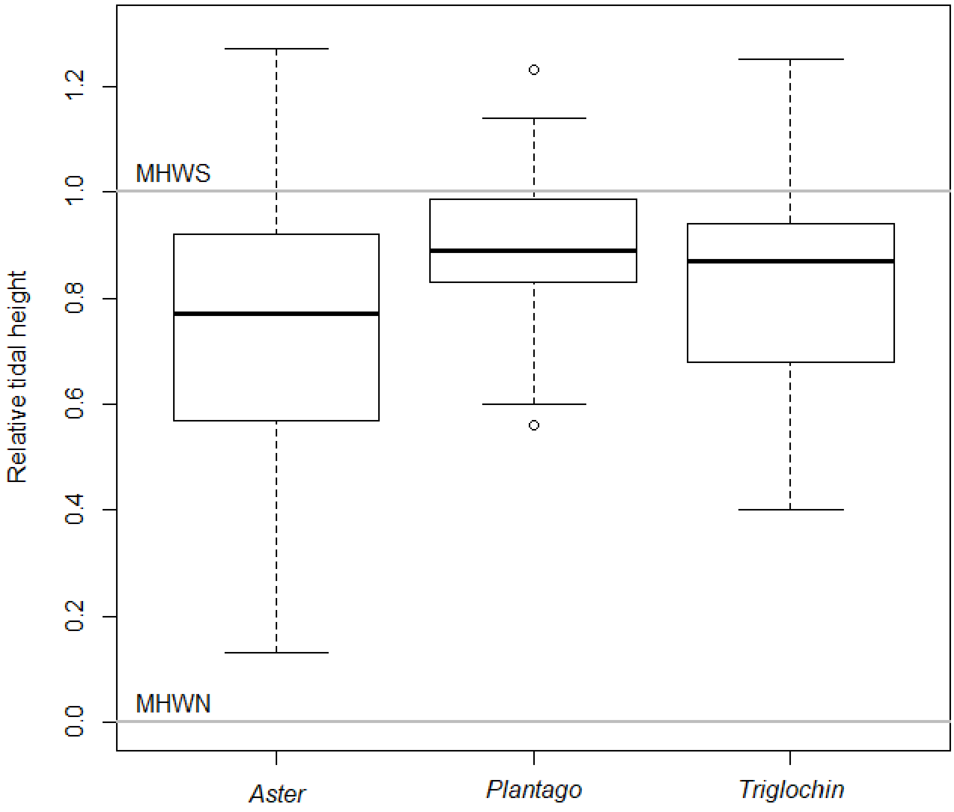

Figure S1. Elevation range of study species. Data are from (Sullivan et al., 2018, Sullivan et al., 2017). Elevations are expressed as relative tidal height, which are standardised relative to mean high water spring (MHWS) and mean high water neap (MHWN) to allow comparison amongst sites with different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

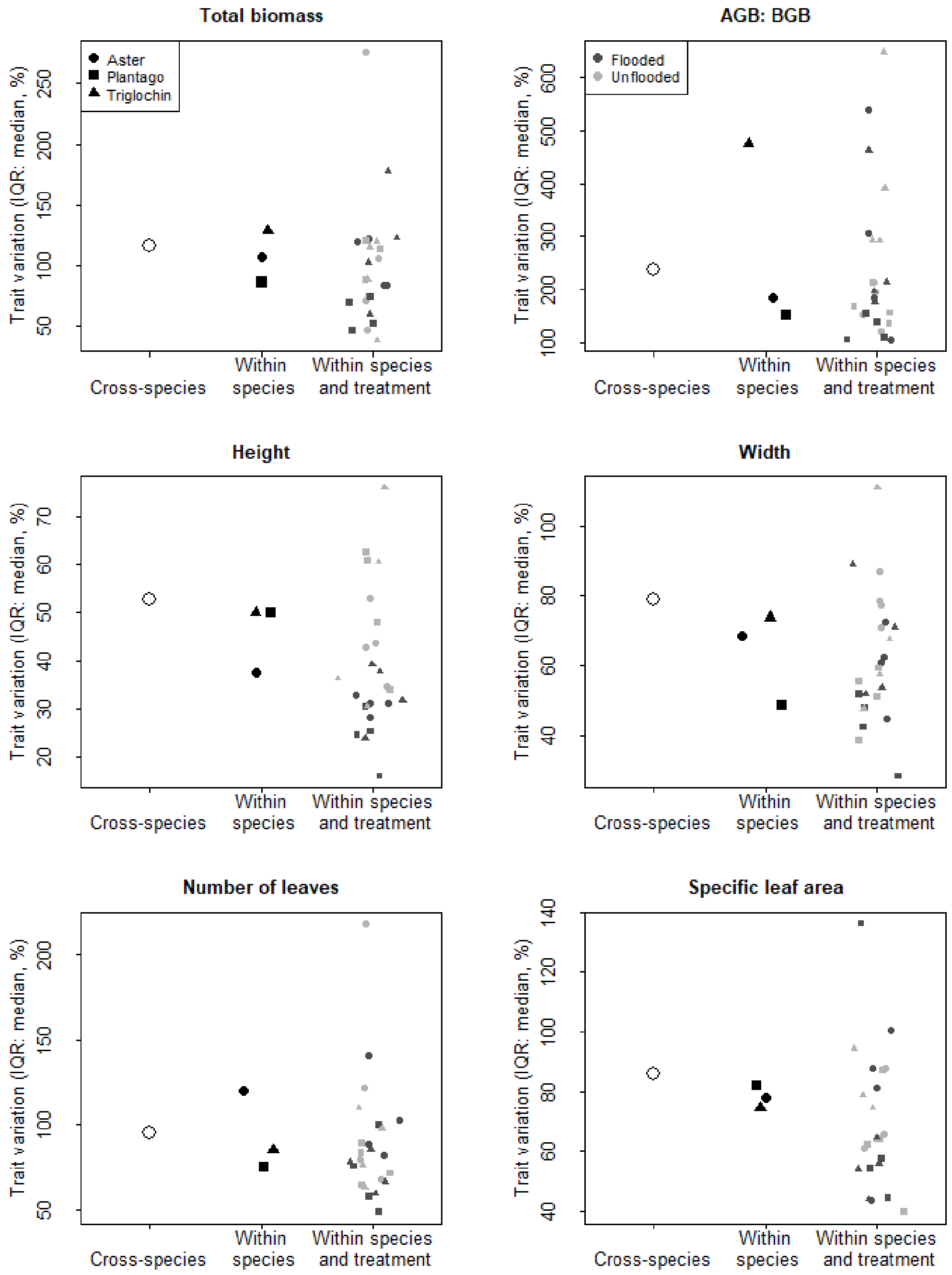

Figure S2. Inter and intra-specific variability in the suite of traits presented in Figure 1. For each trait, a non-parametric analogue of the coefficient of variation, interquartile range/ median × 100, was calculated at three levels (1) cross species, pooling data across species and treatments, (2)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

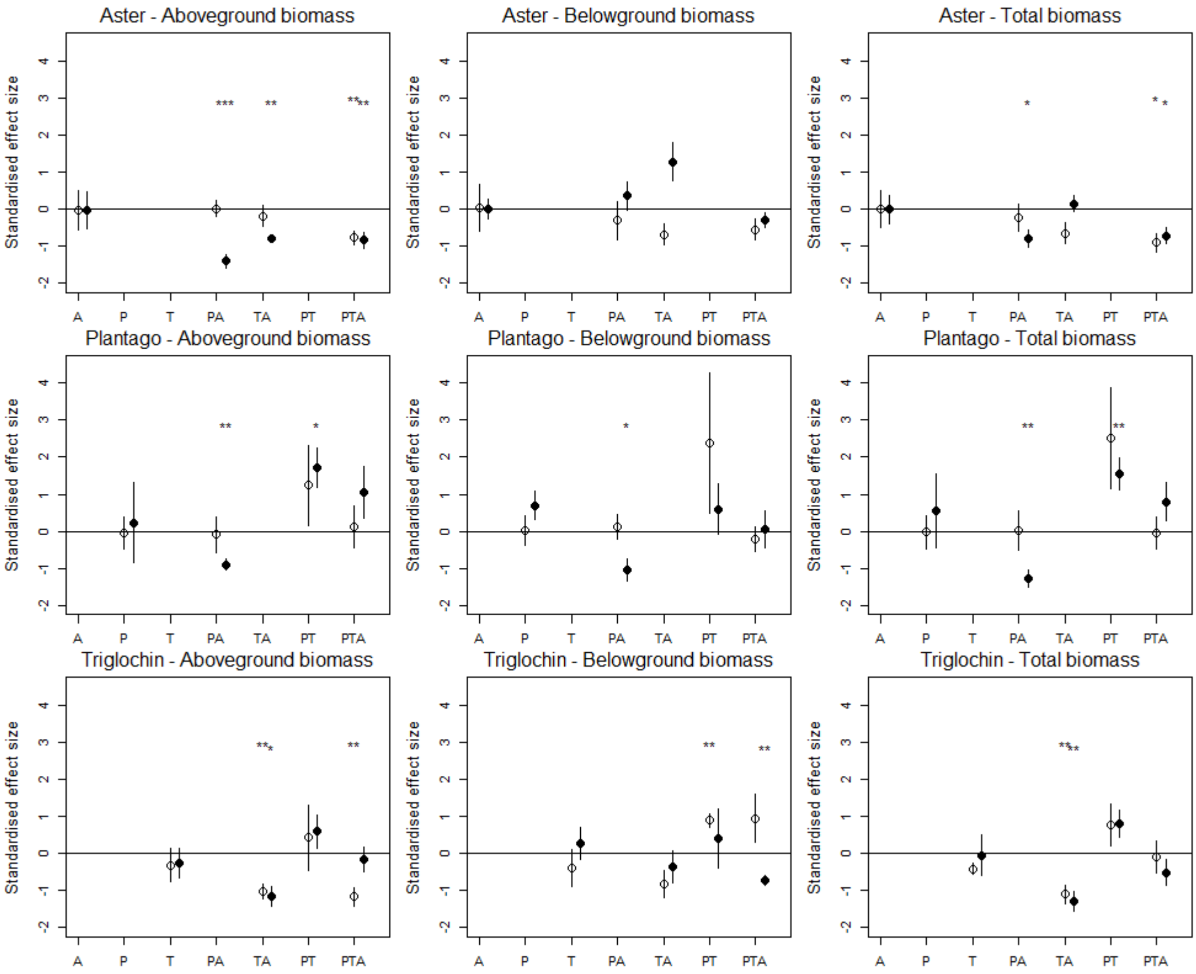

Figure S3. As Fig. 3, but calculating biomass standardised effect sizes for each species separately. Values greater than zero indicate that the species has higher biomass in the treatment than expected based on its performance in monoculture, while negative values indicate that it has lower biomass than expected.

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
Aster[1]	207	207	217	203	202	186
Plantago[2]	222	222	222	214	214	197
Triglochin	224	224	219	211	208	196

[1] Not including the 17 individuals that died; [2] Not including the 2 individuals that died.

Table S1b. Sample size for analyses at the pot level per treatment. Maximum number of pots per 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

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

		Aster		Plantago		Triglochin	
		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

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

* Z score for number of leaves.

Table S4. Coefficients of linear models relating pot-level metrics to flooding treatment, species 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
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	0.432
	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

Additional references

Sullivan MJP, Davy AJ, Grant A, Mossman HL. 2017. Data from: Is saltmarsh restoration success constrained by matching natural environments or altered succession? a test using niche models. Dryad Digital Repository. https://doi.org/10.5061/dryad.380g2.