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The Fight to Capture Light: Functional Diversity Is Related to Aquatic Plant Community Productivity Likely by Enhancing Light Capture

Charlotte Angove[1], Alf Norkko[1,2] and Camilla Gustafsson[1]*

[1] Tvärminne Zoological Station, University of Helsinki, Hanko, Finland, [2] Baltic Sea Centre, Stockholm University, Stockholm, Sweden

Functional diversity (FD) experiments are highly effective for investigating how a community interacts with its environment. However, such experiments using morphological and chemical traits have not been conducted for submerged aquatic plants and their insights would be highly valuable for understanding the ecology of these communities. We conducted a 15-week field experiment in the Baltic Sea where we manipulated the species composition of aquatic plant communities to investigate functional diversity. We constructed artificial triculture communities with different species compositions to change the Community Weighted Means (CWMs) and variability of traits. We measured nine plant traits and tested how community productivity (CP) was related to FD, trait CWMs and community trait ranges. CP varied by more than four times across treatments and functional richness was significantly related to CP. Functional evenness and functional divergence were not significantly related to CP. Height, leaf area and $\delta^{13}C$ were significantly related to CP. Leaf $\delta^{13}C$ trends with CP suggested that the carbon supply is not replete, yet species composition was partly responsible for the relationship. Plant height likely had multifaceted benefits to CP because there was evidence of a competitive height interaction between the tallest and 2nd tallest species, therefore the effects of plant height to CP would have been disproportionally large. The height of the tallest species significantly drove the variability of the community height range, which was significantly related to CP and it had a relatively large influence on the calculation of FD indices. Leaf area, which was strongly correlated to plant height, was also significantly related to CP. The significant relationship between functional richness and CP was most likely driven by the presence of taller plants. FD likely enhanced CP, by selecting for extreme trait values which enhanced production (selection effect), while niche complementarity effects were not observed. This study provides experimental evidence and mechanistic insights into the role of FD and specific traits for CP in submerged aquatic plant communities. To conclude, FD was significantly related to CP of temperate aquatic plant communities likely by selecting for traits which enhanced light capture, with consequences for carbon supply.

Keywords: Baltic Sea, BEF, carbon cycling, functional diversity, functional traits, primary production, *Zostera marina*

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Dongyan Liu,
East China Normal University, China

Reviewed by:
Nianjun Xu,
Ningbo University, China
Kun-Seop Lee,
Pusan National University,
South Korea

****Correspondence:***
Charlotte Angove
charlotte.angove@helsinki.fi

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INTRODUCTION

Functional diversity experiments are powerful tools for understanding how an ecosystem works (Tilman et al., 1997; Díaz and Cabido, 2001; Hooper et al., 2005; Mouillot et al., 2013; Gagic et al., 2015). Not only do they inform us about functional diversity indices, but the volume of traits measured allows us to explore multiple trait–process and trait–trait relationships (McGill et al., 2006; Cadotte et al., 2011). This provides an in-depth understanding of how the study organisms interact with their environment (Hooper and Vitousek, 1997; Tilman et al., 1997; Díaz and Cabido, 2001; Hooper et al., 2005; Gagic et al., 2015).

Plant functional traits are measurable morpho-physio-phenological characteristics of a plant which can improve its performance of processes linked to its fitness, for example increased biomass production (Violle et al., 2007). It is likely that functional traits strongly influence ecosystem properties, as suggested by a consensus of literature (Hooper et al., 2005). They can support the biomass production of plants by many potential mechanisms (Pérez-Harguindeguy et al., 2013), for example by enhancing their ability to capture light (Díaz et al., 2004; Gustafsson and Norkko, 2019), to compete for resources against other plants (Gaudet and Keddy, 1988; Cadotte, 2017), or by increasing their access to nutrient pools (Campbell et al., 1991; Kembel et al., 2008; Angove et al., 2018). These traits constitute the foundation of functional diversity, because their measurements are combined to calculate functional diversity indices. Indeed, the definition of functional diversity is the performance variability of different functions (Garnier et al., 2016), such as the combined performance of light capture and nutrient uptake. It is important to investigate functional diversity because it provides mechanistic insights into the relationships between plant diversity and ecosystem processes, which contributes to the practical management of vegetated ecosystems (Díaz and Cabido, 2001). Functional diversity can increase primary productivity by, for example, selecting for extreme trait values which enhance productivity (selection effects) or by a complementarity of fundamental niches (complementarity effects) (Loreau and Hector, 2001). Functional ecology is an enrichment to traditional taxonomic ecology because it allows us to investigate the underlying mechanisms for diversity effects to processes (e.g., Violle et al., 2007). For example, species richness affects productivity in temperate submerged aquatic plant meadows (Salo et al., 2009; Gustafsson and Boström, 2011), as can functional traits (Gustafsson and Norkko, 2019) and perhaps these functional traits can be used to explain species effects (e.g., Hillebrand and Matthiessen, 2009).

Aquatic plant meadows of the northern Baltic Sea are temperate communities with typical seasonal patterns of pronounced summer growth (Boström et al., 2004; Attard et al., 2019). The brackish seawater conditions allow for marine, brackish and limnic species to coincide within the same meadow (Kautsky, 1988), therefore meadows can be highly diverse communities with a variety of different plant traits (Kautsky, 1988; Gustafsson and Norkko, 2016, 2019; Angove et al., 2018). Such a diversity of traits provides an opportunity to conduct a functional diversity experiment to understand how aquatic plants interact with their environment. Previous functional diversity research for aquatic plants has consisted of surveys along environmental gradients (e.g., Fu et al., 2014; Gustafsson and Norkko, 2019) and controlled mesocosm experiments (e.g., Engelhardt and Ritchie, 2002). However, to our knowledge, no experiment has yet manipulated species composition to investigate functional diversity *in situ*. We conducted a functional diversity experiment *in situ* to investigate how the functional diversity of submerged aquatic plants can be linked to their primary production. When conducting functional diversity experiments, it is necessary to understand the environmental context to select plant traits which are most likely to affect the process being measured (Petchey and Gaston, 2006). Two of the most limiting resources conventionally known to affect aquatic plant growth are light and nutrient availability (Lee et al., 2007). Light intensity can affect the depth limit of aquatic plants (Ralph et al., 2007). Accordingly, the distribution of plants can shift from turbid, nutrient-rich waters to clearer, relatively nutrient-poor waters to favor light capture (Krause-Jensen et al., 2008). Indeed, plant height is significantly related to productivity in temperate plant meadows (Gustafsson and Norkko, 2019). A reduction of light availability, such as by shading, can lead to reduced growth, changes in the biomass investment for light capture, mortality and/or changes in community properties such as shoot density (Longstaff and Dennison, 1999; Ruiz and Romero, 2001; Boström et al., 2004; Gustafsson and Boström, 2013; Salo et al., 2015). Nutrient availability can also affect the growth of aquatic plants (Perez et al., 1991; Ferdie and Fourqurean, 2004; Armitage et al., 2011), as well as the expansion of meadows (Furman et al., 2017) and it can dictate how much biomass plants invest for capturing light (Maurer and Zedler, 2002). Aquatic plants absorb nutrients from the sediment porewater and the water column (Touchette and Burkholder, 2000), and the sediment nutrient source is spatio-temporally variable and finite (Angove et al., 2018). Even in eutrophic environments such as the northern Baltic Sea (Andersen et al., 2009; Gustafsson et al., 2012), plants can deplete nutrients from their surrounding sediments in response to biomass-driven demands (Angove et al., 2018). Therefore, both light and nutrient availability are viable candidates which could limit productivity in temperate aquatic plant communities (Boström et al., 2004; Lee et al., 2007). Resultantly, traits which are linked to light capture and nutrient uptake could be influential to biomass production by submerged aquatic plants.

We investigated the role of plant traits and functional diversity for community biomass production by conducting a 15-week transplant experiment *in situ*. By comparing the relationships between plant traits, functional diversity and biomass production, we could provide novel mechanistic insights about the role of different traits and drivers for the productivity of submerged aquatic plant communities. Previous evidence shows that communities with taller plants are significantly more productive (Fu et al., 2014; Gustafsson and Norkko, 2019). Evidence also shows that resource partitioning might allow submerged aquatic plants to utilize the sediment nutrient pool more effectively (Gustafsson and Boström, 2011). In such conditions, traits which represent nutrient metabolism and sourcing by plants, e.g., leaf tissue $\delta^{15}N$, might be superseded by morphological traits to access nutrients; such as root length (Aerts, 1999). Therefore, we hypothesized that aquatic plant community biomass production would be closely related to plant height and root length range, but not to leaf chemical traits such as leaf tissue $\delta^{15}N$ and $\delta^{13}C$ (H1). Because of such trait variability effects, we hypothesized that plant communities with a higher functional diversity would produce more biomass (H2).

MATERIALS AND METHODS

Study Area and Field Experiment

We conducted the experiment in the shallow archipelago areas of the northern Baltic Sea; our experimental site, Kyan (59.827415, 23.209903 WGS84), is a brackish-water (salinity ca. 5.6 PSU, Gammal et al., 2019) semi-exposed lagoon located on the island Vindskären, Tvärminne archipelago, southern Finland. It is a coarse-sand environment with a relatively low organic matter (OM) content [silt fraction (<0.63 μm) = 0.43%, OM = 0.54%; Gammal et al., 2019]. It is protected from the open Baltic Sea by a partly-submerged rock covered by bladderwrack, *Fucus vesiculosus*. Its moderate levels of wave exposure allowed submerged plant communities to thrive (Worm and Reusch, 2000; Gustafsson and Norkko, 2019). The lagoon is inhabited by a diverse and mixed community of submerged aquatic plants (Gustafsson and Norkko, 2019, **Figure 1A**) and we selected naturally bare sand patches (4 m × 8 m) amongst these communities at approximately 2.5 m depth to conduct the experiment. We conducted a transplant experiment *in situ* by SCUBA diving (e.g., Salo et al., 2009; Gustafsson and Boström, 2011). We defined six experimental zones (8 m × 4 m) within the pre-selected bare patches. Within these patches, we cleared the sand of lone shoots and buried rhizomes then marked out plots, which were evenly spaced and separated by at least 1 m. In each bare patch, we planted three experimental functional diversity communities (total 18 communities). We commenced the experiment on 01/06/2016.

We collected shoots of the six most abundant species which were already existing in the lagoon; these species were *Zostera marina* L., *Potamogeton perfoliatus* L., *Zannichellia major* Boenn. ex Reichenb., *Ruppia cirrhosa* (Petagna) Grande, *Stuckenia pectinata* (L.) Böerner and *Myriophyllum spicatum* L. (based on preliminary checks in 2016 and pre-existing data; Gustafsson and Norkko, 2019). At this time of year, the growth season for these plants had only recently begun (personal observation). We created experimental triculture communities where we manipulated the species composition to change the community weighted means (CWMs) of traits. Thus, our experimental treatment was the mean and variability of heritable traits manifested by different species within a community. We selected each species assemblage using a random number generator, and experimental treatments varied along a continuous scale (total 18 communities, **Supplementary Table S1**). The random selection process could have selected identical communities at random, and resultantly there were 11 unique community assemblages amongst the 18 communities. There were no selection criteria amongst the six experimental species, however we removed one species *M. spicatum* from the random selection process after its maximum possible occurrence (2 experimental plots, 16 shoots) because it was found in lower abundances than the other experimental species. We constructed the communities by randomly assembling 8 individuals of each 3 species onto a 30*30 cm plastic grid using cable ties (total 24 shoots, **Figure 1B**) while keeping the plants submerged. The individuals used to assemble communities were standardized by approximate biomass and we randomly collected 10 individuals of each species to estimate the starting biomass (mg DW).

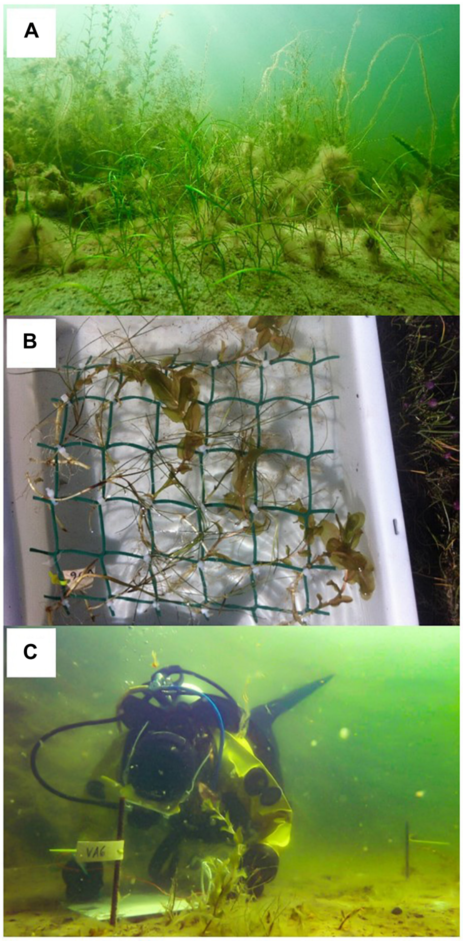

FIGURE 1 | (A) Natural mixed species aquatic plant community in the northern Baltic Sea (image credit Alf Norkko). **(B)** Artificial triculture community ready to be transplanted (image credit Charlotte Angove). **(C)** Regular monitoring of experimental communities (image credit Tiina Salo).

We carefully planted the experimental communities and secured the grids into the sand using two stainless steel hooks. Two weeks after planting we revisited the communities to survey the plant survival rate after the transplant procedure (**Figure 1B**). While most communities had been successfully transplanted, if an individual was lost then we corrected the starting biomass value of the community accordingly. We re-visited the communities every 2–3 weeks to monitor their growth and remove the shoots of non-experimental plants which approached or intruded the plots (**Figure 1C**) until the experiment was terminated after 15 weeks on 14/09/2016, when all the plots were harvested. After harvesting, we collected subsamples of new leaf tissues for nutrient analysis (**Table 1**) then froze the samples (−18°C) for future processing. During the experimental period, we monitored the temperature and light continuously using loggers (HOBO Pendant® Temperature/Light Data Logger 64K, Onset, United States) and the daily maximum temperature varied between 9.1 and 19.6°C ($\bar{x}$ = 15.3°C). We converted

TABLE 1 | Description of the traits which were measured for each species in each community; their abbreviations, the technique used to quantify them, the average frequency of measurements for each species trait value, the relevance of the trait to primary production in aquatic plant communities and the literature from which these relationships are based.

Trait	Technique	$\bar{x}$	Relevance to 1° production	Literature
Median height (cm)	Measured the length of aboveground tissue (cm) for intact shoots using the definition described in text. Measured every shoot of the first 10 individuals (intact collection of shoots) until measurement frequencies were lowered to species-specific counts based on cumulative average analyses. Calculated median height.	26	Increased light capture, greater competitive ability for capturing light	Gaudet and Keddy, 1988; Cadotte, 2017; Gustafsson and Norkko, 2019
Leaf area (mm^2)	Selected the largest intact leaf from at least the first 5 individuals. Leaf sheaths were excluded. Scanned using an Epson flatbed scanner. Measured leaf area (mm^2) using ImageJ (Schneider et al., 2012), calculated median leaf area.	6	Increased light capture	Díaz et al., 2004; Wright et al., 2004
Median max root length (MMRL, mm)	Selected the 10 longest primary roots from at least the first 5 individuals, if present, until at least 30 roots had been collected. Scanned using an Epson flatbed scanner, measured lengths (mm) using SmartRoot (Lobet et al., 2011) on ImageJ (Schneider et al., 2012). Calculated median primary root length (excluding branch lengths).	49	Increased access to new sediment nutrient pools	Campbell et al., 1991; Kembel et al., 2008; Angove et al., 2018
Specific root length (SRL)	The roots which were scanned for MMRL were pooled, dried (48 h, 60°C) then weighed (nearest 0.1 mg). Divided the sum of root lengths (including branch lengths, mm) by their dried weight (mg).	1	Greater investment for reducing the diffusion distance to new sediment nutrient pools compared to benefits of more root mass per unit length (e.g., Transport of solutes, greater penetration force on soil)	Eissenstat, 1992; Aerts, 1999; Pérez-Harguindeguy et al., 2013
Leaf elemental N concentration (%DW), $\delta^{13}C$ and $\delta^{15}\delta N$ isotope ratios	Young leaves were collected immediately after harvest. To collect enough material, multiple individuals were sampled, and the material pooled. The material was rinsed with Milli-Q water, dried (48 h, 60°C), weighed (nearest 0.1 mg), homogenized using a ball mill and analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (UC Davis Stable Isotope Facility, United States). International standards to calculate delta values were Vienna PeeDee Belemnite ($\delta^{13}C$) and Air ($\delta^{15}N$).	1	N: availability of N for metabolic processes in new leaf tissue. $\delta^{15}N$: nitrogen sourcing. $\delta^{13}C$: stronger isotopic fractionation against heavier, more energy-consuming ^{13}C isotopes during growth. Carbon sourcing.	Cloern et al., 2002; Wright et al., 2004; Roscher et al., 2012; Buapet et al., 2013; Gustafsson and Norkko, 2019

This data was used to calculate community-weighted means of traits based on combinations of 3 different species.

the light intensity data (lum ft^{-2}) to photosynthetically-active radiation (PAR, $\mu mol\ m^{-2}\ s^{-1}$) using the methods described by Gustafsson and Norkko (2016). The daily maximum PAR ranged from 168 to 555 $\mu mol\ m^{-2}\ s^{-1}$ ($\bar{x} = 419\ \mu mol\ m^{-2}\ s^{-1}$). While light irradiance and temperature varied throughout the experiment (**Supplementary Figure S1**), conditions were approximately similar across treatments because communities were transplanted at a consistent depth (approximately 2.5 m).

Trait Selection and Measurement

We measured the variability of traits manifested by the plants at harvest (e.g., Roscher et al., 2012). We defrosted the samples and counted the total number of shoots for each species in a community. To define the difference between shoots and branches, we used a guideline to separate biomass between aboveground and belowground material; aboveground biomass began where tissues became photosynthetic. One species could not be classified using this technique (*Zannichellia major*) because its rhizomes were often unpigmented. For this species, we separated aboveground biomass at the location of the last rhizome internode with roots before aboveground material. This adjustment did not affect height measurements because in comparison to the variability of shoot heights it was negligible. We measured traits which were potentially influential for community biomass production (**Table 1**), based on guidance by previous literature and the trait handbook by Pérez-Harguindeguy et al. (2013). We calculated the molar ratio between C and nitrogen (N, C:N ratio) to indicate changes in the availability and investment of C relative to N and vice versa.

We dried the samples at 60°C for at least 48 h and measured the biomass of different plant parts. Biomass measurements were pooled for each species in each plot to collect the value of the total biomass. Primary productivity (mg Dry Weight [DW] d^{-1}) was calculated using the increase in biomass (mg DW) throughout the experimental period (105 days) for each species in each community. Community productivity (CP) was its sum of all species productivities. We removed data for one plot because its growth had noticeably failed, and we suspect that the plants suffered from something which was not included in our experimental treatment.

Functional Diversity Indices

We conducted all analyses using R (version 3.5.2, R Core Team, 2018). We calculated CWMs based on the relative shoot frequencies of each species in a community (Garnier et al., 2004; Gustafsson and Norkko, 2019). These and the CP were calculated manually from communities with no missing values, therefore there were fewer replicates than originally present and their frequency varied between analyses. While CWMs are criticized for inferring trait–environment relationships (Peres-Neto et al., 1991), this criticism does not apply to our experiment because we examined trait–productivity relationships and we sampled the entire experimental population. We calculated trait ranges for communities by subtracting the 10th percentile trait value of the species with the lowest trait value from the 90th percentile trait value from the species with the highest trait value (Schleuter et al., 2010). We did this to calculate height range (cm) and the range of root lengths (mm).

We used Spearman's Rank correlation to check for significant relationships between traits (**Table 1**) and incorporated a False Discovery Rate (Benjamini and Hochberg, 1995) to reduce the likelihood of Type I errors which arise from multiple comparisons. Following this, we excluded leaf area from calculations for functional diversity indices, because it had a strong significant positive correlation to median height (**Supplementary Figure S2**). We used the remaining traits listed in **Table 1** and the "FD" package (Laliberté et al., 2014) to calculate Functional Richness (FRic), Functional Evenness (FEve) and Functional Divergence (FDiv) (Mouchet et al., 2010; Schleuter et al., 2010). FRic describes the volume of functional space occupied by the mixture of traits, while FEve and FDiv describe the distribution of traits within the trait space (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010; Schleuter et al., 2010). Indeed, FEve describes the regularity of the distribution of mean species traits within the trait space for a community, while FDiv describes the position of species' trait clusters within the trait space (Schleuter et al., 2010). To calculate these indices, we estimated the relative weights of different traits for productivity using findings from a spatial survey conducted in the same region which examined the role of temperate aquatic plant traits for primary production across environmental gradients (Gustafsson and Norkko, 2019). When traits were significantly related to primary production across communities, we used standardized versions of their coefficient estimates to represent their relative weights for functional diversity indices (Height = 33, $\delta^{15}N$ = 13, $\delta^{13}C$ = 11) (Petchey and Gaston, 2006). When traits were not significantly linked to productivity across communities, we ranked their weight as 1. The FRic and FDiv estimates represented the variability of traits poorly (quality = 0.28) because of the corrective process to include more traits than species; while FRic indices must traditionally have more species than traits, the model which we used incorporated a corrective process (Laliberté et al., 2014).

Statistical Analysis

We conducted linear regressions between functional diversity indices and CP, then between CWMs of traits and CP to examine the relative relationships between different traits and productivity in this experiment. When necessary, we transformed variables to meet the criteria for parametric analyses; in these cases, the transformations are shown on graphs when present. If data was non-normally distributed by a marginal amount, we maintained the use of parametric regression and used White's test for homogeneous variances in addition to the widely-used Breusch-Pagan test to validate that variances were homogeneous (Godfrey and Orme, 1999).

We tested whether the correlation between leaf area and height was reflected at community level using Pearson's correlation analysis. Additionally, we further investigated the relationship between community $\delta^{13}C$ and CP using a generalized linear model (GLM); we tested whether trends were due to species differences or whether there was a valid independent trend between $\delta^{13}C$ and productivity. For this analysis, we removed one species *Myriophyllum spicatum* because its occurrence in the experimental communities was much lower than other species (2 out of 18 communities). There was collinearity between species identity and δ^{13}C, therefore we centered δ^{13}C to species identity by subtracting mean species δ^{13}C from their corresponding δ^{13}C values to reduce collinearity. We repeated this process for C:N ratios and productivity, however we used factor ceiling analysis (Thomson et al., 1996; Thrush et al., 2003) and non-parametric regression to investigate C:N-productivity trends. Finally, we conducted a permutation-based multiple regression analysis to summarize the combined effect of different traits for productivity (**Table 1**). For this analysis, we included the estimated start biomass for each community to examine its relative effect to biomass production compared to other traits measured. We used Euclidean distances and we implemented a backward-selection process to select a model by its AICc. The main findings were consistent when the backward-selection process was replaced by a forward-selection process, indicating model stability.

RESULTS

By the time of harvest, there was a large variability in growth across our experiment; with overall biomass per community ranging from 1.854 to 8.145 g DW. CP ranged from 11.9 to 57.2 mg DW d^{-1} (tenth and ninetieth percentiles, respectively) which meant that the amount of biomass produced in each community varied by more than four times. Overall, functional diversity metrics were weakly related to biomass production (**Table 2**). While there was a significant relationship between FRic and community biomass production (**Figure 2** and **Table 2**), there was not a significant relationship between community biomass production and FEve ($\bar{x} = 0.78$) or FDiv ($\bar{x} = 0.78$) (**Table 2**).

Linear Regression Analyses

Linear regression analyses identified two types of traits which were relatively strongly related to CP; these were traits that characterized light capture (height and leaf area) and some traits that described nutrient concentrations in the leaves (**Table 3**).

TABLE 2 | Linear regression statistics for the relationship between CP (mg DW d^{-1}) and functional diversity indices; Functional Richness (FRic) and Functional Evenness (FEve).

	Coefficient	**Intercept**	**Regression statistics**			
			r^2	***n***	***F***	***p***
FRic	136.906	9.665	0.298	15	5.517	**0.035**
FEve	−0.0231	3.425	0.0001	15	0.001	0.971

			Rank regression statistics		
	Coefficient	**Intercept**	***n***	**Wald test**	***p***
FDiv	27.573	10.665	15	0.392	0.683

Rank regression statistics for the relationship between CP and Functional Divergence (FDiv). The bold values are statistically significant p-values.

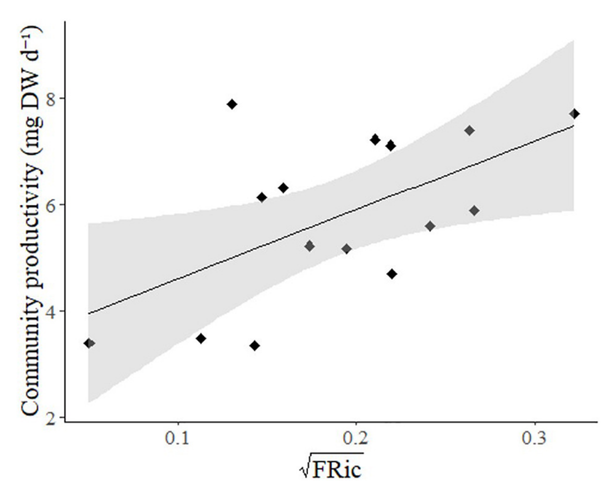

FIGURE 2 | Relationship between Functional Richness (FRic, square root transformed) and community productivity (mg DW d^{-1}). Solid line: line of best fit, shaded area: 95% confidence intervals.

Other traits were not significantly related to productivity in these analyses ($p > 0.05$, **Supplementary Table S2**). These included mean community maximum root length (MMRL, mm), specific root length (SRL), leaf tissue nitrogen (% DW) and δ^{15}N concentrations, as well as the range of root lengths within a community (mm).

Height was strongly related to CP by a variety of mechanisms. Firstly, taller communities were significantly more productive (**Figure 3A** and **Table 4**).

Secondly, the upper height limit of a community drove the height range (**Table 3** and **Supplementary Figure S3**) which was also significantly related to primary production (**Figure 3B** and **Table 3**). This is partly owing to the tallest species being more productive in response to its own increase in height (**Table 3** and **Supplementary Figure S4**). However, it is also a result of the second tallest species being more productive as the community height range increased (**Table 3** and **Supplementary Figure S4**). This is because the second tallest species was significantly more likely to grow taller as the tallest species increased in height (**Figure 3C**, Pearson correlation; $r = 0.8038$, $p < 0.001$). The productivity of the third tallest species was not significantly related to community height range (**Table 3**).

Taller communities were significantly more likely to have larger leaf areas (**Figure 4A**, Pearson correlation, $r = 0.8441$, $p < 0.001$), and leaf area was significantly related to the productivity of a community (**Figure 4B** and **Table 3**).

With increasing productivity of communities, δ^{13}C was significantly likely to be less negative (**Figure 5A** and **Table 3**). There was also a weak, negative relationship between leaf tissue C:N and community production which was marginally non-significant (**Figure 5C** and **Table 3**).

Post hoc Nutrient Analyses

Post hoc analyses showed that the relationship between δ^{13}C and productivity was affected by species identity, because there

TABLE 3 | Linear regression statistics.

	Coefficient	Intercept	Regression statistics			
			r^2	*n*	*F*	*p*
Community productivity (mg DW d^{-1})						
Community height (cm)	2.8416	−8.3139	0.536	14	15	**0.002**
Community height range (cm)	33.73	−70.29	0.482	14	12.09	**0.004**
Community leaf area (mm^2)	11.983	−30.777	0.377	13	7.247	**0.02**
Community $\delta^{13}C$	12.77	192.52	0.457	14	10.93	**0.006**
Community C:N	−44.84	67.88	0.250	14	4.34	0.0575
Community height range (cm)						
Tallest species 90th percentile height (cm)	0.8567	−0.9702	0.954	14	271	**<0.001**
Shortest species 10th percentile height (cm)	1.5712	16.6493	0.179	14	2.833	0.116
Tallest spp. productivity (mg DW d^{-1})						
Community height range (cm)	18.61	−41.26	0.484	14	12.2	**0.004**
***2nd* tallest spp. productivity (mg DW d^{-1})**						
Community height range (cm)	16.965	−42.1	0.289	14	5.276	**0.039**
***3rd* tallest spp. productivity (mg DW d^{-1})**						
Community height range (cm)	13.069	−1.853	0.009	14	0.1108	0.7445

The relationship between community productivity (mg DW d^{-1}) and community traits; height (cm), height range (cm), leaf area (mm^2), leaf tissue $\delta^{13}C$ and leaf tissue carbon: nitrogen (C:N) ratio. The role of the upper (tallest species 90th percentile height) and lower (shortest species 10th percentile height) height limits of community height range (cm) on its variability. The effect of the community height range (cm) on the productivity (mg DW d^{-1}) of the tallest, second tallest and shortest species in a community. The bold values are statistically significant p-values.

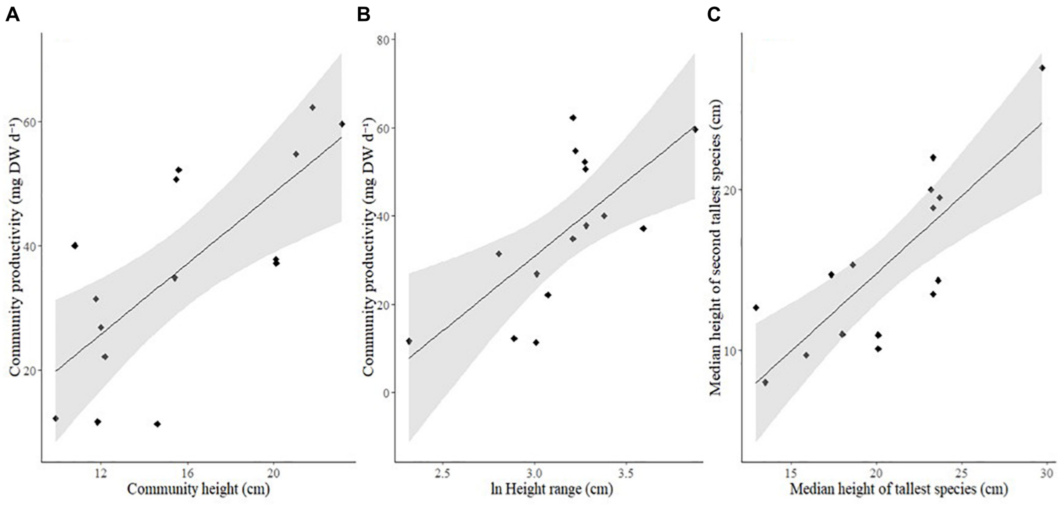

FIGURE 3 | Relationship between **(A)** Community height (cm) and community productivity (mg DW d^{-1}), **(B)** Community height range (ln-transformed, cm) and community productivity (mg DW d^{-1}), **(C)** Median height of tallest species (cm) and median height of second tallest species (cm). Solid line: line of best fit, shaded area: 95% confidence intervals.

was collinearity between species identity and $\delta^{13}C$ (VIF > 100). However, once the collinearity was remediated by centering $\delta^{13}C$ by species identity, a significant relationship between $\delta^{13}C$ and productivity persisted [**Figure 5B**, GLM; $F(1,43) = 21.099$, $p < 0.0001$]. Indeed, while species had significantly different rates of primary productivity [**Figure 5B**, GLM; $F(4,39) = 17.691$, $p < 0.0001$] species identity did not significantly affect the relationship between $\delta^{13}C$ and productivity [**Figure 5D**, GLM; $F(4,35) = 0.794$, $p > 0.05$]. Overall, there appeared to be a validly independent trend between $\delta^{13}C$ and productivity.

For each species in each community, there was a marginally non-significant relationship between the 85th percentile of C:N and productivity (**Figure 5D**, quantile regression; $p = 0.0598$). These trends between C:N and productivity were likely caused by species identity effects because C:N ratios exhibited potential collinearity to species identity (VIF > 10) and once such collinearity was remediated by centering C:N ratios by species identity, the factor ceiling effect was not present ($p > 0.05$) nor was rank C:N significantly related to rank productivity (Overall Wald test = 0.391, $p > 0.05$).

TABLE 4 | Permutation-based multiple regression statistics.

	Pseudo-F	p	
Community productivity (mg DW d^{-1})			
Community height (cm)	11.279	0.0106	
Community start biomass (mg)	3.749	0.0901	
Community leaf area (mm^2)	22.8	0.0015	
Community leaf tissue δ^{15}N	0.91	0.3643	
Community leaf tissue δ^{13}C	10.286	0.0152	
	AICc	**R^2**	***n***
Overall model	28.753	0.999	10

The relationship between community-weighted means for plant traits and community productivity (mg DW d^{-1}), n = 10. Height and leaf area were log-transformed.

Summary Model for Community Trait Relationships to Productivity

The summary model which included the variability of multiple traits (**Table 1**) supported the main findings of the single linear regression analyses; community height, leaf area and leaf tissue δ^{13}C were the most related traits to community productivity (**Table 4**). Also, there were other traits included in the summary model which were not significantly related to productivity when the variability of other traits was not included in the analysis (**Table 4**). Indeed, these traits included in the model were the biomass at the start of the experiment and community leaf tissue δ^{15}N (**Table 4**).

DISCUSSION

Overview

We found FRic to be significantly related to primary production, unlike FEve and FDiv. Also, primary production was more strongly related to specific traits than FD indices, and these traits characterized light capture and nutrient concentrations in the leaves. The summary model supported the main findings of the single linear regression analyses, because it included community height, leaf area, and leaf tissue δ^{13}C. It also included traits which were not significantly related to primary production on an individual basis in the model (**Table 4**) but apparently their variability became relevant after the variability of other traits had been considered. Such traits were the biomass of the community at the start of the experiment and the leaf tissue δ^{15}N; indicative of different N sourcing (e.g., Cloern et al., 2002; Roscher et al., 2012). Overall, the R^2 of the model was very high and indicative of overfitting, however such a high R^2 is also plausible because it included many traits which were strongly related to community productivity. Thus, our results indicated that the traits which we measured in the experiment were strongly linked to primary production.

Some traits had multifaceted benefits for primary production, for example plant height was not only strongly related to community production, but it also could have facilitated a competitive response in the community because the heights of the tallest and second tallest species were correlated. Taller plants were also more likely to have larger leaf areas, and leaf area was also significantly related to productivity. Therefore, these plants were likely to have invested in capturing light more effectively (**Figures 3**, **4** and **Table 1**) and communities with such plants were more productive. Indeed, both height and leaf area were strongly related to community productivity. However, because both traits (height and leaf area) were correlated it is difficult to discern whether productivity was enhanced by both traits independently or only one trait was functionally important for productivity. Many other traits were not significantly related to primary production in the many linear regressions (**Supplementary Table S2**) including those which characterized root properties, leaf tissue N (% DW) concentrations and community δ^{15}N (**Supplementary Table S2**). Trends in δ^{13}C suggested that the ambient carbon supply was likely not replete, because more productive communities were richer in ^{13}C compared to ^{12}C. In this case, they had likely expended more energy to acquire carbon because ^{13}C is heavier and more energy-consuming to metabolize compared to ^{12}C, which is perhaps a consequence of limited carbon availability (Hu et al., 2012). This suggests that carbon availability could have inhibited the increased photosynthesis facilitated to plants (Kiswara et al., 2005; Hu et al., 2012) which had an increased ability to capture light. Therefore, δ^{13}C is likely to have responded to primary productivity, and it is possible that in our experiment, δ^{13}C represented environmental carbon availability in response to productivity rather than affecting it. Thus, an opportunity for further study would be to manipulate, for example, the nutrient availability to experimental communities to explore the dynamics between effect and response traits. With this information, there would be potential to construct an informed and predictive response-effect trait framework for aquatic plants.

Functional Diversity Enhanced Productivity by Selecting for Extreme Trait Values to Capture Light

The relationship between FRic and primary production was likely driven by the variability of height, because height was heavily weighted for the FRic calculation and height range was significantly related to productivity. However, results also showed that the height range of communities was driven by the height of the tallest species. Therefore, FRic was likely related to biomass production due to the presence of taller plants. This was supported by indices which incorporated the distribution of species abundances within the trait space; FDiv and FEve, because their results suggested that it was not the distribution of traits within a community but instead the expression of specific traits. Perhaps also, FEve and FDiv would become more informative in more species-rich communities or in an experiment which accounts for intraspecific variability in the indices. It is apparent from our findings that here, functional diversity could have benefited productivity by selecting for extreme trait values for light capture (selection effect) rather than a complementarity of fundamental niches (complementarity effect) (Loreau, 2000). Cadotte (2017) hypothesized that the

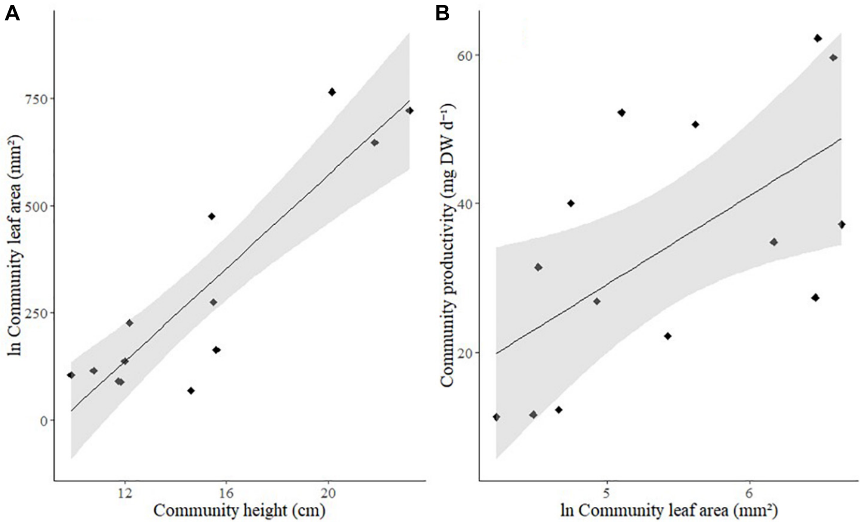

FIGURE 4 | Relationship between **(A)** Community height (cm) and community leaf area (ln-transformed, mm^2), **(B)** Community leaf area (ln-transformed, mm^2) and community productivity (mg DW d^{-1}). Solid line: line of best fit, shaded area: 95% confidence intervals.

selection effect was strongest for plants with similar trait values, which is partly supported by our findings because the two tallest species competed for light, however in this case it did not appear that the shortest species benefited from a complementarity effect with an increased height range. Thus, the benefit of light capture for these submerged aquatic plant communities appears to be unidirectional. Perhaps for emergent plants its effects are not unidirectional once plants reach the water-air interface. Indeed, plant biomass investment in height can change with water depth (Fu et al., 2012).

Plant height is renowned to be a fundamental trait for influencing community productivity (Díaz et al., 2004; Cadotte, 2017; Gustafsson and Norkko, 2019). This study has provided evidence that the benefits of aquatic plant height to community production are multifaceted, because the height of the tallest species was significantly related to community productivity, and its height likely stimulated a competitive height response in the community (**Figure 3**, Hector et al., 1997). Therefore, there is a disproportional increase in productivity in response to the manifestation of this trait (Hector et al., 1997; Cardinale et al., 2002). Such findings show that while it is arbitrary that larger plants (taller plants with larger leaf areas) are strongly related to biomass production, the manifestation of height is clearly related to biomass production for more reasons than its facilitation of plant size.

Increased Productivity Had Carbon Consequences

Temperate aquatic plant meadows are unlikely to have a replete supply of C (Buapet et al., 2013), and C depletion can limit their productivity (Hellblom and Björk, 1999; Buapet et al., 2013). Indeed, it may have been limiting to the more productive communities in this experiment because they had become enriched with the heavy isotope δ^{13}C. Their increased ability to capture light, thus photosynthesize, and uptake carbon at higher rates (Kiswara et al., 2005; Hu et al., 2012), could have facilitated energy-consuming consequences because of their increased demand for C (Kiswara et al., 2005) which led to their enrichment with the heavy isotope ^{13}C. It is noteworthy to recognize that while N and P can be the most limiting to growth in terrestrial communities (Güsewell, 2004), it is also important to incorporate C availability in aquatic environments as a possible limiting factor for growth (Beer and Rehnberg, 1997; Zimmerman et al., 1997; Buapet et al., 2013; Campbell and Fourqurean, 2013). At community level, species differences in δ^{13}C also contributed to the relationship between community δ^{13}C and productivity; which could be related to, for example, their ability to use bicarbonate (HCO_3^-) as a carbon source (Lepoint et al., 2004). Leaf C:N ratios were largely affected by species identity, which is accordant to findings by Li et al. (2015) that species differences in the allocation of nutrients are likely to be more important for the variability of C:N rather than growth rates of aquatic plants. The marginally non-significant relationship between leaf tissue C:N and productivity indicated that there could have been an underlying role for relative species abundances to affect productivity. Indeed, it is clear from these results that species identity was likely to have had an integral role to the results of this experiment; results depended on whether species could manifest certain trait values. However, this was expected because we manipulated the species composition to change the variability of plant traits.

Generalizing Local Findings to Larger Spatial Scales

Gustafsson and Norkko (2019) surveyed aquatic plant meadows which included the natural meadow next to this experimental site. They found that aquatic plant height was the only plant trait with a strong significant relationship to productivity across

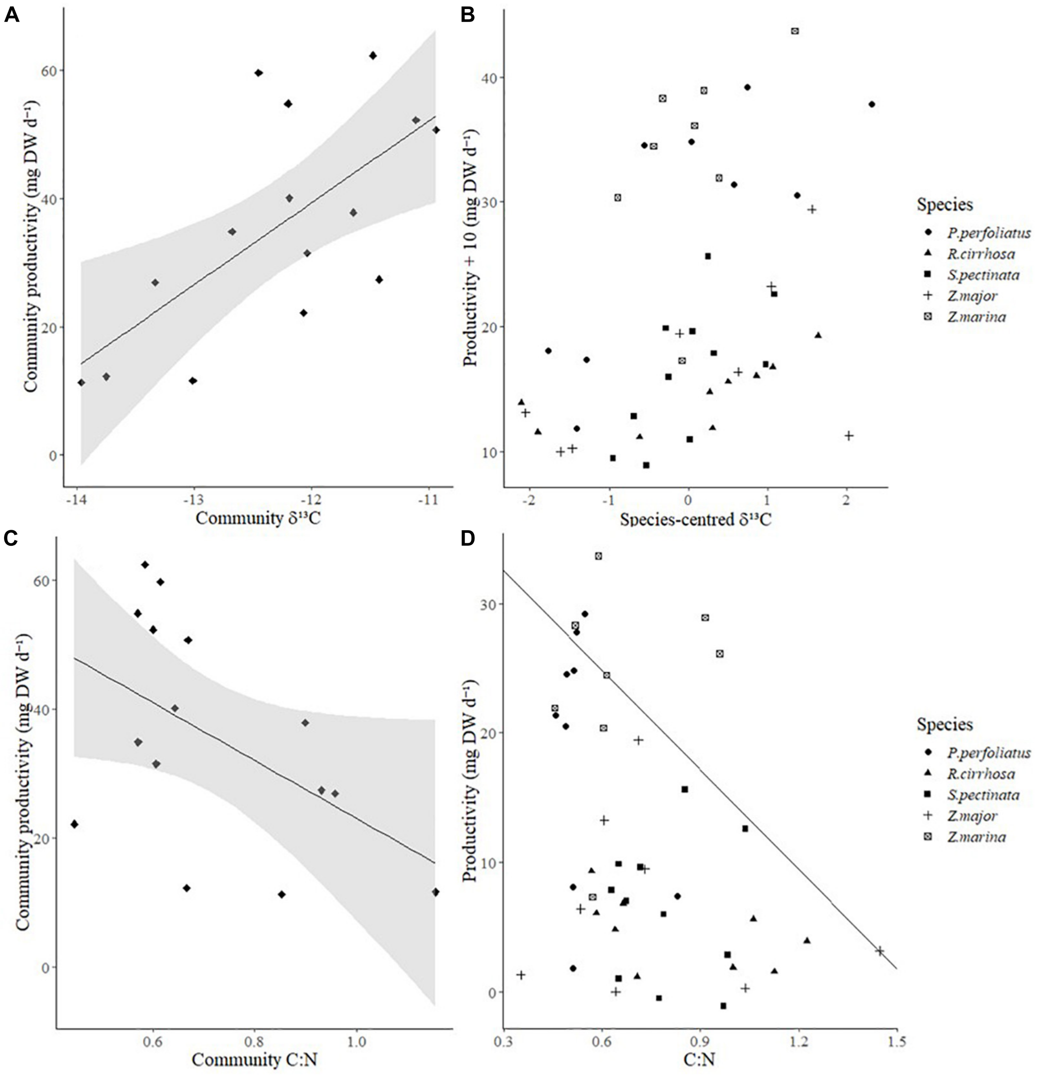

FIGURE 5 | (A) Relationship between community leaf tissue δ^{13}C and community productivity (mg DW d^{-1}); solid line: line of best fit, shaded area: 95% confidence intervals. **(B)** Relationship between species-centered leaf tissue δ^{13}C of each species in each community and their productivity (+ 10 in accordance to its entry in a generalized linear model with error family Gamma, mg DW d^{-1}). **(C)** Relationship between community leaf tissue carbon: nitrogen (C:N) ratios and community productivity (mg DW d^{-1}); solid line: line of best fit, shaded area: 95% confidence intervals. **(D)** Relationship between leaf tissue C:N of each species in each community and their productivity (mg DW d^{-1}); solid line: 85th percentile of productivity with changes in C:N.

environmental scales, and the location of this study was included in their range. Our findings complement this survey because it provides experimental evidence that height is likely to be one of the most related traits to primary productivity. Fu et al. (2014) also found that height was significantly related to primary production along a water depth gradient in freshwater lakes, amongst other traits. In our study, we found that leaf area was also significantly related to primary production and that it was significantly correlated with height, strengthening inferences for the potential generality of our findings. The strong link between leaf area and height indicates that the interaction between closely related traits likely contributes to the overall functioning of aquatic plant communities. For example, in our experiment, the taller plants could have invested in strategies to optimize light capture so that they could facilitate high productivity. This may have catalyzed the increase in productivity relative to height. The relationship between δ^{13}C and productivity were much less variable in our experiment than as observed by Gustafsson and Norkko (2019), and in the local region of this site the relationship was reverse to our observations. This could have been due to the environmental variability in carbon sources across different communities at a larger spatial scale. However, we found no significant relationship between δ^{15}N and productivity like the local region by Gustafsson and Norkko (2019), and potentially the source of nitrogen is not as closely related to productivity compared to other local factors. Whereas, Gustafsson and Norkko (2019) found that δ^{15}N was more closely related to productivity at larger spatial scales, maybe because

$\delta^{15}N$ represented the influence of N sourcing at larger spatial scales, or it became more influential in other conditions. It was included in our summary model which examined the overall relationship between traits and productivity; therefore, perhaps it is also related to productivity for a reason that we have not yet identified, which is linked to the variability of other traits. Overall, Gustafsson and Norkko (2019) suggested that while height is strongly related to productivity across communities, the combination of plant traits which are related to productivity is highly context-dependent. Following our mechanistic study, we build on this to hypothesize that traits linking to light capture are prioritized (i.e., Height and leaf area) (Cadotte, 2017). These findings show that CWMs have been related to productivity so strongly that their changes led to a relationship between functional diversity and productivity. Such findings are accordant to those by Fu et al. (2014) which show that CWMs are likely more related to aquatic plant productivity than a metric for functional diversity. Our results provide further evidence that the dynamics for plants in aquatic environments are significantly different to those in the terrestrial realm (e.g., Carbon availability, water availability and light-nutrient dynamics; Hemminga and Duarte, 2000; Peterson and Heck, 2001; Lee et al., 2007). Furthermore, it is important to acknowledge the ecological independence of aquatic plants to the terrestrial realm and to conduct an informed evaluation. Indeed, with this approach the studies of aquatic plants are not only exploring a relatively new environment, but it also challenges the paradigms for terrestrial environments by exploring how they interact with extremely different environmental conditions (e.g., Refraction of light in the water column which is related to increased nutrient availability; Krause-Jensen et al., 2008). Further studies which investigate the underlying mechanisms of function for aquatic plants would greatly benefit our understanding of the ecology of aquatic and perhaps even terrestrial plants.

CONCLUSION

This is, to our knowledge, the first experiment to manipulate species composition to investigate functional diversity in aquatic plant meadows *in situ*. It shows how functional diversity experiments can be conducted *in situ* in ecosystems beyond terrestrial grasslands, also for those which have a relatively low species-diversity. We found that functional richness was related to community productivity, likely because of a selection effect which enhanced community light capture (height and leaf area). Indeed, there were multifaceted benefits for communities with taller species, because of observed competition between species. It appeared that biomass production came at a consequence to carbon supply, and species identity participated an integral role for the relationship between carbon and productivity. An opportunity for further study would be to explore plant trait responses and build a predictive plant response-effect trait framework.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

CG and CA conceived the ideas and designed methodology. CA, CG, and AN conducted the experiment in the field, analyzed the data, and wrote the manuscript. CA led laboratory processing of the samples.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00140/full#supplementary-material

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