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Quantifying the importance of functional traits for primary production in aquatic plant communities

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Abstract

1. Aquatic plant meadows are important coastal habitats that sustain many ecosystem functions such as primary production and carbon sequestration. Currently, there is a knowledge gap in understanding which plant functional traits, for example, leaf size or plant height underlie primary production in aquatic plant communities.

2. To study how plant traits are related to primary production, we conducted a field survey in the Baltic Sea, Finland, which is characterized by high plant species and functional diversity. Thirty sites along an exposure gradient were sampled (150 plots), and nine plant morphological and chemical traits measured. The aim was to discern how community-weighted mean traits affect community production and whether this relationship changes along an environmental gradient using structural equation modelling (SEM).

3. Plant height had a direct positive effect on production along an exposure gradient ($r = 0.33$) and indirect effects through two leaf chemical traits, leaf $\delta^{15}N$ and leaf $\delta^{13}C$ ($r = 0.24$ and 0.18, respectively) resulting in a total effect of 0.28. In plant communities experiencing varying exposure, traits such as root N concentration and leaf $\delta^{15}N$ had positive and negative effects on production, respectively.

4. *Synthesis*. Our results demonstrate that the relationship between aquatic plant functional traits and community production is variable and changes over environmental gradients. Plant height generally has a positive effect on community production along an exposure gradient, while the link between other traits and production changes in plant communities experiencing varying degrees of exposure. Thus, the underlying biological mechanisms influencing production differ in plant communities, emphasizing the need to resolve variability and its drivers in real-world communities. Importantly, functionally diverse plant communities sustain ecosystem functioning differently and highlight the importance of benthic diversity for coastal ecosystem stability.

KEYWORDS

biodiversity, ecosystem function, effect trait, environmental gradient, macrophytes, seagrass, structural equation modelling, *Zostera marina*

1 | INTRODUCTION

There is general consensus that species identity and the functional traits of species are key to understand the role of biodiversity for ecosystem functioning and how ecosystems respond to environmental disturbance (Díaz & Cabido, 2001; Lavorel & Garnier, 2002). Functional traits can be defined as different morphological, physiological, and phenological traits that influence the fitness of an individual by affecting its growth, reproduction and survival (Violle et al., 2007). Furthermore, traits that determine how a species interacts with its environment can be divided into response and effect traits, for example, how species respond to environmental factors and disturbances (response traits) and which traits in a species reflect its effects on ecosystem functions (effect traits) (Díaz & Cabido, 2001; Garnier, Navas & Grigulis, 2016; Suding et al., 2008; Violle et al., 2007). In general, the positive relationship between biodiversity and ecosystem functioning is thought to be driven by two mechanisms; niche complementarity which includes complementary resource use and selection (dominance) effects where a few dominating species have a proportionally large effect on the relationship (Díaz & Cabido, 2001; Loreau & Hector, 2001). Cadotte (2017), for example, showed that plant assemblages with low trait dissimilarity tend to affect biomass production mainly through selection effects, whereas communities with high trait dissimilarity influence functioning through niche complementarity to a greater extent.

Plant traits linked to ecosystem functioning are often related to the acquisition and resource use, size, and regeneration of plants (Garnier et al., 2016; Westoby, Falster, Moles, Vesk & Wright, 2002). Globally, certain traits, such as adult height, leaf area, and leaf nitrogen content per mass have been found to be central for the ecological strategy of a plant (Díaz et al., 2016). Specific leaf area (SLA) and leaf nitrogen concentration (Leaf N) are considered important for the leaf economic spectrum and may in turn, have large impacts on ecosystem processes, such as on primary production (Garnier et al., 2004; Wright et al., 2004). Trade-offs are common, however, and species with high Leaf N tend to have a lower leaf life span and faster growth, whereas species with lower Leaf N have a higher investment in leaf structure and resource conservation and accordingly, tend to have a longer leaf life span with slower growth (Westoby & Wright, 2006; Wright et al., 2004).

Despite increasing numbers of studies on plant functional traits and ecosystem processes in the terrestrial realm (e.g., Garnier et al., 2004, 2016), analogous studies in marine environments and particularly seagrasses and other aquatic plants are very few. This is unfortunate as humans heavily depend on coastal ecosystems such as seagrass meadows for goods and services (Cullen-Unsworth et al., 2014; Orth et al., 2006). In addition to maintaining biodiversity and modifying the abiotic and biotic environment, seagrasses and other aquatic plants extensively contribute to the high overall productivity found in coastal ecosystems (Duarte, 2000; Fourqueran et al., 2012). To bridge this knowledge gap, a functional group approach including the identification of important effect and response traits is needed. Seagrasses and other aquatic vascular plants have been classified according to categorical traits such as life-history and morphological traits, for example, growth form and reproduction strategy (Blomqvist, Wikström, Carstensen, Qvarfordt & Krause-Jensen, 2014; Carruthers et al., 2007; Unsworth, Collier, Waycott, Mckenzie & Cullen-Unsworth, 2015; Walker, Dennison & Edgar, 1999; Willby, Abernethy & Demars, 2000). de los Santos et al. (2016) in turn, explored leaf mechanical traits among a variety of seagrass species. Moreover, Kilminster et al. (2015) developed a form-functional model using life-history trait data where seagrass species are grouped based on species response to environmental disturbance, while Blomqvist et al. (2014) have studied the trait composition of vegetation along environmental gradients in the Baltic Sea using biological trait analysis (BTA) although not linking it to any particular ecosystem function. Aquatic plant diversity increases primary production with different species having various effects on production (Gustafsson & Boström, 2011; Gustafsson & Norkko, 2016), but the recognition of which underlying continuous effect traits affect such patterns has never been specifically tested prior to this study and thus, remain unknown.

The archipelago areas of the northern Baltic Sea are comprised by complex habitat mosaics which are defined by strong environmental gradients in, for example, exposure and salinity. These areas can generally be divided into three zones; outer, middle, and inner, based on the proportion of land versus water in the landscape and the degree of exposure (Hänninen, Toivonen, Vahteri, Vuorinen & Helminen, 2007; Häyrén, 1900). Gradients in environmental variables, such as salinity, water clarity, and nutrient concentrations, occur when moving from the outer to the inner archipelago (Hänninen et al., 2007). The plant communities in the area are diverse due to the mixture of marine and limnic species (Gustafsson & Boström, 2011; Kautsky, 1988). The species composition and dominance changes between the archipelago zones with marine, biomass-storing species, such as *Zostera marina* and *Ruppia* spp., being common in the more exposed, saline outer areas, while limnic canopy-forming species, for example, *Potamogeton* spp. and *Myriophyllum* spp. occur more frequently in sheltered, less saline inner areas (Kautsky, 1988; Pitkänen, Peuraniemi, Westerbom, Kilpi & von Numers, 2013). Some of these species such as *Stuckenia pectinata* show significant morphological phenotypic plasticity, which may reflect in certain traits exhibiting high intraspecific variability, for example, root:shoot ratio or leaf area (Garnier et al., 2016; Kautsky, 1987). Thus, as the plant species communities and the dominance patterns change along environmental gradients the inter- and intraspecific trait values within communities are likely to change as well (Garnier et al., 2016). This, in turn, might influence the potential relationships between plant traits and primary production on a community-level.

Despite the overall physiological and morphological differences in aquatic plants compared to their terrestrial counterparts such as the lack of stomata, development of aerenchyma and the affinity for different inorganic carbon sources (Kuo & den Hartog, 2006), our aim was to investigate whether similar relationships between continuous plant effect traits and primary production found in terrestrial plant communities (e.g., Díaz et al., 2004; Garnier et al.,

2016) are found in aquatic plant communities. Consequently, we used structural equation modelling (SEM) to test hypotheses on trait–production relationships and, for example, hypothesized that adult height and Leaf N would affect primary production positively (Cadotte, 2017; Garnier et al., 2016). Furthermore, we expected SLA and adult height to indirectly affect primary production through, for example, effects on Leaf N, because correlations between SLA and Leaf N are common among terrestrial plants (Garnier et al., 2016) and tall fast-growing competitive aquatic plants can have rapid nutrient uptake and thus, potentially higher concentrations of nitrogen in their tissues (Kautsky, 1988). The direct effect of SLA on production could be weak or potentially lacking due to differences in seagrass leaf structure compared to terrestrial plants (Cambridge & Lambers, 1998). In addition, as root lengths can indicate the rooting depth and nutrient acquisition potential of seagrasses (Hughes, Stachowicz & Willimas, 2009), we expected root length to have a direct positive effect on primary production and indirect positive effects on production through tissue nutrient concentrations (Root N and Leaf N). The gradient approach taken in this study further allows us to better understand how the changes in the species composition and dominance patterns and the potential plastic responses in intraspecific trait values might affect community primary production differently along an exposure gradient, and consequently, we predicted the links between plant effect traits and primary production to change between archipelago areas. Despite some traits potentially changing along the gradient (response traits) and overlapping with the measured effect traits (Lavorel & Garnier, 2002; Suding et al., 2008), our study aimed at solely evaluating the link between effect traits and production.

2 | MATERIALS AND METHODS

2.1 | Study area and field sampling

A field survey was conducted in the Ekenäs-Hanko archipelago, Finland. 30 sites (Figure 1) were sampled in August 2014 during peak biomass season using SCUBA diving. The area is characterized by strong seasonality in environmental variables (e.g., temperature, photosynthetic active radiation [PAR]) with a marked seasonal succession in production and biomass. The sites were chosen based on their position in the archipelago, whether in more exposed outer, semiexposed middle or more sheltered inner areas, and a priori knowledge of species-rich plant meadows occurring at the site (M. Westerbom pers. comm.). At each site, a 20-m long transect was laid out in species-rich and dense vegetation, and five plots (1 m^2) were randomly sampled along the transect totalling 150 plots. If no vegetation was present where the quadrat was randomly assigned, it was moved until vegetation was found. Horizontally along each transect, depth varied by <0.5 m, while the vertical depth ranged between 1.6 and 3.6 m between different sites. The vertical depth was thus, enough for the plant community not to have been heavily impacted by common disturbances such as water level fluctuations and ice scouring. All plant material (above- and below-ground) was collected from within the plot by careful digging, sometimes to depths of 20–30 cm to access all below-ground material. At each site, two sediment samples were collected with a syringe ($\varnothing$ 2 cm) to approximately 10 cm depth and three sediment porewater NH_4^+ samples were collected using Rhizon soil moisture samplers (type SMS: length 100 mm, $\varnothing$ 2.5 mm). The samplers were inserted 10 cm into the sediment and connected to 125 ml vacuum bottles.
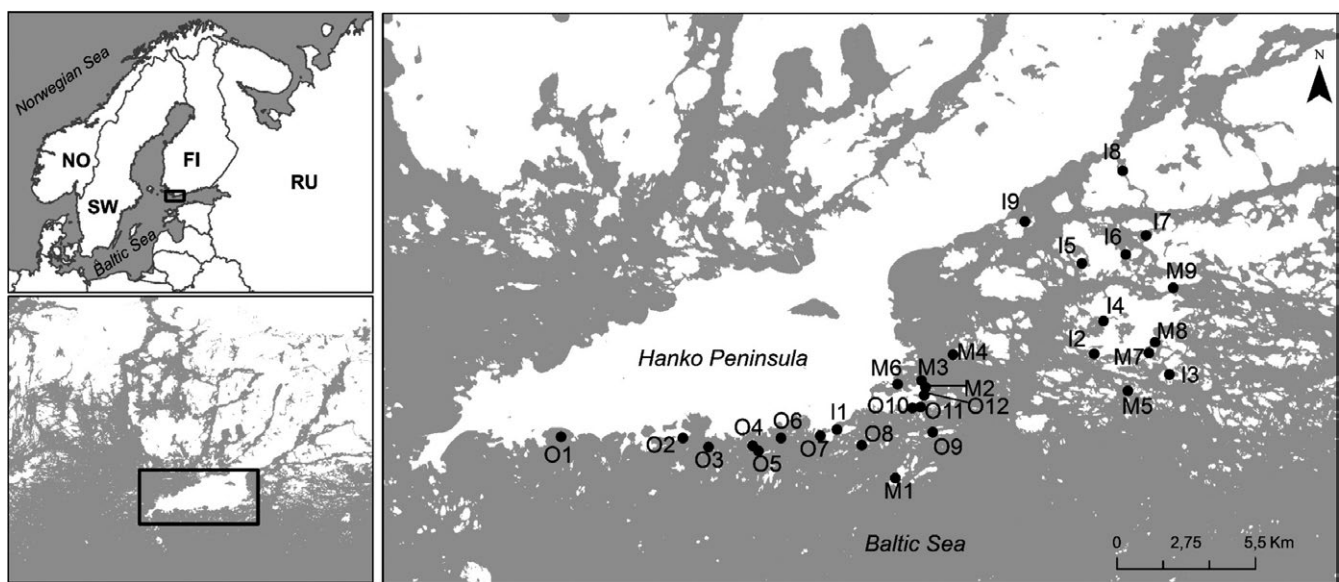

FIGURE 1 Map of the study area with sites featured. The site classification was based on principal component analysis (PCA) where sites were clustered along an exposure gradient based on three abiotic sediment variables (Figure S1, grain size > 0.25 mm, % silt fraction (< 0.063 mm) and mean grain size). Site labels denote O = exposed outer sites, M = semiexposed middle sites and I = sheltered inner sites, respectively. The coordinates of the sites were imported into ARCGIS 10.1 software (Esri). Map sources: Countries, 2014—European Commission, Eurostat/GISCO. Administrative boundaries: ©EuroGeographics, ©FAO (UN), ©TurkStat Source: European Commission—Eurostat/GISCO. Contains data from the National Land Survey of Finland Topographic Database 10/2017

The porewater samples were kept on ice in the dark upon arrival to the laboratory. In addition, one water column sample for the determination of NH_4^+-N was collected from each site and treated as mentioned above. To obtain information on the range in environmental conditions (light and temperature) at the time of sampling, we measured PAR (μmol photons m²/s) and temperature at three sites every 5–15 min using light loggers (HOBO Pendant® Temperature/Light Data Logger 64 K; Onset) deployed at canopy height at 2.2–2.8 m depth for 1 week each in August 2014. The light data from the loggers (lumens/ft²) was converted to PAR using the equation in Gustafsson and Norkko (2016) and converted to daily PAR (mol m⁻² day⁻¹). The salinity in the water column was measured with a portable conductivity meter VWR EC 300.

2.2 | Laboratory analysis

Plant and sediment samples were frozen (−18°C) immediately upon arrival in the laboratory. Water column and porewater samples were filtered (Whatman GF/F), frozen (−18°C), and later analysed spectrophotometrically for NH_4^+-N using an autoanalyzer (Aquakem 250) based on the analytical methods by Hansen and Koroleff (1999). Plant and sediment samples were thawed, the number and identity of different species and shoot densities of each species were recorded, and plant biomass were sorted into leaf and stem (aboveground), rhizome, and root biomass (below-ground) per species, while the sediment samples were analysed for grain size and organic content (LOI method). Prior to the grain size analysis, hydrogen peroxide (H_2O_2, 6%) was added to the sediment samples to dissolve any organic material present. The grain size distribution was determined by sieving sediment samples through a series of sieves (2, 1, 0.5, 0.25, 0.125, and 0.063 mm). The sediment retained in the sieves was dried (48 h, 60°C) and weighed. To retrieve the mean grain size (phi) (Folk & Ward, 1957) of each site, we used the program GRADISTAT v8.0 (Blott & Pye, 2001).

2.3 | Trait selection and measurement

In the laboratory, nine different morphological and chemical traits were measured on each species within a plot following standardized trait measurement protocols by Pérez-Harguindeguy et al. (2013). The maximum vegetative height (hereafter H_{max}) of each species was determined by measuring the two tallest shoots from the top of the photosynthetic tissue to where the shoot is attached to its rhizome. H_{max} is, for example, related to the light interception of the plant (Pérez-Harguindeguy et al., 2013) and thus, likely linked to primary production. If no intact specimens were retrieved from a sample, an average H_{max} from the other plots from the same site was used. The specific leaf area (SLA, mm²/mg) was determined by selecting two mature and intact leaves of each species from two different shoots. In terrestrial studies, SLA has a considerable impact on primary production across genera and latitude (Díaz et al., 2004). The leaf sheath was excluded, where after the leaf was weighed for the wet weight, scanned with an Epson flatbed scanner, dried (48 h, 60°C),

and weighed for the dry weight. The areal measurements were done by using the image processing program ImageJ (Schindelin, Rueden, Hiner & Eliceiri, 2015). If no intact leaves were found in a plot, an average SLA derived from the other plots from the same site was used. The leaf and root nitrogen (Leaf and Root N) concentrations (mg/g) were measured on species from 1 to 2 plots from each site. Material was collected from young leaves and roots and to get enough material of each species, the material was pooled from several individuals within the plot. The material was dried (48 h, 60°C) and ground to a fine powder with a ball mill (Retsch MM 400). The elemental concentrations, and leaf and root $\delta^{15}N$ and $\delta^{13}C$ were determined from the same samples by using an elemental analyser interfaced to an isotope ratio mass spectrometer (UC Davis Stable Isotope Facility). The stable isotope signatures are reported in delta notation in relation to the international standards for C (Vienna PeeDee Belemnite) and N (Air). The $\delta^{15}N$ values indicate which available nitrogen pools a plant species utilizes. For example, higher values (more positive) are usually found in plants that utilize nitrogen derived from aquatic sediments where microbial processes tend to yield inorganic nitrogen enriched in $\delta^{15}N$ (Cline & Kaplan, 1975; Cloern, Canuel & Harris, 2002). In turn, values closer to 0 indicate that the plant species uses nitrogen derived from nitrogen-fixing bacteria such as cyanobacteria (Cloern et al., 2002). $\delta^{13}C$ is used to assess the differences in the photosynthetic pathway and source of inorganic carbon (Cloern et al., 2002). In seagrasses, increasing $\delta^{13}C$ can potentially be linked to increased photosynthetic C demand (Hu, Burdige & Zimmerman, 2012; Roca et al., 2015). In general, the $\delta^{13}C$ of aquatic plants tends to be quite variable due to, for example, changes in the isotopic ratio of DIC in the water column (Cloern et al., 2002). For maximum root length (Root), the 5–10 longest intact roots were measured on each species from a plot. The maximum root length can indicate the potential rooting depth with subsequent nutrient acquisition potential (Hughes et al., 2009) assuming that the roots grow vertically. As all the biomass of species was divided into foliage, rhizomes, and roots, it was possible to calculate the root:shoot ratio (R:S-ratio), which indicates the amount of biomass allocated to roots for nutrient uptake and foliage to increase light capture (Poorter et al., 2012).

Primary production estimates for the different plant species were obtained from Kautsky (1988) and extrapolated to m⁻² by multiplying with the amount of biomass per species/m², consequently summing the community production for every plot. For species with no net production data (e.g., *Myriophyllum sibiricum*), estimates for species from the same genus (e.g., *Myriophyllum spicatum*) were used.

2.4 | Data analysis

Community-weighted mean (CWM) trait values (Garnier et al., 2004) were calculated for each plot (*n* = 150) with the *FD* package in R (Laliberté, Legendre & Shipley, 2014) using shoot density as a weighting variable. For the CWM calculations, the average SLA per species from one plot was used (pooled from two measurements). The maximum root length per species (Root) in each plot was the median value of minimum five, maximum ten roots from a minimum

of three individuals. The average nutrient concentration and isotope values derived from two samples of each species per site were used as representative values of each species per site and used for all plots from each site. The CWM values were standardized to have a mean of 0 and variance of 1 (Magurran & McGill, 2011). All trait values hereafter are community-weighted means.

Sites were clustered along a gradient of wave exposure into three different archipelago areas using principal component analysis (PCA). The distribution of the data was inspected by histograms and draftsman plots. Skewed variables were either square-root or log-transformed to retrieve a normal distribution (Clarke, Gorley, Somerfield & Warwick, 2014). After the transformation, data was standardized to have a mean of 0 and variance of 1 (Clarke et al., 2014), where after a PCA was conducted. The data was further clustered using CLUSTER analysis on a resemblance matrix based on Euclidean distance followed by a SIMPROF test (significance level 0.05, 9,999 permutations). In the PCA, long-term integrators of environmental conditions, that is, mean grain size, % silt fraction (<0.063 mm), and grain size >0.25 mm were the focal abiotic variables, while other environmental variables such as temperature, salinity, and water column nutrients were considered short-term descriptors of site environmental conditions, and thus prone to high variability caused by stochastic events within short time periods. The sites clustered into four clusters based on grain size >0.25 mm, % silt fraction (<0.063 mm), and mean grain size (phi) (Folk & Ward, 1957) (Figure S1). Sites located in the outer and middle areas formed two obvious clusters, whereas two clusters were formed for the more sheltered sites in the inner area. The sites in the two clusters (I-sites) were more closely related on a Euclidean distance measure

than the two other clusters (O and M) and as one of the clusters only contained three sites (I2, I5, I8, Figure S1), we opted to merge them with the other sheltered cluster (containing 6 sites, I-sites, Figure S1) to increase replication for further analyses. In addition, the sites from the two combined clusters all had a mean grain size >3.4 and a % silt fraction >37% in common, both indicating a lower energy environment, that is, less exposure (Valanko, Norkko & Norkko, 2010).

To explore similarity in community species and trait composition at different sites, we conducted nonmetric multidimensional scaling (nMDS) based on $\sqrt{\sqrt{}}$-transformed densities (species composition) and log-transformed community-weighted trait values (trait composition) and Bray–Curtis similarities. In order to match the MDS with the number of samples of environmental variables ($n = 30$), the ordination was based on species average shoot densities or the average trait composition per each site calculated on the five samples collected from each site. For the species density, we opted to $\sqrt{\sqrt{}}$-transform the data to take into account rarer species (Clarke et al., 2014) and to improve the data distribution of the trait composition, it was log-transformed. Furthermore, to explore how the three environmental variables derived from the PCA and the average shoot density of each species or average trait composition were correlated to the MDS axes we overlaid a vector (Pearson correlation >0.3) on the nMDS plot. To study whether differences in species community or trait composition were statistically solid, we conducted a two-way nested ANOSIM with 9,999 permutations where factor Site was nested within factor Archipelago area. The analysis was performed on the full dataset with five plots per site ($n = 150$). Furthermore, to discern which species contributed the most to the found dissimilarities in community composition between different
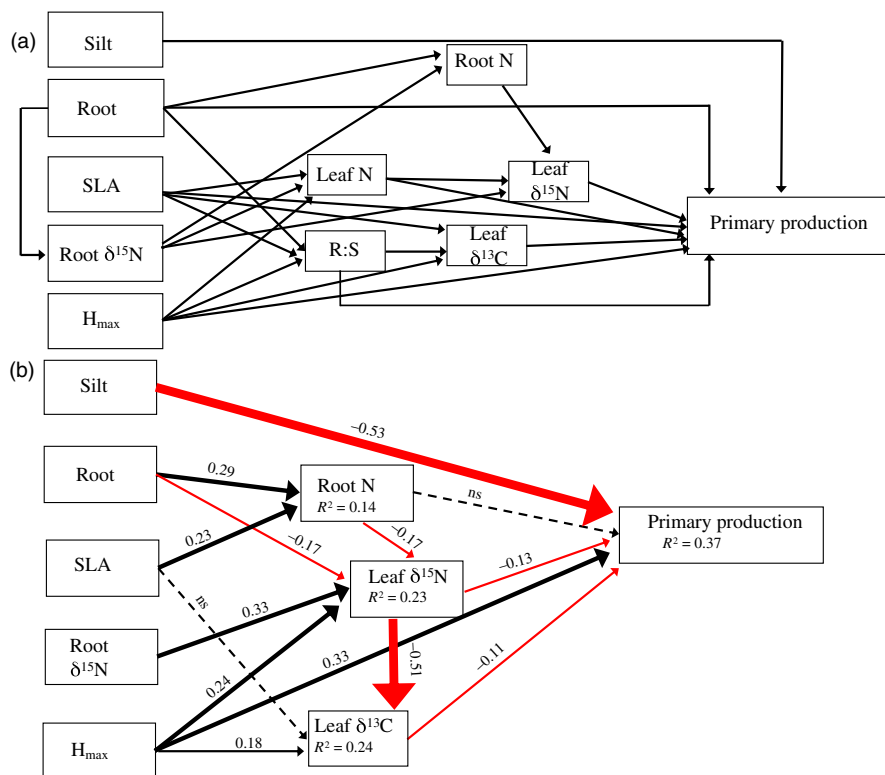

FIGURE 2 (a) Conceptual model of the hypothesized relationships for all variables and paths included in the whole model. (b) Best-fit whole model (based on the complete dataset) showing significant relationships between variables. All trait variables are community-weighted by shoot density and primary production denotes production/m^2. Silt (% sediment silt fraction <0.063 mm) is an abiotic variable used as a proxy for wave exposure. The red denotes negative and black positive relationships, respectively, and the arrow width represents the standardized path coefficients. The dashed line denotes an insignificant relationship. The marginal R^2 values are given for endogenous variables [Colour figure can be viewed at wileyonlinelibrary.com]

Archipelago area groups, we conducted a similarity breakdown analysis, SIMPER. All multivariate analyses were carried out in PRIMER v7 (Clarke et al., 2014).

To investigate relationships between plant traits and primary production, we used SEM. Before proceeding to the modelling of the data, we inspected the data for outliers, nonlinear relationships and non-normal distributions. Primary production and silt fraction were log-transformed (ln-transformed) to improve normality. A random effect was included to model variation in the intercepts among the 30 sites and the responses were fit with linear mixed models using the function lme from the NLME package in R (Pinheiro, Bates, DebRoy & Sarkar, 2013). Due to the hierarchical random structure of the data with five plots nested within each site (150 plots in total), we used piecewise SEM to fit the path models using the package *piecewiseSEM* in R (Lefcheck, 2015), which in contrast to traditional variance–covariance-based SEM, can be used for nested data (Lefcheck, 2015). We constructed a full model of hypothesized paths between traits and primary production (Figure 2a) where we considered root, SLA, H_{max}, and silt exogenous variables, that is, the other variables included in the model would not explain them. We hypothesized that, for example, SLA, Leaf N, and H_{max} would influence primary production (Cadotte, 2017; Díaz et al., 2004; Garnier et al., 2004), after which we assessed the goodness-of-fit of the model (Fisher's *C* statistic) using the Shipley's test of directional separation (Shipley, 2009). The D-separation test reveals significant missing relationships between variables and by including a significant missing path the model fit can be improved. Models with an adequate fit ($p > 0.05$) were considered candidate models and their AICc computed (AIC corrected for small sample size) and compared. The model with the lowest AICc value was considered the best-fit model. To assess model validity, we plotted residuals against fitted values for each component model.

As piecewise SEM cannot handle latent variables (such as a PCA axis incorporating a combination of observed variables, Lefcheck, 2015), we chose the % silt fraction as a proxy for wave exposure. The % silt fraction indicates the hydrodynamic forcing with less silt (lower accumulation of fine particles) being found in wave-exposed high-energy environments (Valanko et al., 2010). In the graphical assessment of variables prior to fitting the SEMs, we noticed a negative relationship between plant community biomass and silt fraction and a positive relationship between biomass and primary production. Because primary production was standardized to gram biomass, biomass was not included as a separate endogenous variable in the SEM-analysis, but instead, we used primary production as a proxy for biomass and silt as a predictor of primary production. We constructed one SEM for the whole data. Once the best-fit candidate model was derived for the whole dataset by conducting Shipley's *D*-separation tests (see above) the best-fit model was used as the hypothesized full model for each of the three different areas along an exposure gradient, that is, the outer, middle and inner areas. For every area, we constructed a set of candidate models with a fit $p > 0.05$ and compared the AICc for each model (see above). Subsequently, we were able to evaluate links between

community-weighted traits and community primary production for each area separately and reveal potential differences in the relationships between traits and primary production in each area.

3 | RESULTS

3.1 | Environmental variables and plant communities along an exposure gradient

Variations in salinity were marginal and ranged between 4.4 and 5.7 but the sediment organic content tended to be higher at the more inner sites (Table S1). The results from the PCA revealed that sites clustered along a wave exposure gradient into more exposed outer, semiexposed middle, and sheltered inner archipelago areas in response to three environmental variables; grain size >0.25 mm, % silt fraction (<0.063 mm), and mean grain size, which were all considered proxies of wave exposure. PCA axes 1 and 2 together almost explained 95% of the variation (Figure S1). A vector overlay with length 0.3 on a nMDS revealed that grain size >0.25 mm increased with MDS 1, which is indicative of more exposed sites with a similar plant community composition (Figure S2a). In turn, both mean grain size and silt fraction decreased with MDS 1 and thus, indicated more sheltered sites. Furthermore, we aimed at investigating how the structure and diversity of the plant communities in terms of shoot density, species composition, and plant richness varied along the wave exposure gradient. An MDS revealed that on average, the species composition changed from the outer to the inner archipelago (Figure S2). In addition, the average biomass and shoot densities increased when moving from the inner to the outer sites (Figure S3, Table S1). In total, 14 species were found along the gradient (Table S2) with the peak richness (i.e., number of species), 9 species at a site (average 4 species/replicate) found in the exposed archipelago and the lowest richness, 1 species found at a site (average 1 species/replicate) in the inner archipelago. The average shoot densities of *Z. marina*, *S. pectinata*, *Ruppia cirrhosa*, and *Zannichellia major* all tended to increase towards the more exposed sites (Figure S2b). Species more common in sheltered environments such as *Ceratophyllum demersum*, *Najas marina*, and *Callitriche hermaphroditica* in turn, had fairly strong negative relationships with MDS 1. In addition, *N. marina*, *C. demersum*, and *Potamogeton perfoliatus* showed quite strong relationships to MDS 2. This axis mainly separates sites within the inner area and indicates large variability in species communities at the more sheltered sites. To investigate whether the species communities differed between archipelago areas, we performed an ANOSIM analysis that revealed that the species communities differed between the different archipelago areas (Global $R = 0.42$, $p < 0.01$). Pairwise tests further showed that plant communities growing in outer and inner areas and outer and middle areas, respectively, differed the most (Table 1), while the differences between communities in the middle and inner areas were not as marked (Table 1). The analysis also revealed that Site had an effect on plant communities (Global $R = 0.76$, $p < 0.01$) but as we wanted to explore how plant community composition might change

TABLE 1 Results from ANOSIM showing how dissimilar (%) the plant species communities were on average between the different archipelago areas (Global test, *R*, and *p*-values) and the contribution of each species to the observed dissimilarities between areas based on SIMPER. Data is √√-transformed and based on shoot densities of plant species

Outer vs. Middle (Global test, *R* = 0.409, *p* < 0.01) Average dissimilarity = 68.91			
Average shoot density			
Species	**Outer**	**Middle**	**Contribution %**
Zostera marina	1.88	0.16	17.86
Stuckenia pectinata	2.01	0.74	15.8
Zannichellia major	1.72	0.44	15.21
Ruppia cirrhosa	1.35	0.38	11.38
Zannichellia palustris	0.33	1.03	9.74
Potamogeton perfoliatus	1.45	1.9	8.88
Outer vs. Inner (Global test, *R* = 0.609, *p* < 0.01) Average dissimilarity = 80.25			
Average shoot density			
Species	**Outer**	**Inner**	**Contribution %**
Zostera marina	1.88	0	16.49
Stuckenia pectinata	2.01	0.51	14.94
Zannichellia major	1.72	0	13.72
Potamogeton perfoliatus	1.45	1.24	10.58
Ceratophyllum demersum	0.33	1.31	9.8
Ruppia cirrhosa	1.35	0	9.04
Middle vs. Inner (Global test, *R* = 0.159, *p* < 0.05) Average dissimilarity = 68.41			
Average shoot density			
Species	**Middle**	**Inner**	**Contribution %**
Potamogeton perfoliatus	1.9	1.24	15.92
Ceratophyllum demersum	0.59	1.31	14.26
Zannichellia palustris	1.03	0.53	13.14
Callitriche hermaphroditica	0.04	1.02	11.26
Stuckenia pectinata	0.74	0.51	10.34
Myriophyllum spicatum	0.35	0.22	6.11

along an exposure gradient, the community composition between sites within an archipelago area was not deemed important. Thus, we conducted a SIMPER analysis on the Archipelago area to investigate how similar the species composition was within each area. The analysis revealed that the species composition was on average >45% similar in the outer areas with *S. pectinata*, *Z. marina*, and *Z. major* all contributing >20% to the similarity in community composition. The middle communities were on average 43% similar with *P. perfoliatus* contributing with >60% to the similarity in species community composition. The innermost plant communities were more variable than the aforementioned and only had a 37% similar species composition with *C. demersum* and *P. perfoliatus* contributing with >65% to the observed similarities. Not surprisingly, plant communities

in the outer and inner areas differed the most (Table 1) with three species, *Z. marina*, *S. pectinata*, and *Z. major*, contributing by almost half (>45%) to the found differences in plant communities. The same three species also contributed by almost 50% to the differences between plant communities in the outer and middle areas (Table 1). Furthermore, we aimed at exploring how the average trait composition of the communities might differ by conducting an ANOSIM analysis. The results revealed that the division between sites was not as clear as with species shoot densities (Figure S2c). The average trait composition in the outer and middle, and middle and inner areas were not significantly different (Global *R* = 0.02, *p* > 0.05 and Global *R* = 0.17, *p* > 0.05, respectively); however, the trait composition differed between inner and outer areas (Global *R* = 0.32, *p* < 0.05).

3.2 | Relationship between plant traits and primary production

Our best-fit model on the whole dataset (Fisher's *C* = 14.35, *p* = 0.94) revealed that overall, 37% of the variation in community primary production could be explained by the % silt fraction (a proxy for wave exposure) and four different community-weighted trait variables; H_{max}, Leaf $\delta^{13}C$, Leaf $\delta^{15}N$, and Root N (Figure 2b). Silt had a strong negative effect on primary production while H_{max} had a positive effect on primary production (Figure 2b, Table 2). The total effect of H_{max} on primary production was 0.28. Leaf N and R:S-ratio had no effects on primary production and the model including these pathways had a poor fit (Fisher's *C* = 120, *p* < 0.001) with a higher AICc value compared to the best-fit model (287.36 and 91.41, respectively). SLA had no direct effect on primary production, even though it indirectly influenced primary production through Root N and Leaf $\delta^{13}C$ (Figure 2b).

To explore how the relationship between community-weighted traits and community primary production might vary in different archipelago areas, we conducted separate models for each area with results revealing that different biological mechanisms were likely operating in the different areas. In the best-fit model for the outer area (Fisher's *C* = 17.5, *p* = 0.62), H_{max} and Root N showed a positive relationship with primary production, while Leaf $\delta^{13}C$ showed a negative effect (Figure 3a, Table S3a). These three plant traits explained almost 20% of the total variance associated with community primary production. In addition, H_{max} showed a strong positive effect on Leaf $\delta^{15}N$, but Leaf $\delta^{15}N$ was not causally linked to primary production. SLA had no effect on any other variables and was consequently dropped from the model to increase fit. In the middle area, the best-fit model (Fisher's *C* = 15.79, *p* = 0.90) discerned no significant links to primary production (Figure 3b). H_{max} showed a positive, albeit nonsignificant effect on primary production (Table S3b). In contrast to the plant communities in the outer areas, SLA affected Root N positively, while it had a negative effect on Leaf $\delta^{13}C$ (Figure 3b, Table S3b). The maximum root length (Root) in turn, was dropped from the model due to no clear effect on any other variables. In contrast to the outer area, Leaf $\delta^{13}C$ had a negative effect on Root N (Figure 3a,b). Another difference to the outer model was the absent

TABLE 2 Path coefficients for the best-fit model (Figure 2b). Silt (% silt fraction <0.063 mm) and primary production (Primprod) are ln-transformed. The trait values are community-weighted means and standardized to have a mean of 0 and variance of 1

Response		Predictor	Unstandardized estimate	SE	Standardized estimate	SE	p value	
Root N	←	Root	0.29	0.08	0.29	0.08	<0.001	***
Root N	←	SLA	0.23	0.08	0.23	0.08	0.005	**
Leaf δ^{15}N	←	Root δ^{15}N	0.33	0.07	0.33	0.07	<0.001	***
Leaf δ^{15}N	←	H_{max}	0.24	0.08	0.24	0.08	0.002	**
Leaf δ^{15}N	←	Root N	−0.17	0.08	−0.17	0.08	0.032	*
Leaf δ^{15}N	←	Root	−0.17	0.08	−0.16	0.08	0.041	*
Leaf δ^{13}C	←	Leaf δ^{15}N	−0.51	0.08	−0.51	0.08	<0.001	***
Leaf δ^{13}C	←	H_{max}	0.18	0.08	0.18	0.08	0.026	*
Leaf δ^{13}C	←	SLA	−0.15	0.08	−0.15	0.08	0.065	ns
Primprod	←	H_{max}	0.35	0.05	0.33	0.05	<0.001	***
Primprod	←	Silt	−0.53	0.12	−0.55	0.12	<0.001	***
Primprod	←	Leaf δ^{15}N	−0.14	0.06	−0.13	0.05	0.017	*
Primprod	←	Leaf δ^{13}C	−0.11	0.05	−0.11	0.05	0.040	*
Primprod	←	Root N	0.09	0.05	0.08	0.05	0.080	ns

Note. ns: non-signifcant. *p < 0.05, **p < 0.01, ***p < 0.001.

effect of H_{max} on Leaf δ^{15}N, which in turn was prominent in the outer plant communities (Figure 3a). In the innermost area, the best-fit model (Fisher's C = 30, p = 0.36) revealed that H_{max} and Leaf δ^{15}N had medium-strong direct effects on primary production; Leaf δ^{15}N a negative and H_{max} a positive effect, respectively. In addition, Root had an indirect effect on production through Leaf δ^{15}N (Figure 3c, Table S3c). The total variance of primary production explained by these variables was close to 20%. Similar to the plant communities in the middle area, we found a strong negative relationship between Leaf δ^{15}N and Leaf δ^{13}C, while Root influenced Root N positively, akin to the relationship found in the outer plant communities (Figure 3a,c).

4 | DISCUSSION

In contrast to the various terrestrial studies that have focused on continuous plant functional traits (e.g., Leaf N, SLA) and the links to ecosystem functioning (Garnier et al., 2016), this is to our knowledge, the first study that explores the relationship between continuous aquatic plant traits and primary production along an environmental gradient. Our results demonstrate that the relationship between plant traits and production is variable and context-dependent, and this further emphasizes the importance of trying to resolve variability in real-world communities. Only one of the measured traits, H_{max}, was clearly linked to primary production, while two leaf traits, Leaf δ^{15}N and Leaf δ^{13}C had a weak effect. Traits such as Leaf N and SLA were not related to production, which suggests that in aquatic plant communities, the influence of these traits on production is insignificant compared to terrestrial ecosystems. Accordingly, the general patterns found in terrestrial plant communities with a few traits having a considerable effect on primary production (Díaz et al., 2004;

Garnier et al., 2004) is not as evident in aquatic plant communities. Aquatic macrophytes function differently compared to their terrestrial counterparts, probably caused by both morphological and physiological adaptations to the surrounding medium (Kuo & den Hartog, 2006) and key abiotic factors influencing plant growth such as temperature or light differ greatly in range in aqueous media (Bornette & Puijalon, 2011). Our results further reveal how different plant communities perform along an exposure gradient and discern that the underlying biological mechanisms affecting primary production are different depending on the plant community. This is an important notion as functionally diverse communities sustain primary production in different ways with further implications for the ecosystem stability and the sustenance of functioning in a changing environment (Díaz & Cabido, 2001).

4.1 | General relationship between plant traits and primary production

Dominance and competitive ability among plants can be enhanced by certain traits such as individual plant biomass and height (Gaudet & Keddy, 1988). Such traits can explain ecosystem processes, for example, primary production to a larger extent than traits leading to resource complementarity (Roscher et al., 2012). Complementarity and selection effects underlie positive relationships in plant communities in the Baltic Sea (Gustafsson & Boström, 2011; Salo, Gustafsson & Boström, 2009). Cadotte (2017) noted that for primary production, the selection effect is frequently best explained by one trait only, plant height. Our results corroborate our hypothesis that overall, plant height, H_{max}, had a direct positive effect on primary production (Figure 2b) and in more detail, also in plant communities in the outer and inner areas (Figure 3a,c). Seagrasses and other submersed macrophytes are often controlled by light-limitation (Barko, Adams
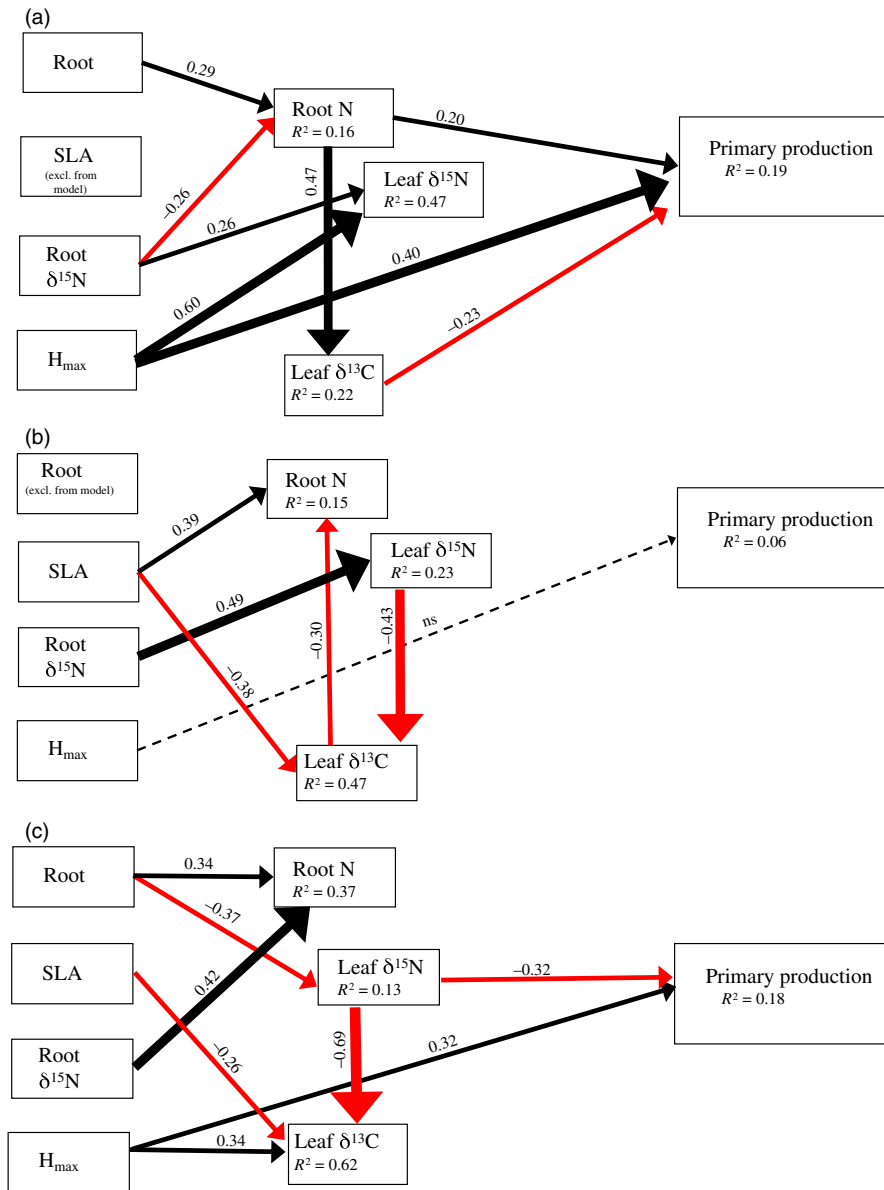
FIGURE 3 The best-fit models for different areas with the best-fit model for the whole area (Figure 2b) used as the base model. Significant relationships between variables shown in the (a) outer (b) middle, and (c) inner archipelago, respectively. All trait variables are community-weighted by shoot density and primary production denotes production/m^2. The sampled sites were divided into three archipelago areas based on a principal component analysis (PCA) with three abiotic variables relating to wave exposure used as clustering variables (see Figure S1). Red denotes negative and black positive relationships, respectively, and the arrow width represents the standardized path coefficients. The dashed line denotes an insignificant relationship. The marginal R^2 values are given for endogenous variables [Colour figure can be viewed at wileyonlinelibrary.com]

& Clesceri, 1986; Ralph, Durako, Enríquez, Collier & Doblin, 2007) so it is not very surprising that H_{max}, which is related to the light capture influences primary production in aquatic meadows. Similar results have also been found for saltmarsh plant communities, where canopy height exerted a positive influence on above-ground production (Minden & Kleyer, 2015). Our results further indicate that tall species, for example, *Z. marina* and *S. pectinata* that dominated the species community in the outer areas and *P. perfoliatus* in the inner areas (Table 1, Figure S2b) also had a large effect on the production. Both *S. pectinata* and *P. perfoliatus* are fast-growing competitors with high nutrient acquisition potential that form large canopies, whereas

Z. marina is a ruderal, biomass-storing species with slower production rates (Gustafsson & Norkko, 2016; Kautsky, 1988). However, as *Z. marina* was a frequent community component of several outer sites, it influenced the community-weighted H_{max} considerably at a number of sites with further implications for community production. In addition to H_{max}, two leaf chemical traits (Leaf δ^{15}N and Leaf δ^{13}C) had a weak negative effect on primary production, indicating that in communities with high primary production the light availability was lower and/or the DIC source highly variable (negative δ^{13}C, Durako & Hall, 1992; Cloern et al., 2002; Hu et al., 2012) and the plants derived their nitrogen from nitrogen-fixing bacteria such as cyanobacteria

(Cloern et al., 2002). The former relationship was only found to be significant in the outer area, whereas the latter (Leaf δ^{15}N and primary production) in the innermost area (Figure 3a,c). Noticeably, H_{max} exerted a positive effect on both leaf chemical traits, thus also affecting primary production indirectly (Figure 2b). Surprisingly, Leaf N had neither direct nor indirect effects through other variables on primary production. This contrasted our hypothesis based on terrestrial work where Leaf N can be linked to the leaf economics spectrum and further to enhanced production (Garnier et al., 2016; Wright et al., 2004). The absent relationship can have been caused by the fact that light is often the limiting factor for growth in eutrophic environments such as the Baltic Sea (Gustafsson et al., 2012), whereas in more oligotrophic conditions, nutrients are of higher importance (Burkholder, Tomasko & Touchette, 2007). As discussed above, the negative relationship between Leaf δ^{13}C and production could indicate low light availability and further corroborate light being a limiting factor for production.

The strong negative effect of silt on primary production reflected the change in biomass moving from the outer to the inner archipelago (Figure S3, Table S1) since primary production was standardized to g biomass. The high biomass in the outer archipelago was influenced by the occurrence of meadow-forming species (e.g., *Z. marina* and *Ruppia* spp., Figure S2) with high average biomass and shoot densities/m^2 (Table S1), whereas the communities in the inner areas were mainly composed of canopy-forming species such as *Myriophyllum* spp. and *P. perfoliatus* (Madsen, Chambers, James, Koch, & Westlake, 2001) with lower biomass and shoot densities/m^2 (Table S1). As we hypothesized, SLA did not have a direct effect on primary production in our study. Cambridge and Lambers (1998) proposed that among seagrasses, SLA is not an important trait for growth because seagrasses have a modified leaf structure compared to terrestrial plants and the epidermis, for example, contains most of the photosynthetic apparatus. Conversely, SLA is an important trait for the leaf economics spectrum of terrestrial plants and often show a strong correlation with photosynthesis and relative growth rate (Garnier et al., 2004, 2016), further supporting the notion that terrestrial and aquatic plants function somewhat differently. In salt-marsh plant communities that occur in the terrestrial-marine interface, both SLA and the CN-ratio of the whole plant have also been linked to the decomposition of biomass (Minden & Kleyer, 2011), but whether these traits influence the same process in submerged plant communities remains to be tested.

4.2 | Plant traits and the link to production along an exposure gradient

Traits often respond to environmental gradients and different ecological processes such as abiotic and biotic filtering, selection, and plasticity may all influence observed patterns between traits and the environment (Garnier et al., 2016). The species in our study conform to different ecological strategies based on the CSR model by Grime (1979). Thus, species belonging to a certain strategy can have very similar characteristics, for example, competitors tend to have rapid growth

and nutrient uptake rates, in our study represented by canopy-forming species such as *P. perfoliatus* and *Myriophyllum* spp. (Kautsky, 1988). On the other hand, biomass-storing species such as *Z. marina*, have slower growth but still possess large above- and below-ground biomass. Environmental gradients shape the strategies of plants and thus, the value of traits that respond to environmental changes or disturbances, that is, response traits (Díaz & Cabido, 2001) often change along environmental gradients. H_{max}, SLA, and Leaf N are all examples of traits that can change depending on environmental factors, for example, in terrestrial environments H_{max} and SLA tend to increase with nutrient availability (Garnier et al., 2016). Both abiotic and biotic filters act as selective forces that influence species distributions and the functional structure of communities. *Z. marina*, for example, thrives in the outer archipelago where wave exposure is higher resulting in increased physical disturbance. It has an extensive rhizome-root mat that anchors it firmly to the seafloor and flat, flexible strap-like leaves reducing drag (Madsen et al., 2001), both important characteristics for a species tolerating local environmental conditions that include frequent strong water movement. *Z. marina* also manifests a quite unique trait combination for a Baltic Sea aquatic plant species with overwintering biomass, energy storage capacity, and salinity tolerance (Blomqvist et al., 2014). Other species that could competitively exclude *Z. marina* in terms of growth rate or nutrient uptake, for example, the competitive species *P. perfoliatus* or *C. demersum* cannot thrive in exposed areas because of their shoot morphology (*P. perfoliatus* rigid stem with broad leaves) or lack of roots (*C. demersum*) and generally occur in areas with less wave exposure (Kautsky, 1988). Some species are morphologically plastic, for example, the biomass allocation of *S. pectinata* distinctly changes with wave exposure (Kautsky, 1987), which in turn affects the intraspecific variability in R: S ratios. The change in trait values along gradients is caused by both intraspecific variation and inherent differences between species (Garnier et al., 2016). As such changes in trait values exist within and among communities, it can manifest in very different community trait values over spatial scales with varying effects on primary production. In such circumstances, response and effect traits can overlap and the same traits having an effect on a function also respond to an environmental change along a gradient (Lavorel & Garnier, 2002; Suding et al., 2008).

The negative effect of Leaf δ^{13}C on production in the outer archipelago was surprising in that seagrasses that were common or even dominating the communities at a few sites in the outer areas also often have more enriched Leaf δ^{13}C values (more positive values) than other marine/aquatic autotrophs. This can partly be explained not only by their use of HCO_3^- as a Ci source but also other factors such as photosynthetic rate, light availability, and water flow can cause variation in δ^{13}C with a higher value indicating carbon-limited photosynthesis (Hu et al., 2012; Lepoint, Dauby & Gobert, 2004). However, many freshwater angiosperms are also able to use HCO_3^- as a Ci source (Keeley & Sandquist, 1992; Maberly & Madsen, 1998). A possible reason to the negative relationship may, for example be, low light availability causing lower photosynthetic activity with lower Ci demand (Hu et al., 2012). Overall, the δ^{13}C of aquatic plants is often highly variable, partly because of the isotopic variability in the

dissolved inorganic carbon (DIC) source pool (Cloern et al., 2002). Thus, the high variability in Leaf δ^{13}C probably obscured any clear relationships with community production in the more sheltered areas. However, the marked difference between areas was the influence of other variables on Leaf δ^{13}C. In the outer areas, Root N had a strong positive effect on Leaf δ^{13}C, while in the middle and inner areas Leaf δ^{15}N had a negative effect on Leaf δ^{13}C (Figure 3). A plausible explanation to the positive relationship between Root N and Leaf δ^{13}C is that with increasing nitrogen available for growth the demand for photosynthetic carbon also increases (enriched δ^{13}C values). The negative relationship between Leaf δ^{15}N and Leaf δ^{13}C could in turn indicate that in the innermost areas the nitrogen used by plants is derived from nitrogen-fixing bacteria such as cyanobacteria (δ-values close to 0, Cloern et al., 2002) and that these plants have more negative δ^{13}C values due to, for example, increased light attenuation in the innermost areas (Durako & Hall, 1992; Hänninen et al., 2007) or increased use of CO_2^- due to lower water alkalinity (Maberly & Madsen, 1998). In addition, plants with lower Leaf δ^{15}N had a higher primary production, which gave rise to the negative effect of Leaf δ^{15}N on primary production (Figure 3c). Maberly and Madsen (1998) showed that freshwater macrophytes that had a higher affinity to CO_2^- (with a more negative δ^{13}C-value) also had a smaller SLA. In our study, SLA had a negative effect on Leaf δ^{13}C in both middle and inner areas, which further suggests that some of the freshwater species with low SLA found in the more sheltered areas, used CO_2^- as a Ci source.

5 | CONCLUSIONS

Despite generalities in the relationship between plant functional traits and primary production in terrestrial environments the patterns are not similar in aquatic environments. Our results demonstrate that the relationship between plant effect traits and community production is variable and changes over environmental gradients. Plant height generally has a positive effect on community production along an exposure gradient, while the link between other traits and production changes in plant communities experiencing varying degrees of exposure. Thus, the underlying biological mechanisms influencing production differ in plant communities. Effect–response trait frameworks have been tested in terrestrial and saltmarsh plant communities (Minden & Kleyer, 2011, 2015; Suding et al., 2008) and the natural next step would be to develop one for aquatic plants. Such a framework could reveal how environmental factors interact with response traits and how these traits in turn, are related to effect traits and ecosystem functioning (Suding et al., 2008). In addition, we are lacking an understanding of how temporal scales may change the link between plant functional diversity and ecosystem functioning. Communities are not static and the trait composition in a community changes over temporal scales in terms of ecological succession. Moreover, it is likely that many of the measured traits that lacked a direct link to the focal process in this study, for example, root length is important for other functions such as nutrient uptake and nutrient cycling (Angove et al.,

unpublished), which further highlights the importance of ecosystem multifunctionality (Hector & Bagchi, 2007; Lefcheck et al., 2015; Minden & Kleyer, 2015). In future studies where the relationship between traits and ecosystem functioning is explored, integrating environmental factors, time and multifunctionality will become even more relevant. Importantly, functionally diverse plant communities sustain ecosystem functioning differently and highlight the importance of benthic diversity for coastal ecosystem stability.

AUTHORS' CONTRIBUTIONS

C.G. conceived the ideas and designed methodology, C.G. and A.N. collected the data; C.G. analysed the data. C.G. wrote the first draft of the manuscript, and both C.G. and A.N. contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The dataset used for the structural equation modelling is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad. jd8f99n (Gustafsson & Norkko, 2018).

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