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RESEARCH PAPER

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Latitudinal variation in plant defence against herbivory in a marine foundation species does not follow a linear pattern: The importance of resource availability

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Abstract

Aim: Studies on latitudinal patterns in plant defence have traditionally overlooked the potential effect that resource availability may have in shaping plant defence. Likewise, latitudinal patterns of tolerance traits have rarely been studied, yet they can be a critical component of plant defence. Therefore, the aim of our study was to examine latitudinal variation in the production of tolerance and resistance traits against herbivory along a latitudinal range and a natural gradient of resource availability from upwelling conditions.

Location: North America (Canada, USA, Mexico).

Time period: Summer months of 2015.

Major taxa used: The seagrass *Zostera marina*.

Methods: We conducted experiments simulating macroherbivore (e.g., bird, fish) damage on the seagrass *Z. marina* at 10 sites across the Eastern Pacific coast (Canada–Mexico) and Quebec and analysed several traits related to resistance and tolerance strategies against herbivory. In addition, we examined the effects of potential seagrass changes in defence strategies by performing a series of feeding experiments with mesoherbivores in a subset of sites.

Results: We found that eelgrass resistance defences did not follow a linear latitudinal pattern but rather followed a bell-shaped curve which correlated with bottom-up control. In sites with higher nutrient availability, plants allocated resources to tolerance strategies and had lower resistance traits. Furthermore, seagrasses did not respond linearly to increased herbivory pressure; while they tolerated moderate levels of herbivory, they underwent a significant reduction in tolerance and resistance under high herbivory levels, which also made them more susceptible to consumers in feeding experiments.

[Correction added on 21 November 2020, after first online publication: the affiliation for Katharyn Boyer has been updated.]

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Main conclusions: Our results highlight the importance that nutrient availability has in shaping latitudinal patterns of plant defence against herbivory and show how these defences may not respond linearly to increased herbivory pressure in seagrasses.

KEYWORDS
herbivory, latitudinal gradient, limited resource model, nutrients, phenolic compounds, plant–herbivore interactions, resource availability, seagrass, upwelling, *Zostera marina*

1 | INTRODUCTION

Biotic interactions such as herbivory strongly influence plant fitness and distribution patterns (Wisz et al., 2013) and consequently plants have evolved diverse defence strategies to tolerate and resist herbivory (Núñez-Farfan et al., 2007; Strauss & Agrawal, 1999). Tolerance strategies mitigate the negative effects of herbivory to plant fitness, for example, by compensating the biomass lost through herbivory with compensatory growth or by accumulating resources belowground to invest in regrowth (Rosenthal & Kotanen, 1994; Tiffin, 2000). Resistance strategies reduce the feeding preference or performance of herbivores by, for instance, reducing plant palatability or nutritional quality (Fritz & Simms, 1992). The strength of trophic interactions, and thus herbivory, is hypothesized to follow a latitudinal gradient with higher interactions towards lower latitudes (i.e., biotic interactions hypothesis, BIH; Schemske et al., 2009). This phenomenon has led to the proposal that plants are better defended towards lower latitudes (i.e., the latitudinal-herbivory-defence-hypothesis; LHDH; Coley & Aide, 1991). For instance, salt marsh plant palatability decreases towards lower latitudes as a result of lower leaf nitrogen content, higher toughness or higher content of secondary compounds (Ho & Pennings, 2013; Pennings et al., 2001; Siska et al., 2002). In the marine environment, algae collected from tropical sites have higher chemical defences (phenolic compounds), and thus lower palatability, when compared to temperate sites (Bolser & Hay, 1996; Demko et al., 2017).

However, both the BIH and the LHDH remain topics of controversy (Anstett, Nunes, et al., 2016; Hillebrand, 2004; Moles, 2013) and recent reviews have found weak support for the LHDH both in terrestrial and marine environments. There is conflicting evidence in relation to plant chemical defences (e.g., plants have more chemical defences in temperate regions; Moles et al., 2011), and contradictory results in feeding patterns (Moles et al., 2011; Poore et al., 2012; Zhang et al., 2016). Importantly, these reviews, as well as many of the works therein, do not consider important aspects that can drive plant–herbivore interactions when examining these relationships besides chemical defence, such as nutritional quality, tolerance strategies or environmental resources. In fact, other mechanisms (e.g., changes in cost of defence due to biogeography; Kooyers et al., 2017) may explain the latitudinal variability observed in plant defence. It has been pointed out that the solution to this controversy requires new investigations that encompass broad latitudinal geographic areas and that use consistent standardized methods among sites. Also, studies need to consider more types of defence traits (Anstett, Nunes, et al., 2016; Schemske et al., 2009) including defence induction (Anstett, Chen, et al., 2016) and nutritional quality (Moles et al., 2011), and incorporate the use of feeding preference experiments to understand the mechanisms of interaction.

Most studies exploring latitudinal patterns in plant defence have focused on herbivore damage and resistance strategies, while latitudinal patterns in tolerance strategies have been largely unexplored (Anstett, Nunes, et al., 2016), yet they are a critical element of plant defence strategies (Núñez-Farfan et al., 2007; Strauss & Agrawal, 1999). The few existing tolerance studies have only measured compensatory growth, and have yielded inconsistent results likely due to biogeographic effects such as similar regrowth responses driven by different selective pressures (e.g., leaf loss by freezing at high latitudes, and herbivore damage at low latitudes; Wieski & Pennings, 2014; Woods et al., 2012). Importantly, plants have several other tolerance traits against herbivory (e.g., belowground reserves) whose variations have not been examined in a latitudinal context.

The availability of resources greatly influences the production of defensive traits, since resources allocated to defence can trade-off with growth and reproduction (Strauss et al., 2002). The resource availability hypothesis (RAH; Coley et al., 1985) postulates that plants in resource-rich environments invest in induction of secondary metabolites (produced in response to herbivory) instead of investing in constitutive resistance (produced regardless of the risk of attack; Agrawal & Karban, 1999). However, recent works assessing the predictions of the RAH for intraspecific variations in plant defence (intraspecific-RAH), propose the opposite; that is, that plant populations from resource-rich environments have higher constitutive resistance, which is mediated by the higher herbivory pressure often found in these environments. Accordingly, in low-resource environments, inducibility of resistance traits should be more

effective and would trade-off with constitutive resistance (Hahn & Maron, 2016). Regarding tolerance strategies, resources have also been postulated to drive their production. For instance, the limiting resource model (LRM) proposes that plants are more tolerant to herbivory when limiting resources are available and if herbivore damage does not actually hamper the acquisition or use of those resources (Wise & Abrahamson, 2007).

Since environmental resources (e.g., light, nutrients) change with latitude, latitudinal patterns of both resistance and tolerance defence strategies are also likely to be influenced by resource availability in addition to herbivore pressure or damage. Furthermore, the level of herbivore pressure (i.e., duration and/or intensity) can also shift plant defence responses. While some traits may be more prevalent under high herbivory rates (e.g., induction of secondary metabolites; Dostálek et al., 2016), others are induced under moderate pressure (e.g., compensatory growth; Vergés et al., 2008). Understanding how resource availability and herbivory may interact to modify plant defence traits in a latitudinal context is highly relevant, especially in marine environments, given that eutrophication is usually a concern in coastal areas and upwelling events are predicted to increase their intensity due to climate change (García-Reyes et al., 2015; Xiu et al., 2018). However, to our knowledge no studies have analysed these interactions in a wide latitudinal range.

Beyond environmental factors, the suite of defence traits that plants exhibit against herbivory involve different traits that are heritable and influenced by genetic constraints that modulate the expression of these traits (e.g., genetic variation; Andrew et al., 2007; O'Reilly-Wapstra et al., 2002). In fact, reduction of genotypic richness or increased inbreeding reduce plant resistance to herbivory (Du et al., 2008; Moreira et al., 2014). Therefore, it is important to consider genetic variations in influencing patterns of plant defence, especially in wide spatial range investigations such as latitudinal studies.

Plant–herbivore interactions can have profound effects in ecosystems, especially when involving foundation species, due to direct (e.g., loss of feeding resources) and indirect (e.g., loss of refuge) impacts on associated species as well as on ecosystem properties (e.g., nutrient cycling; Silliman et al., 2013). As foundation species, seagrasses create critical coastal ecosystems and contribute to many ecosystem services (e.g., carbon burial, reduction of coastal erosion; Nordlund et al., 2016). Seagrasses are chemically defended (Zidorn, 2016) and studies have shown that some seagrass traits such as below- and aboveground biomass vary with latitude (Clausen et al., 2014; Ruesink et al., 2018; Soissons et al., 2018), yet, to our knowledge, no works have studied latitudinal variations in defences against herbivory in seagrasses. Importantly, given their critical role as foundation species, variations in the ecological roles of seagrasses are expected in concert with variations in plant traits and interactions with herbivores.

The aim of this study was to investigate the applicability of the resource hypotheses (RAH, LRM) in explaining latitudinal patterns of plant tolerance and resistance traits against herbivory and the potential inductive responses to different herbivory rates. Integrating these elements is necessary in wide latitudinal studies because plants are exposed to gradients of herbivory and resource availability, and thus, their allocation of resources to defence is likely constrained by the interaction between these two factors. We predicted that marine plants from regions with more resources available (e.g., upwelling sites) would allocate more resources to tolerance (following the LRM), having higher (following the intraspecific-RAH) constitutive resistance and lower inducibility of secondary metabolites under grazing pressure. Consequently, we expected that herbivores would modify their feeding behaviour in response to changes in plant traits. We tested these predictions by performing a simulated herbivory experiment with the seagrass *Zostera marina*. *Zostera marina* is a dominant foundation species in estuaries and coastal areas across the Northern Hemisphere and is consumed by a wide variety of grazers including birds and small invertebrates (e.g., amphipods, isopods), which can strongly influence eelgrass abundance and distribution (Kollars et al., 2017; Reynolds et al., 2012; Tomas et al., 2011). Although, to our knowledge, there are no comprehensive studies on the levels of herbivory along the sites of this study, numerous herbivores that feed on seagrass such as isopods, amphipods and waterfowl are present in the study sites (personal observation, G.H., K.B., S.K., F.T., Duffy et al., 2013; Hayduk et al., 2019; Kollars et al., 2017; Reynolds et al., 2012). While the studies that have explored patterns in herbivory pressure in seagrasses do not find a consistent latitudinal tendency (Vergés et al., 2018), temperate seagrasses are expected to suffer increasingly higher herbivory damage due to the poleward expansion of tropical herbivores (Hyndes et al., 2016; Vergés et al., 2014).

We replicated a simulated herbivory experiment on several sites across the US west coast, Mexico and Quebec to (a) examine the influence of latitude (and associated changes in some environmental factors) on plant defence strategies against herbivory and to (b) assess the effects of latitude (and associated changes in environmental factors) and herbivory on these strategies and their trade-offs. We followed these manipulative experiments with feeding choice experiments to (c) investigate how herbivore-driven changes in plant traits affect seagrass palatability to other herbivores within the community.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We performed simulated herbivory experiments at 10 study sites (nine of them along the eastern coast of the Pacific Ocean) ranging approximately 20 degrees in latitude (52–32° N), from Calvert Island in Canada to Ensenada in Mexico (Figure 1, Supporting Information Figure S1 and Table S1). Along this latitudinal range, mean coastal sea surface temperature (SST) decreases from south to north (Figure 1) while the mean nutrient (i.e., NO_3) concentration exhibits a maximum off the coast of California where coastal upwelling is most intense (Figure 1b and Supporting Information Figure S2). This upwelling

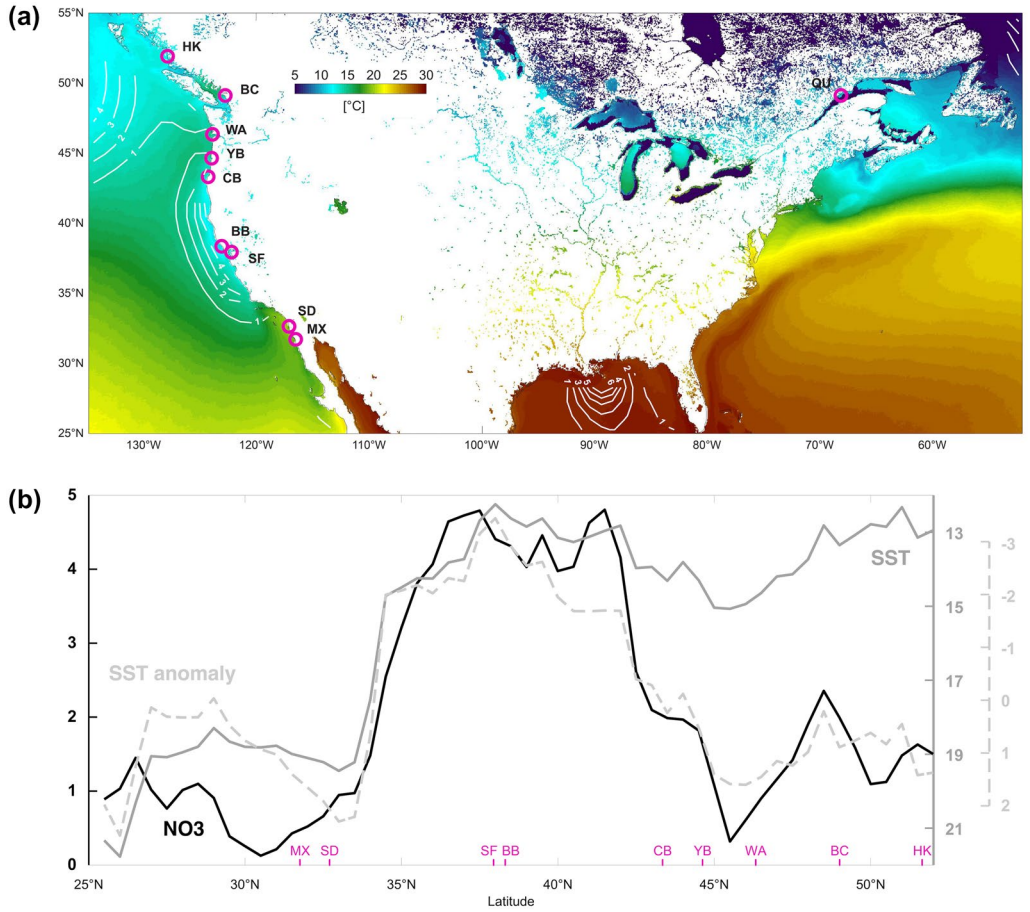

FIGURE 1 (a) Mean May-June-July satellite sea surface temperature (SST) derived from the 1982–2008 Advanced Very High Resolution Radiometer Pathfinder Project data set. White contours indicate mean May-June-July NO_3(μmol/L) from the 1878–2012 World Ocean Atlas data set. The locations of the study sites; Calvert (Hakai, Canada; HK), Baie St. Ludger (Quebec, Canada; QU), Tsawwaseen (British Columbia, Canada; BC), Willapa (Washington, US; WA), Yaquina Bay (Oregon, US; YB), Coos Bay (Oregon, US; CB), West side Regional Park (Bodega Bay, California, US; BB), Point Molate (San Francisco, California, US; SF), San Diego Bay (San Diego, California, US; SD) and Punta Banda Estuary (Ensenada, Baja California, Mexico; MX), are indicated with magenta circles. (b) Comparison of the May-June-July NO_3(μmol/L; black) with the May-June-July SST (°C; grey) and the SST anomaly (SST without latitudinal gradient; dashed light grey) along the Pacific coast. Note the reverse axis for the SST and the SST anomaly (i.e., detrended SST)

strongly influences the nutrient availability and community structure of coastal reefs (Menge & Menge, 2013) and estuaries in the US west coast (Hayduk et al., 2019; Hessing-Lewis & Hacker, 2013). Indeed, leaf N of seagrasses in study sites exhibits a significant positive correlation with NO_3 values (Supporting Information Figure S3). Further descriptions about the abiotic factors of the study sites are provided in the Supporting Information (Study Site Description S1).

The experiment started the first week of May 2015 and was maintained for a total of 10–11 weeks in order to capture plant chemical and size changes. A total of fifteen 4-m^2 experimental plots, five per treatment, were randomly distributed in shallow subtidal (0.5–1 m at low tide) homogeneous monospecific meadows of *Z. marina* (low wave exposure and low natural herbivory) avoiding the edges of meadows or patchy areas. Plots were separated by 3 m and the treatments were randomly assigned to each plot.

The experimental treatments consisted of three simulated herbivory levels; control (i.e., natural low levels), moderate (i.e., removal of 40% of maximum leaf length) and high (i.e., removal of 80% of maximum leaf length), with maximum leaf length being quantified initially as the average maximum leaf length of five plants measured per plot. Herbivory simulation was performed by leaf clipping, a standard procedure for simulating herbivory from macroherbivores such as fish or birds in seagrasses (Holzer & McGlathery, 2016; Sanmartí et al., 2014; Tomas et al., 2015; Valentine et al., 2004; Vergés et al., 2008) that produces similar effects to natural grazing in seagrasses (Fourqurean et al., 2010; Holzer & McGlathery, 2016). All the seagrass shoots in the plot and 20 cm outside the plot were clipped every 2 weeks throughout the experimental period. At the end of the experiment, five to ten shoots were collected from the experimental plots to perform analyses of tolerance and resistance traits (see below and Supporting Information Table S2).

2.2 | Plant tolerance traits

Leaf relative growth rate and shoot size are tolerance traits related to compensatory growth response (Tiffin, 2000; Vergés et al., 2008;

Supporting Information Table S2). Leaf relative growth rate (RGR; per day) was measured in five to ten shoots per plot by hole punching leaves 2 weeks before the end of the experiment following the method of Zieman (1974) and dividing the growth area by the total leaf area of the shoot and the number of days elapsed since punching. Leaf width, maximum leaf length, number of leaves, total leaf area, leaf biomass, sheath area (proxy of shoot size and unaffected by clipping; Ruesink et al., 2018), rhizome biomass and number of rhizome internodes were measured at the end of the experiment.

Nitrogen, carbon and sucrose of the three newest formed leaves (hereafter young leaves) and of rhizomes as well as belowground (i.e., rhizome) starch content were analysed from pooled plant material collected at the end of the experiment. All these chemical traits are considered tolerance traits (Supporting Information Table S2) since belowground resources can be reallocated to reproduction or regrowth after herbivory (Stowe et al., 2000; Tiffin, 2000). N and C in all tissues were analysed using a Carlo-Erba Instruments (Egelsbach, Germany) elemental analyser. Sucrose and starch were analysed with the anthrone assay. A more extensive explanation for the categorization of tolerance traits, and detailed methods for chemical analyses of plant traits are described in the Supporting Information (Methodology S1, Table S2).

2.3 | Plant resistance traits

Specific phenolic compounds, nitrogen, carbon, and fibre content in leaves are considered resistance traits (Supporting Information Table S2) due to their effects on the palatability or digestibility of the plant, and therefore herbivore preference (Hernán et al., 2019; Sieg & Kubanek, 2013). These traits were analysed in young leaves from pooled plant material collected at the end of the experiment. Specific phenolic compounds were analysed with ultra-performance liquid chromatography-tandem mass-spectrometry as in Hernán et al. (2017) with modifications (see Supporting Information Methodology S1). We identified seven phenolic compounds; rosmarinic acid (RA), and six flavonoids [i.e., apigenin-7-sulphate, APS; diosmetin-7-sulphate, DS; luteolin-7-sulphate, LUTS; luteolin-7-O-β-glucoside, LUTG; luteolin-7,3'-disulphate, LUTS2; luteolin-7-O-β-(6''-malonyl) glucoside, LUTMG]. Specific leaf area (SLA = leaf area/ leaf weight; cm^2/g), which is used to evaluate leaf toughness (with high SLA indicating low toughness; Paul et al., 2012), was quantified in five to ten shoots per plot at the end of the experiment. A detailed methodology for all chemical analyses of plant traits can be found in the Supporting Information (Methodology S1).

2.4 | Genetic metrics

Allelic richness and genotypic diversity (clonality) may follow a linear or unimodal latitudinal gradient, reflecting phylogeographic history in which range edges show low diversity and an overall attenuation from south to north. These variables were assessed to be used as covariates to control for genetic variance. Genetic metrics (allelic richness and genotypic richness) were assessed on 20 shoots per site (maintaining 2 m between shoots) with 24 microsatellite loci. Details about the methodology for genetic metrics of eelgrass can be found in the Supporting Information (Methodology S2).

2.5 | Herbivore feeding assays

To examine the effect of simulated herbivory-driven changes on feeding behaviour of other herbivores within the community, we conducted a series of three-choice feeding experiments in which we measured tissue consumption (i.e., tissue consumed from one treatment relative to the total tissue consumed). The experiments were performed with an invertebrate grazer commonly found in *Z. marina* seagrass beds along the Central and North Pacific coast, the isopod *Pentidotea resecata*. The isopods were collected from two sites (Coos Bay and Yaquina Bay) and were offered fresh eelgrass leaves without epiphytes collected from all three simulated herbivory treatments of their own sites. Additionally, in order to examine if the feeding patterns observed were driven by mechanical-structural or chemical traits, we performed three-choice feeding experiments with agar-based artificial food (Siska et al., 2002; Tomas et al., 2015). The experiments consisted of 10–15 replicates and ended when approximately 50% of initial material was consumed. Further details about the methodology of the feeding assays are provided in the Supporting Information (Methodology S3).

2.6 | Statistical analyses

We calculated one mean value of the response variables measured per plot having thus five replicates per treatment and site. We performed a principal component analysis (PCA) with all the 31 plant response variables measured or calculated from the variables measured (e.g., rhizome biomass per internode = rhizome biomass/number of internodes; SLA; RGR) in order to visualize possible patterns of plant defence strategies across clipping treatments and sites (Figure 2). We tested our predictions (effects of latitude, resource availability and simulated herbivory treatments, and their interactions) while controlling for potential covariation introduced by the genetic traits using univariate general linear models (GLMs). Prior to performing the GLMs, we explored the correlation among our response variables to reduce the number of GLMs to fit (Supporting Information Figure S3) and selected 15 response variables that are also the more relevant as defence traits (i.e., leaf RGR, number of leaves, sheath area, rhizome biomass per internode, leaf nitrogen, carbon and sucrose content, rhizome nitrogen, carbon, sucrose and starch content, SLA, leaf fibre content, total flavonoids and specific phenolic compounds) to test our

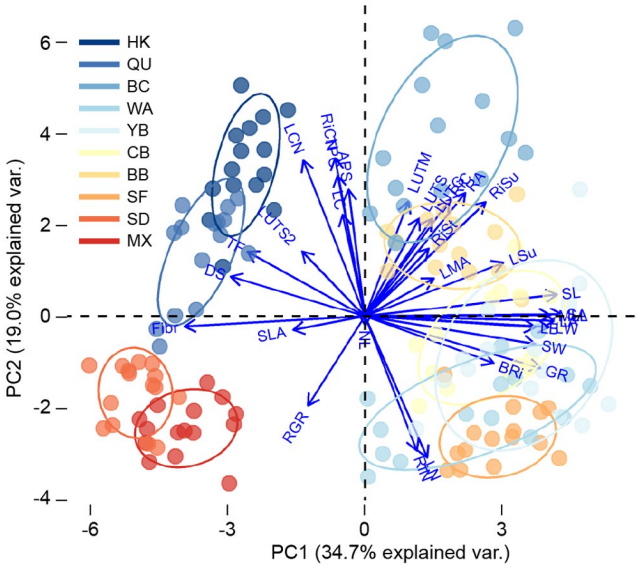

FIGURE 2 Principal component analysis. Arrows represent the loading of the variables. Dots represent the score of each replicate on principal component 1 (PC1) and PC2. Circles group the replicates within each site and sites are coded as in Figure 1. RGR = leaf relative growth rate; NL = number of leaves; LW = leaf width; LB = leaf biomass; LA = leaf area; MLL = maximum leaf length; SA = sheath area; LMA = leaf mass area; SL = sheath length; SW = sheath width; BRi = biomass of rhizome per internode; LSu = leaf sucrose content; RiSt = rhizome starch content; RiSu = rhizome sucrose content; RiN = rhizome nitrogen content; RiC = rhizome carbon content; RiCN = rhizome C/N; SLA = specific leaf area; LN = leaf nitrogen content; LC = leaf carbon content; LCN = leaf C/N; Fibr = leaf fibre; TF = total flavonoids; TPC = total phenolic compounds; flavonoids [LUTG = luteolin-7-O-β-glucoside; LUTS2 = luteolin-7,3'-disulphate; LUTM = luteolin-7-O-β-(6''-malonyl) glucoside; LUTS = luteolin-7-sulphate; APS = apigenin-7-sulphate; DS = diosmetin-7-sulphate]; RA = rosmarinic acid

hypotheses. We also explored the correlation between potential explanatory variables (genetic covariates, SST, latitude and NO_3) to avoid collinearity in the model fitting and discarded SST due to its high negative correlation with NO_3 and latitude ($R^2 = -.7$ for both; Supporting Information Figure S3). Consequently, NO_3 and latitude were use as explanatory variables and genotypic richness as a covariate. We reduced the full GLM of each response variable using a stepwise selection procedure to find the model with the lowest Akaike information criterion (AIC) value to avoid type I errors (Supporting Information Table S3). The coefficients, standard errors and *p*-values of fixed effects in all minimum adequate models were estimated via iteratively reweighted least squares using the glm function of the core R-package (R Core Team, 2007). Standardized generalized variance-inflation factors were also calculated as an index of multicollinearity. All models were fitted considering a Gaussian (i.e., normal) distribution of errors. Hence, the distribution of the residuals (errors) was checked for normality and response variables were transformed when the distribution of the residuals deviated from normality.

For the results of the feeding assays, we tested whether the level of simulated herbivory affected the amount of eelgrass biomass consumed by *P. resecata* using the multivariate Hotelling's T^2 test without transformation of the variables. Post hoc analyses were performed with Tukey multiple comparisons of means. The detailed methodology for all statistical analyses is described in the Supporting Information (Methodology S4).

3 | RESULTS

3.1 | Latitudinal variation of defence traits

We found that both tolerance and resistance traits (except number of leaves and rhizome biomass per internode) varied with latitude.

The PCA (Figure 2) differentiates two groups in axis 1 (PC1); the sites at the extremes of the *Z. marina* distribution range, and the sites at intermediate latitudes where the shoots reach larger sizes with higher growth rates and belowground resources (PC1, Figure 2). The results of the analyses on tolerance and size traits show that leaf sucrose, sheath area and correlated morphometric traits (Supporting Information Figure S3) peaked at mid-latitudes (Figure 3 and Supporting Information Figure S4). Carbon-based belowground resources (i.e., rhizome starch, sucrose and C) increased with increasing latitude (Table 1, Figure 3), whereas belowground N and leaf relative growth rate were lower towards higher latitudes (Table 1, Figure 3). Genotypic richness statistically influenced all tolerance traits, except rhizome C, but there were no overall consistent patterns with latitude (Table 1).

The PCA also shows a separation between mid-latitude and extreme-range populations in relation to resistance traits. In particular, marginal populations seem to invest in mechanical and phenolic defences (Figures 2 and 4). SLA increased with increasing latitude, while leaf fibre, leaf C, and total flavonoids (driven by the most abundant compound; DS) exhibited their minimum values at mid-latitudes (Figure 4 and Supporting Information Figure S5). However, some less abundant flavonoids and RA exhibited the opposite pattern (Supporting Information Figure S5, Table S4). On the other hand, leaf N content peaked at mid-latitudes, decreasing more towards higher latitudes (Table 1, Figure 4).

3.2 | Resource availability and defence traits

Sheath area as well as rhizome C, N, sucrose and biomass (and correlated traits, Supporting Information Figures S3, S6 and S7) increased with nitrate availability, while number of leaves and rhizome starch decreased (Table 1, Figure 5). Leaf N, phenolic compounds and flavonoids increased with higher nitrate availability, whereas leaf fibre content exhibited the opposite pattern (Table 1 and Figure 6, Supporting Information Table S4, Figures S6 and S7).

3.3 | Latitudinal patterns of defence traits in response to herbivory

Plant traits did not differ between the control and the moderate herbivory treatments, and only the high herbivory treatment

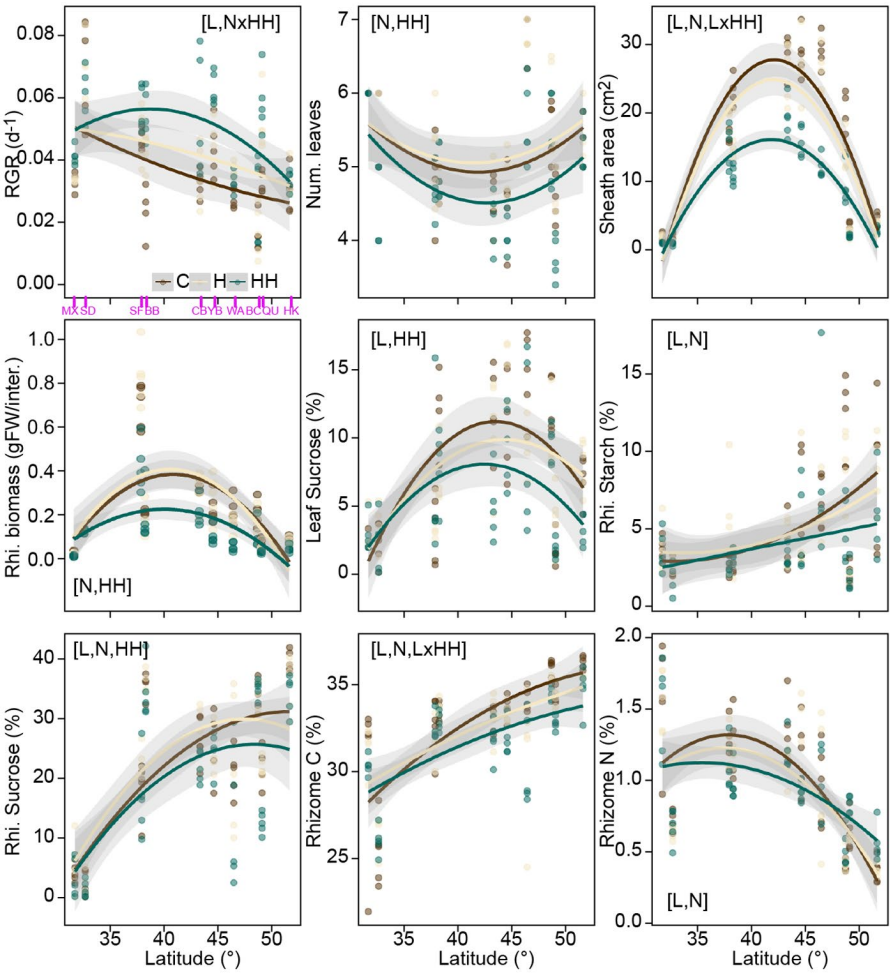

FIGURE 3 Distribution of tolerance traits along the latitudinal gradient. Grey bands indicate 95% confidence boundaries for the control (C; dark brown), moderate (H; beige) and high (HH; green) herbivory treatment fitted curves (general linear models). Letters indicate statistical differences due to latitude (L), nitrate (N), high herbivore treatment (HH), and interactions. Rhi = rhizome; RGR = relative growth rate; g FW/inte r= grams of fresh weight per internode. The first panel shows in magenta the latitude of the study sites ($n = 5$ per treatment and site). Sites are coded as in Figure 1

had effects on defence traits in *Z. marina*, which affected most of the tolerance traits. For instance, plants exhibited a higher relative growth rate under high simulated herbivory, which was further enhanced under high nutrient availability (Table 1, Figure 5). Number of leaves, rhizome biomass per internode, and sucrose content of both leaves and rhizomes were lower under the high herbivory treatments. In addition, rhizome C and sheath area only exhibited a significant decrease in high herbivory treatments at high and mid latitudes, respectively (Table 1, Figure 3). The only traits related to resistance that increased significantly under the high herbivory treatment were SLA and leaf N, with the increase in leaf N being greater towards higher latitudes (Table 1, Figure 4).

3.4 | Herbivore responses to simulated herbivory-driven changes in plant palatability

Isopods from both Coos Bay and Yaquina Bay consumed significantly higher amounts of fresh leaf biomass and agar-base food from the high herbivory treatment when compared to the control treatment in the three-choice experiments (Figure 7).

4 | DISCUSSION

This work shows that most eelgrass defence traits against herbivory follow a bell-shaped distribution, which suggests that latitudinal differences in defence traits of *Z. marina* are strongly driven by bottom-up forces, supporting the RAH. Tolerance traits (six of the nine traits) were strongly associated with high resource availability (i.e., upwelling) as expected by the LRM. On the other hand, we found higher investment in resistance traits towards both extremes of the distribution of eelgrass (and not only at lower latitudes), likely influenced by lower resources at these extremes in comparison to mid-latitudes (as proposed by the RAH and contrary to the intraspecific-RAH). Furthermore, none of the *Z. marina* traits analysed was significantly affected by moderate (i.e., 40% loss) herbivore damage, while high herbivory induced compensatory growth, decreased resistance, and increased palatability, which further enhanced susceptibility to herbivory by other grazers within the community.

Most tolerance traits were higher in the sites with higher nutrient availability, coincident with the region of strong upwelling (Schwing & Mendelssohn, 1997). Upwelling brings nutrient-rich waters, which also have higher pCO_2 (Feely et al., 2008), thus providing resources that generally limit seagrass productivity

TABLE 1 Results of general linear model (GLM) on defence traits

Variable		*i*	β_{lat}	β_{H}	β_{HH}	β_{NO3}	$\beta_{G.R.}$	β_{lat*H}	β_{lat*HH}	β_{NO3*H}	β_{NO3*HH}
Sqrt (relative growth rate (per day)]	Est.	0.39	−0.003	0.002	0.013	−0.003	−0.099			0.007	0.011
	SE	0.033	<0.001	0.012	0.012	0.004	0.026			0.005	0.05
	p	**< .001**	**< .001**	.892	.284	.45	**< .001**			.149	**.027**
Number of leaves	Est.	2.825		0.106	−0.396	−0.239	3.117				
	SE	0.469		0.14	0.139	0.039	0.5				
	p	**< .001**		.452	.06	**< .001**	**< .001**				
Sheath area (cm^2)	Est.	22.102	0.757	4.214	12.944	2.324	−45.043	−0.148	−0.489		
	SE	8.28	0.159	9.423	9.423	0.386	5.008	0.225	0.225		
	p	**.009**	**< .001**	.655	.172	**< .001**	**< .001**	.512	**.031**		
Ln (rhizome biomass (gFW/internode))	Est.	0.665		−0.078	−0.671	0.387	−3.487				
	SE	0.512		0.153	0.153	0.042	0.546				
	p	.196		.61	**< .001**	**< .001**	**< .001**				
Leaf sucrose (%)	Est.	5.276	0.318	−0.483	−1.855		−11.55				
	SE	3.966	0.058	0.878	0.878		3.155				
	p	.186	**< .001**	.583	**.037**		**< .001**				
Logit (rhizome starch (%))	Est.	0.216	0.03			−0.8					
	SE	0.33	0.008			0.032					
	p	.514	**< .001**			**.016**					
Arcsine (rhizome sucrose (%))	Est.	−0.027	0.002	0.001	−0.004	0.006	−0.011				
	SE	0.009	<0.001	0.002	0.002	0.006	0.007				
	p	**.003**	**< .001**	.537	**.025**	**< .001**	.135				
Logit (rhizome C (%))	Est.	−1.674	0.018	0.217	0.248	0.029	0.14	−0.006	−0.007		
	SE	0.125	0.002	0.142	0.142	0.006	0.076	0.003	0.003		
	p	**< .001**	**< .001**	.13	.084	**< .001**	.066	.105	**.037**		
Rhizome N (%)	Est.	2.829	−0.027			0.044	−0.835				
	SE	0.309	0.005			0.019	0.247				
	p	**< .001**	**< .001**			**.023**	**< .001**				
SLA (cm^2/g)	Est.	−419.589	23.442	23.189	178.176						
	SE	176.321	4.111	62.413	62.413						
	p	**.019**	**< .001**	.711	**.005**						
Logit (fibre (%))	Est.	−0.157	−0.034			−0.148	1.326				
	SE	0.25	0.004			0.015	0.2				
	p	.532	**< .001**			**< .001**	**< .001**				
Logit (leaf C (%))	Est.	−0.929	0.005				0.097				
	SE	0.076	0.001				0.061				
	p	**< .001**	**< .001**				.112				
Logit (leaf N (%))	Est.	−1.231	−0.007	−0.045	−0.116	0.286	−0.231	0.001	0.005	−0.001	−0.016
	SE	0.081	0.002	0.092	0.092	0.07	0.049	0.002	0.002	0.009	0.009
	p	**< .001**	**< .001**	.629	.21	**< .001**	**< .001**	.533	**.02**	.876	.081
Sqrt (TF (mg/gDW))	Est.	3.613	−0.045			0.078	1.81				
	SE	0.802	0.012			0.05	0.643				
	p	**< .001**	**< .001**			.118	**.006**				
Sqrt (TPC (mg/gDW))	Est.	3.007	0.027			0.143					
	SE	0.646	0.015			0.064					
	p	**< .001**	.077			**.027**					

Note: Intercept (*i*) and slopes of latitude (β_{lat}), herbivory simulation moderate (β_{H}) and high level (β_{HH}), nitrate (β_{NO3}), their interactions (marked with asterisk), and genotypic richness ($\beta_{G.R}$). Sqrt, Ln, arcsin and logit indicate square root, Napierian logarithm, arcsine and logit transformation, respectively. SLA = specific leaf area; TF = total flavonoids; TPC = total phenolic compounds; gDW = grams of dry weight; gFW = grams of fresh weight; Est. = estimate; *SE* = standard error; *p* = *p*-value (*n* = 5 per treatment and site). Statistically significant results are shown in bold.

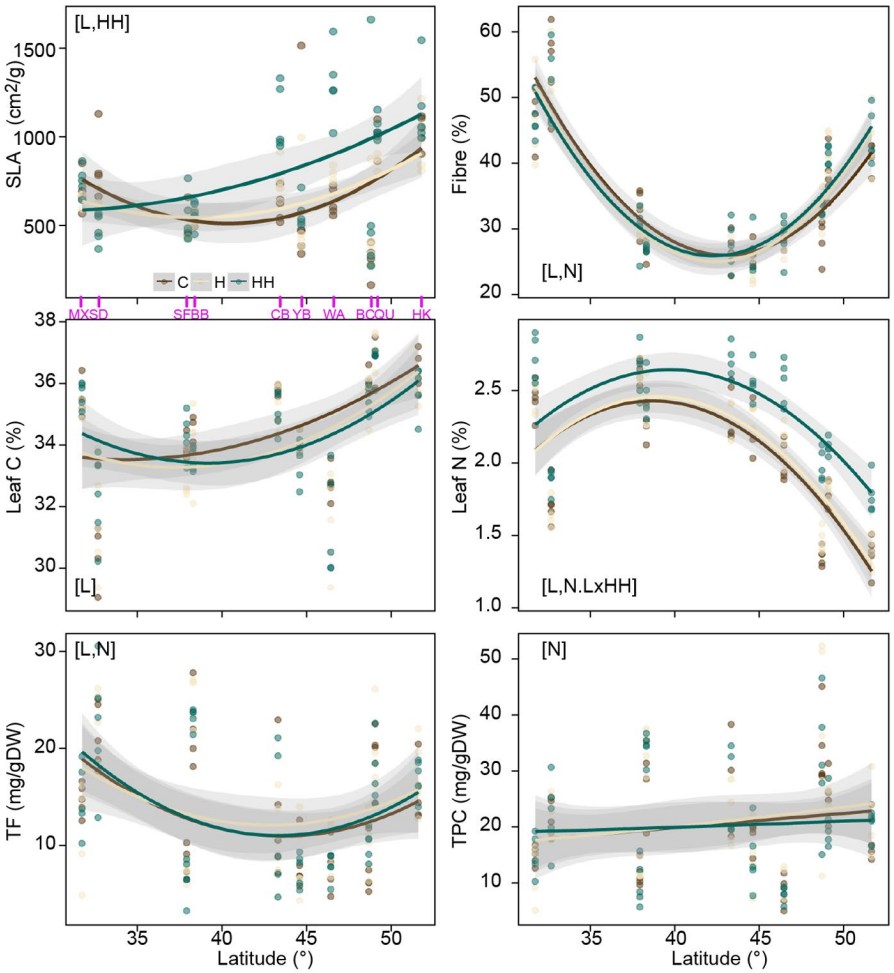

FIGURE 4 Distribution of resistance traits along the latitudinal gradient. Grey bands indicate 95% confidence boundaries for the control (C; dark brown), moderate (H; beige) and high (HH; green) herbivory treatment fitted curves (general linear models). Letters indicate statistical differences due to latitude (L), nitrate (N), high herbivore treatment (HH), and interactions. SLA = specific leaf area; TF = total flavonoids; TPC = total phenolic compounds; gDW = grams of dry weight. The first panel shows in magenta the latitude of the study sites (n = 5 per treatment and site). Sites are coded as in Figure 1

(Beer et al., 2002; Lee et al., 2007). In accordance with the LRM, we observed higher belowground resources and aboveground growth rates with higher nutrient availability under herbivory. At mid-latitudes, higher resource availability appears to translate into higher aboveground (Ruesink et al., 2018) and belowground per capita biomass. Consequently, populations in high resource availability environments are likely to be better prepared to tolerate herbivory or other disturbances that can remove aboveground biomass (e.g., harsher hydrodynamic conditions), having more resources to invest for regrowth. Our study also indicates that summertime leaf relative growth rate decreases with increasing latitude, perhaps due to lower temperatures in northern sites, which has been suggested as an important factor controlling annual seagrass productivity (Clausen et al., 2014). In addition, towards the northern sites, carbon mainly accumulates into carbohydrate reserves in belowground tissues rather than being invested in plant growth, probably as an adaptation to overwintering (Clausen et al., 2014; Robertson & Mann, 1984; Soissons et al., 2018). Indeed, the non-linearity of the relationship of some of the variables with nutrient availability is likely due to this adaptation, leading to lower values of some variables (e.g., number of leaves) at intermediate levels of nitrate concentrations, which correspond to high latitude sites. Moreover, genotypic richness appears to influence most seagrass size traits, which may be related to previous findings of higher eelgrass biomass in more genotypically diverse sites (Hughes & Stachowicz, 2004; Reusch et al., 2005). It has been suggested that higher genetic diversity increases positive interactions such as resource partitioning, improving performance in more genotypically diverse populations (Hughes et al., 2008).

The production of resistance traits also appears to be strongly influenced by available resources. As predicted by the RAH, plants from the sites with high nutrient availability tended to have higher nitrogen and lower fibre contents in leaves, and thus lower constitutive resistance. Indeed, experimental evidence shows that increases in nutrient availability usually lead to higher nutrient content (Hernán et al., 2019; Tomas et al., 2015) and lower fibre production in plant tissues (Goecker et al., 2005; Hernán et al., 2019). On the other hand, the pattern that we detected of lower resistance in high-resource areas does not follow the predictions of the intraspecific-RAH, which predicts that resistance is mediated by the higher herbivory suffered at resource-rich sites. In fact, some plant species inhabiting high resource environments do not undergo high herbivory rates and thus, the predictions of the intraspecific-RAH may not always be applicable (Lamarre et al., 2012). Such lower investment in structural defences and higher nutritional quality typically enhance plant susceptibility to herbivory (e.g., Goecker et al., 2005; Hernán

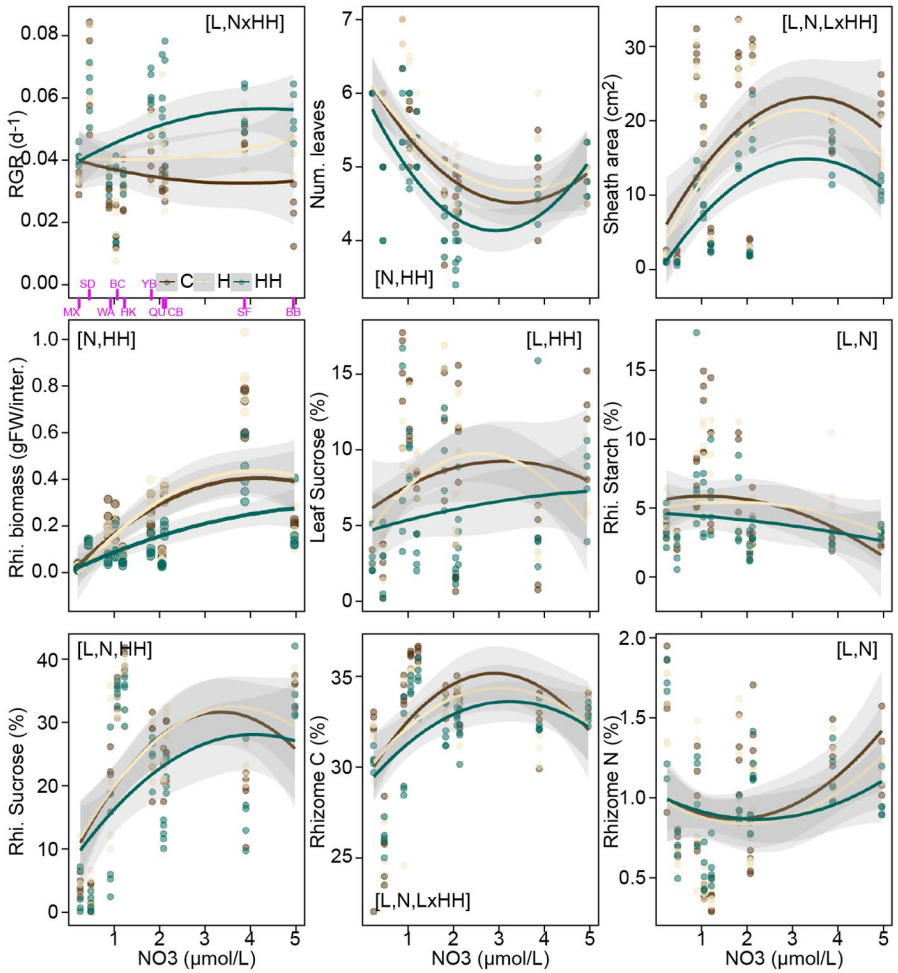

FIGURE 5 Distribution of tolerance traits along the nitrate availability gradient. Grey bands indicate 95% confidence boundaries for the control (C; dark brown), moderate (H; beige) and high (HH; green) herbivory treatment fitted curves (general linear models). Letters indicate statistical differences due to latitude (L), nitrate (N), high herbivore treatment (HH), and interactions. Rhi = rhizome; RGR = relative growth rate; gDW = grams of dry weight; g FW/inter = grams of fresh weight per internode. The first panel shows in magenta the latitude of the study sites (n = 5 per treatment and site). Sites are coded as in Figure 1

et al., 2019; Lucas, 2000; Tomas et al., 2011), and thus would likely make mid-latitude plants more susceptible to consumers.

Furthermore, according to the LHDH, we would expect a negative linear relationship between the concentrations of phenolic compounds and latitude (Anstett, Nunes, et al., 2016; Rasmann & Agrawal, 2011), and we would also expect an induction in the production of chemical defences in response to herbivory. Yet, we did not observe either of those phenomena. In fact, in our system, the production of chemical defences appears to be driven by resource availability rather than herbivory pressure. We found that total flavonoid compounds and total phenolic compounds were slightly higher in higher nutrient availability conditions. Nevertheless, specific compounds exhibited contrasting responses. The most abundant flavonoid (DS) was lower at mid-latitudes (Supporting Information Figure S5) while other less abundant flavonoids (LUTG, LUTMG, LUTS), some of which have been related to UV protection (LUTG, LUTMG; Mierziak et al., 2014), exhibited the opposite pattern (Supporting Information Figure S5), increasing with higher nutrient availability (Supporting Information Figure S7). Likewise, RA was one of the most abundant phenolic compounds found in this study. RA has been found to have antibacterial activity (Guan et al., 2019) and has been suggested to play a role in pathogen and herbivore protection (Khan et al., 2019; Simmonds et al., 2019). This compound exhibited higher concentrations at mid-latitudes (Supporting Information Figure S5) and, in fact, previous studies have found a strong positive correlation between RA and leaf N in seagrasses (Ravn et al., 1994). The idiosyncratic responses in the content of specific phenolic compounds may affect the capacity of plants to defend against pathogens, herbivores and UV-radiation. However, further studies need to be performed in order to actually determine the specific function of many of these particular compounds in seagrasses. On the other hand, genotypic richness seemed to influence some chemical resistance traits such as leaf N, total flavonoids and half of the phenolic compounds identified. Genetic identity influences the production of total phenolic compounds in *Z. marina* (Tomas et al., 2011), and intraspecific (genetically driven) differences in production of secondary metabolites have major ecosystem effects on *Populus*-based ecosystems (see reviews by Schweitzer et al., 2008; Whitham et al., 2006) highlighting the potential role that intraspecific genetic variations may have in driving chemical composition in eelgrass and consequently influencing herbivory and other important ecological processes (e.g., decomposition, nutrient cycling; Schweitzer et al., 2008; Whitham et al., 2006).

The only resistance trait that followed the predictions of the LHDH (i.e., more investment in defence at lower latitudes) was SLA, with southern populations having tougher leaves (i.e., lower SLA). While lower SLA could potentially be a response to higher grazing impact at the southern sites, it may also be related to higher temperature stress that plants

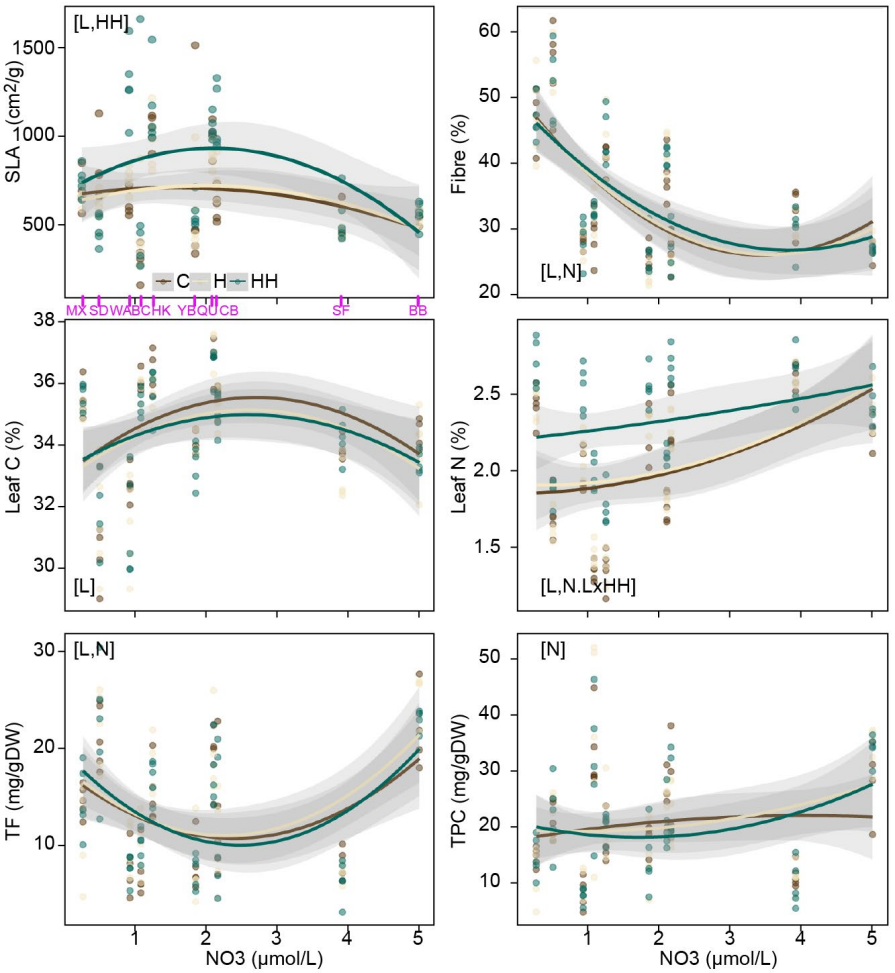

FIGURE 6 Distribution of resistance traits along the nitrate availability gradient. Grey bands indicate 95% confidence boundaries for the control (C; dark brown), moderate (H; beige) and high (HH; green) herbivory treatment fitted curves (general linear models). Letters indicate statistical differences due to latitude (L), nitrate (N), high herbivore treatment (HH), and interactions. SLA = specific leaf area; TF = total flavonoids; TPC = total phenolic compounds. The first panel shows in magenta the latitude of the study sites (n = 5 per treatment and site). Sites are coded as in Figure 1

suffer during low tides in southern sites (Ramírez-Valiente et al., 2014). On the other hand, higher SLA at northern sites may be a consequence of the need to increase plant photosynthetic capacity (and thus leaf area) due to light limitation (Enriquez & Sand-Jensen, 2003).

Regarding impacts of simulated herbivory, *Z. marina* plants appear to be able to tolerate moderate levels of herbivory throughout the latitudinal range examined, as those plants had similar traits to control plants, even though they were regularly being denuded of 40% in leaf length. Thus, plants under moderate treatments were able to compensate for leaf loss, and this may have been achieved by increasing photosynthetic activity of the remaining leaf tissue (Tiffin, 2000). On the other hand, high leaf denudation rates did cause negative effects on plants. For example, *Z. marina* exhibited a compensatory growth response, which has been linked to a reduction in belowground resources (Sanmartí et al., 2014), and which was also observed in our study, with an important reduction in rhizome biomass per internode, and in sucrose content. Importantly, this reduction was attenuated at mid and high latitudes, likely as a result of higher resource availability (LRM; Wise & Abrahamson, 2007). Furthermore, rhizomes suffered a stronger reduction of carbon reserves towards northern latitudes, which may be driven by a limitation in carbon uptake often observed at high latitudes as a result of light limitation (Reich & Oleksyn, 2004). In addition, given that at these northern sites leaves had higher nitrogen content (see below), lower C reserves may also be due to the use of carbon for nitrogen assimilation (Touchette & Burkholder, 2000).

Interestingly, plants under intense herbivory did not increase their resistance against consumption. On the contrary, we observed that high herbivory rates made leaves more palatable (with decreased toughness and higher nitrogen content), which may have resulted in part from a stimulation of nitrogen uptake due to defoliation under high herbivory (Jaramillo & Detling, 1988; Valentine et al., 2004). The increase of nitrogen pools under intense herbivory was particularly great at the northern sites, and this may be a consequence of a lower use of nitrogen for growth (Kerkhoff et al., 2005; Reich & Oleksyn, 2004). The changes that we observed in SLA and nutrients under high herbivory would likely make these plants even more attractive to grazers. In fact, herbivores are known to perform 'cultivation' or 'gardening' grazing whereby they maintain certain species or plant tissues that optimize their foraging (Bjorndal, 1985; Preen, 1995), and we indeed observed that this herbivory-driven decrease in resistance made plants consistently more susceptible to consumption by isopods. Consequently, negative impacts of macroherbivores such as fish or waterfowl on eelgrass may be further enhanced by facilitating susceptibility to other consumers within the community. Indeed, isopods from both populations tended to prefer the most clipped leaves, which were also the more nutritious (i.e., higher

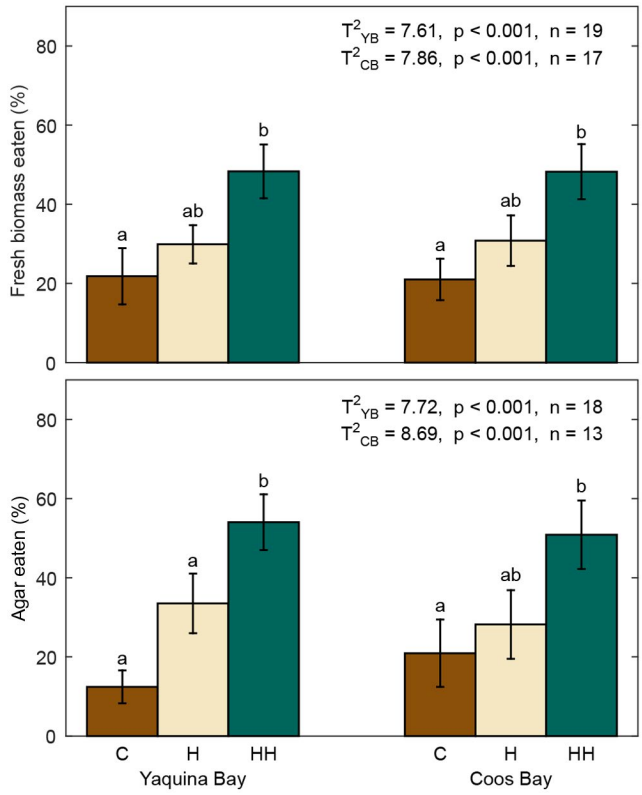

FIGURE 7 Meanpercentage of (a) fresh biomass and (b) agar-based reconstructed food of plant material from different experimental treatments eaten by isopods collected in Yaquina Bay and Coos Bay and fed seagrass from their respective bays. Error bars indicate standard error, and different letters indicate statistically significant differences across treatments (Tukey). Hotelling test results (T^2) from samples collected in Yaquina Bay (T^2_{YB}) and Coos Bay (T^2_{CB}), *p*-value (*p*), and number of replicates (*n*) shown. C = control herbivory treatment; H = moderate herbivory treatment; HH = high herbivory treatment

leaf nitrogen content), more tender (i.e., higher SLA) and which had not exhibited any induction of phenolic compounds or other resistance traits. The fact that isopods exhibited the same preferences when we performed the agar-base feeding experiment suggests that nutritional quality and possibly structural traits are driving the feeding behaviour of this herbivore (Tomas et al., 2011, 2015).

Our study highlights the importance that resource availability has in shaping latitudinal patterns of plant defence strategies against herbivory in a dominant foundation species. Furthermore, our results also indicate that while eelgrass populations are highly tolerant to moderate levels of herbivory, they are not adapted to high herbivory. Importantly, tolerance to high herbivory was enhanced in the sites with high resource availability. Although there are no comprehensive studies on patterns of herbivory pressure on *Z. marina*, this adaptation to moderate herbivory could be primarily driven by consumption by waterfowl (Kollars et al., 2017; Rivers & Short, 2007). Importantly, warming-driven range expansion of tropical herbivores, such as fish or sirenians, into temperate areas is already occurring in many regions (e.g., Mediterranean Sea, Gulf of Mexico, Australian coast), strongly enhancing consumption pressure on benthic macrophytes (Hyndes et al., 2016; Vergés et al., 2014, 2016). The establishment of these new species will increase herbivory pressure on these systems, particularly at the lower edge of their distribution. Moreover, migration patterns of waterfowl species are being altered with climate change and degradation of habitats (Ward et al., 2005) and may shift spatial patterns of grazing pressure. These new scenarios of grazing could have strong detrimental effects on temperate seagrasses, not only by directly reducing plant standing stock, but also by reducing resistance traits and facilitating herbivory by other grazers in the community. Such processes could be especially problematic under conditions of high resource availability, because while more resources may initially enable plants to better tolerate herbivory, they also make plant tissues less resistant to herbivores.

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AUTHOR CONTRIBUTIONS

FT and GH conceived the experiment. GH, FT, JH, KB, SC, MC, CH, MH-L, SK, NK, KH, PJ, MIO, PLR, JR, EV performed the field experiment. GH performed the chemical analyses. MJO performed phenolic compounds analyses. JO performed the genetic analyses. GH and JA performed the statistical analyses. VC analyzed the SST, NO3 and solar radiation data. FT, KB, MC, MJO, CH, MH-L, KH, PJ, MIO, JO and JR contributed with funding, field and laboratory material and analyses. GH and FT prepared the manuscript. All authors discussed and contributed to the manuscript.

DATA AVAILABILITY STATEMENT

All data supporting the results in the paper are publicly available in the Figshare data repository: 10.6084/m9.figshare.13048871.

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BIOSKETCH

We are a group of researchers of the Zostera Experimental Network (http://zenscience.org/) interested in conducting coordinated research in beds of eelgrass (*Zostera marina*) throughout the Northern Hemisphere to tackle big questions about how biodiversity, climate change, and natural variability across the globe influence ecosystem structure and functioning.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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