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RESEARCH ARTICLE

Small-scale thermal habitat variability may not determine seagrass resilience to climate change

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Abstract

Seagrass ecosystems are integral components of coastal marine environments, but they face global threats from climate change. The ability of seagrass to withstand these challenges depends on trait variation among individuals, which is influenced by genetic background and plasticity. In this study, we explore how small-scale thermal habitat variability contributes to intraspecific trait variation in the eelgrass *Zostera marina* and how this variation affects resilience to climate change. We hypothesize that eelgrass meadows with higher mean and more variable summer temperatures exhibit greater resilience. Despite their proximity (maximum distance of 14 km), the 10 assessed meadows exhibited distinct thermal microclimates and were genetically differentiated from each other. We conducted a common garden experiment subjecting eelgrass shoots from these meadows to increased temperature and decreased salinity to represent a projected future climate. The treatment led to a significantly increased mortality, higher prevalence of the eelgrass wasting disease, reduced development of new leaves, and overall diminished growth of *Z. marina*. Responses varied among meadows, independent of their natural thermal summer microclimates. We discuss this mismatch between local microclimate and phenotypic response with a strong focus on the potential of microclimates (higher summer temperature, lower winter temperatures, pronounced variability) to impede differences in intraspecific trait variation among meadows. Overall, our study emphasizes the need for comprehensive habitat characterization paired with the assessment of (thermal) performance curves to unravel the complex effects of microclimates on intraspecific trait variation and, consequently, species resilience to climate change.

Seagrass ecosystems are vital components of coastal marine environments, providing a wide array of ecosystem services and functions (Cole and Moksnes 2016) and fostering diverse communities (Boström et al. 2014). For example, seagrass meadows play a central role in primary productivity, nutrient absorption, and carbon sequestration, as well as serving as crucial nursing and foraging areas (Ruiz-Frau et al. 2017; do Amaral Camara Lima et al. 2023). The cumulative effects of human activities, including eutrophication, habitat destruction, over-exploitation, pollution and diseases (Orth et al. 2006), have led to a significant decline in seagrass coverage (Waycott et al. 2009). The decline of this foundation macrophyte can have strong community effects (Saha et al. 2020; Sawall et al. 2021) with potentially far-reaching consequences for coastal ecosystems (Waycott et al. 2009). Since the 2000s, seagrass's declining trends have stabilized globally, recently shifting toward recovery trajectories in some regions (de Santos et al. 2019; Dunic et al. 2021). However, across Europe, the eelgrass *Zostera marina*, the most widespread seagrass in the Northern Hemisphere, continues to decline along most coastal areas, with meadows in southwest Sweden facing particular losses (de Santos et al. 2019). Restoration efforts support recovery, but outcomes depend heavily on habitat quality and environmental characteristics (van Katwijk et al. 2016; Orth et al. 2020), as well as genetic diversity, adaptive potential and

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connectivity among eelgrass populations (Jahnke et al. 2015; Ries et al. 2023). Recovery is further threatened by the increasing multiple impacts of climate change. Of these, marine heatwaves pose an especially significant threat to the future of eelgrass meadows (Marbà et al. 2022), while local drivers and their extreme events may add considerable stress interactions (Wahl et al. 2021).

Marine heatwaves have increased globally in frequency (34%) and duration (17%) from 1925 to 2016 (Oliver et al. 2018), trends that are projected to continue and even increase. Heatwaves are defined as prolonged and anomalously warm events that exceed the 90^{th} percentile of the historical baseline for 5 or more consecutive days (Hobday et al. 2016). Extreme events rarely occur uniformly or in isolation. Combinations of anomalous levels of environmental drivers (e.g., temperature, salinity, oxygen and pH; Wahl et al. 2021) vary naturally at different temporal and spatial scales, affecting ecological systems (Jackson et al. 2021). Consequently, it is crucial to consider the timing and interactions among these drivers (Boyd et al. 2018). Yet, identifying the most relevant combination(s) of drivers remains difficult, as they are species- and site-specific (Boyd et al. 2018). An example of two significant drivers that can act in tandem is temperature and salinity (Supporting Information Fig. S1), while, overall, salinity is projected to decrease stronger than average in southwest Sweden (Gröger et al. 2019). Previous studies have shown that increased temperatures and decreased salinity individually induce stress in eelgrass, resulting in the upregulation of heat shock proteins (Bergmann et al. 2010), differentially expressed genes (Winters et al. 2011; Jueterbock et al. 2016), and adjustment of organic osmolytes (Ye and Zhao 2003; Touchette 2007), leading to reduced growth (Niu et al. 2012; Hammer et al. 2018) and other negative impacts on trait performances. Furthermore, the combination of both factors has been demonstrated to have negative synergistic effects on *Z. marina* (Salo and Pedersen 2014).

The ability of seagrasses to withstand and recover from anomalous levels of single or multiple drivers depends on an interplay of local environmental conditions, species diversity, and within-species genetic diversity. In ecosystems like dense seagrass meadows, where species diversity is limited, within-species diversity is suggested to be of particular importance for communities to withstand (Ehlers et al. 2008; Salo and Gustafsson 2016) and recover from extreme climatic events (Reusch et al. 2005). The diverse structure of coastal habitats, including mosaics of islands, small bays, river mouths, and depth gradients, fosters a variety of subtidal marine microclimates that may provide shelter from extreme events but also opens the possibility for adaptive differentiation among populations on fine spatial scales (Gorospe and Karl 2011; Woodson et al. 2019).

Environmentally driven selection plays a pivotal role in shaping locally adapted populations, aligning their genotypes to the demands of their habitats (Kawecki and Ebert 2004). For example, seagrass populations exhibit differences in thermal niche space on a global scale (Marbà et al. 2022). This may be due to local adaptation as well as individual-level variation in trait expression through phenotypic plasticity, which collectively gives rise to intraspecific trait variation. Thus, both temperature optima and resistance to heatwaves vary depending on the thermal environments experienced by different populations (Marbà et al. 2022). However, this process can be influenced by gene flow, which has the potential to counteract the diversifying effects of selection (Nosil 2009). Thus, species with limited dispersal are more likely to exhibit local adaptation. Eelgrass, like all seagrasses, is a marine flowering plant that reproduces both clonally and sexually. Clonal propagation via rhizomes allows for rapid expansion but limits genetic diversity (Reusch and Boström 2011). Sexual reproduction allows for dispersal via pollen and negatively buoyant seeds but is mainly limited to the parental meadow (Ruckelshaus 1996), favoring the development of local ecotypes. However, reproductive shoots can drift for tens to hundreds of kilometers and may then release seeds, which in turn sink to the seafloor (Källström et al. 2008; Jahnke et al. 2018). Differences in population connectivity can, on top of environmental variation, thus influence traits on regional scales. Several studies have suggested that adaptation at smaller spatial scales is also possible in seagrass, especially in Mediterranean and tropical climates (Bennett et al. 2022; DuBois et al. 2022; Hernawan et al. 2023). For example, eelgrass populations situated within approximately 10 km of each other in northern California, encountering up to 5°C temperature disparities, have exhibited in situ adaptation to divergent temperature regimes (DuBois et al. 2022). Similarly, populations from distinct salinity gradients within the Baltic Sea display different growth abilities, with individuals from populations experiencing higher environmental fluctuations exhibiting more plasticity (Salo et al. 2014). Recognizing that small-scale thermal habitat variability can lead to differential sensitivity to global change (DuBois et al. 2022), fine-scale regional data are urgently needed to better understand and predict species responses to climate change (King et al. 2018).

In this study, we aimed to investigate the role of intraspecific trait variation of *Z. marina* for resilience to climate change. The individuals under examination were collected from 10 meadows located on a small spatial scale (maximum distance of 14 km) along the Swedish west coast. Genetic differentiation among meadows was assessed from 1639 single-nucleotide polymorphisms obtained via restriction-site associated DNA (2b-RAD) sequencing. Temperature loggers, placed at the different meadows in summer, suggest microclimate niche variation, which is likely due to variations in bathymetry and exposure. We hypothesized that both microclimate and dispersal, affected by exposure, would also be reflected in the level of genetic differentiation in eelgrass. To explore the responses of eelgrass from different microclimates to a combined treatment of increased temperature and decreased salinity, we conducted a common garden experiment in an outdoor mesocosm facility.

We anticipated divergent responses among the individuals from different meadows, with plants from the most sheltered meadows, which naturally experience higher mean temperatures and variability in temperature and other abiotic parameters (e.g., salinity), exhibiting greater resilience.

Materials and methods

Sampling of eelgrass and sediment

Eelgrass was collected between June 28, 2021 and July 2, 2021 by scuba diving at a depth of 1–3 m from 10 meadows in the Kosterhavet Archipelago, Swedish west coast (Fig. 1a; Supporting Information Table S1). The average distance between meadows was ca. 7 km, ranging from a minimum of 1.5 km to a maximum of 14 km. In the study area, summer marine heatwaves coincide with freshening events, representing abrupt fluctuations in salinity (Supporting Information Fig. S1). From each meadow, five genets with a minimum of three connected clonal shoots were collected, placed in water-filled Zip-loc© bags underwater, and transported to the laboratory in cooling boxes. The plants were kept in flow-through surface seawater at the Tjärnö Marine Laboratory to acclimatize for about 20 d. At the start of the experiment, two clonal shoots of similar size from each genet were selected and subjected to either the ambient or climate change treatment (paired design; details below). Sediment was collected from all 10 meadows, mixed, homogenized, and sieved through a 2-mm sieve to remove larger particles, plant pieces, and associated sediment organisms.

Characterizing microclimates in eelgrass meadows

Over the experimental period, seawater temperature measurements were conducted continuously (15-min intervals) at the 10 seagrass meadows (Supporting Information Table S1), using HOBO loggers (ONSET, USA) installed 1 m above the bottom. While shoot length varied across meadows, this was approximately at the top of the eelgrass canopy. Standardization to 1 m, rather than adapting the height to the canopy height, was done to enable comparison between the meadows and to establish a baseline on habitat-specific thermal variability throughout the peak summer of 2021 (Supporting Information Fig. S2). The data collected by the logger placed at Ramnekroken had to be excluded due to the logger being buried in the sediment. For comparability among meadows, data were used for the period July 5–29, 2021. The difference in microclimates between the nine meadows was illustrated by plotting the temperatures recorded as a density plot (Fig. 1b), and meadow-specific thermal daily maximum, diurnal variability, and daily means were extracted (Fig. 1c–e). The diurnal variability values were determined by first identifying the daily maximum and minimum temperature values and then subtracting the minimum from the maximum. Due to limited access to high-resolution salinity loggers, this approach was not possible for salinity, necessitating the assumption that increased thermal variability (due to increased shelter) will equally increase variability in other parameters, such as salinity.

Characterizing genetic differentiation among eelgrass meadows

Field sampling for the genetic assessments of the 10 meadows was conducted in July 2021 (Koster) and May–June 2022 (remaining meadows, Supporting Information Table S1). At each site, 20 individual shoots of *Z. marina* were collected using a "random swim" method that consisted of sampling across the meadow at 1–1.5 m intervals to try to avoid sampling two shoots belonging to the same ramet (Arnaud-Haond et al. 2007; Jahnke et al. 2018). DNA extractions and 2b-RAD library preparations were carried out as described in Ries et al. (2023). For each sampling site, 22 DNA samples were amplified using sample-specific barcoded adaptors (2 of the 20 individuals sampled were sequenced twice using different barcodes and were used as technical replicates). Single-read sequencing (51 bp read-length) using the NovaSeq 6000 system and v1.5 sequencing chemistry (Illumina Inc.) was conducted at the SNP&SEQ Technology Platform at Uppsala University. The bioinformatic analysis was carried out on the Rackham cluster of the Swedish National Infrastructure for Computing following the pipeline developed by Mikhail Matz (2021, available at https://github.com/z0on/2bRAD_denovo) and aligned to the *Z. marina* reference genome (NCBI BioProject Accession number PRJNA701932). The final dataset consisted of 189 individuals successfully genotyped with 1639 single-nucleotide polymorphisms. In the first step of the population genomic analyses, the genetic distance between technical replicates was used to estimate the sequencing error threshold. This threshold allowed us to define which individuals should be considered as distinct genotypes and which should be considered clones of each other. The unweighted pair group method with arithmetic mean algorithm in the *poppr* package (v. 2.9.4; Kamvar et al. 2014) in R (v. 4.3.0; R Core Team 2023), RStudio (2023.3.0.386; Posit Team 2023) was then used to cluster all genotyped individuals based on Hamming distance (i.e., the number of differences) and define a unique multilocus lineage when the average distance between every pair of points between clusters was below 0.0114. While this particular threshold is specific to this dataset, the threshold and the resulting multilocus lineages are very comparable to other studies in the area (Ries et al. 2023). Replicate clones were then removed, leaving only one individual of each multilocus lineage for all further analyses.

To visualize genetic differentiation and population structure among the 10 assessed meadows, we performed principal component analysis using the R package *ade4* (v. 1.7-22; Dray and Dufour 2007) and genetic structure analysis using the sparse nonnegative matrix factorization (*snmf*) algorithm in the landscape and ecological association analyses (*LEA*)

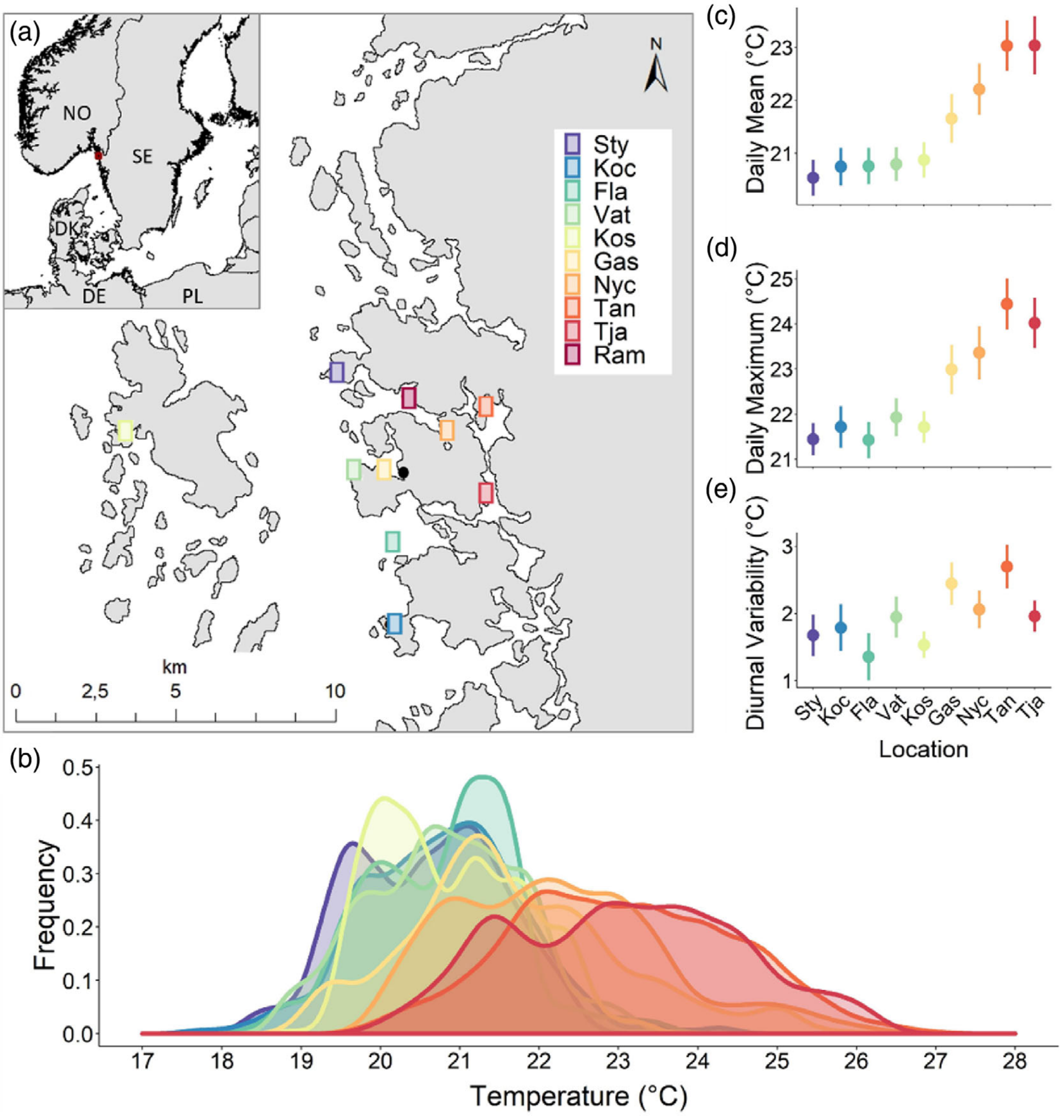

Fig. 1. (**a**) Map of the 10 eelgrass meadows sampled in the Kosterhavet Archipelago. The location of the Tjärnö Marine Laboratory, where the experimental part was conducted, is displayed as a black dot (Map produced in ArcMap 10.8 GIS). (**b**) Density plot for temperatures at the nine meadows, illustrating the frequency of measured temperatures. The temperature attributes (**c**) mean temperature, (**d**) maximum temperature, and (**e**) diurnal variability at the nine meadows, are ordered from lowest to highest mean temperature; (**b–d**) are based on high-resolution, 15-min interval measurements from the nine meadows between July 5–29, 2021. The site Ramnekroken was removed from further analysis as the logger had been buried in the sediment throughout the summer. Fla, Flatskär; Gas, Gåsholmen; Koc, Kockholmen; Kos, Koster; Nyc, Nycklebykilen; Ram, Ramnekroken; Sty, Styrsö, Tan, Tångeholmen, Tja, Tjärnöbo; Vat, Inre Vattenholmen.

package (v. 3.12.2; Frichot and Francois 2015). LEA analyses were run 50 times per K for 1–10 maximum number of ancestral populations (K).

Experimental setup, design, and treatments

The experimental work for this study was conducted using the BALTOTRON outdoor mesocosms at the Tjärnö Marine Laboratory, Sweden (58.876043°N, 11.146222°E; Fig. 1a). The mesocosm system (Supporting Information Fig. S3) is comprised of five compartments, each divided into two separate large open 900-L tanks (250 × 104 × 31 cm). Within these 10 tanks, a total of 100 twelve-liter plastic bags (experimental units) filled with 750 mL of the mixed natural sediment were distributed, with each bag containing one shoot from one of the 10 meadows of the eelgrass *Z. marina* (Supporting Information Fig. S3). The experimental units were exposed to natural sunlight throughout the experimental period, covered with a layer of thin white garden fleece, thereby alleviating ultraviolet light stress.

The experiment consisted of two treatments with differing temperatures and salinity conditions. Each treatment was replicated five times in independent BALTOTRON compartments.

The “ambient” treatment served as a control. It implemented the same temperature and salinity regime recorded at the Tjärnö Marine Laboratory during the experimental period, which included short-term variability representing most natural environmental conditions. Since none of the meadows is directly located within this vicinity (Fig. 1), we do not expect this choice to introduce any bias favoring specific shoots. The “climate change” treatment implemented increased temperatures and lower salinities. More specifically, we aimed to increase the temperature by +4.7°C and to reduce salinity by −5.5 relative to ambient while keeping natural diurnal variabilities. These offsets in temperature and salinity were derived from daily temperature and salinity data collected by the Tjärnö Marine Laboratory between 1980 and 2014, modeled using the “heatwaveR” package (Schlegel and Smit 2018). The treatments represented deviations in (i) seawater temperatures that exceeded the upper 90th percentile and in (ii) salinity that exceeded the lower 30th percentile (Supporting Information Fig. S1).

The system received sea surface water (1 m depth) from Tjärnö Bay, which was directly pumped into 300-L mixing tubs provided for each of the 10 mesocosms. The water for the ambient treatment was not manipulated, whereas the water for the climate change treatment was warmed and freshened within mixing tubs. For each system, the water from the mixing tub was pumped (Eheim 1262) into a header tank, from where the water was distributed by gravity into the experimental units. Effluent water from the experimental units was allowed to overflow into the thermally controlled water baths and was never reused within the experimental units.

The temperature and salinity of water in the mixing tubs were controlled using Profilux 4 computers (GHL) connected to 600-watt heaters (Schego, Germany) and by mixing with tap water. The temperature in the 900 L water baths was maintained by Cygnet pool heaters (Cygnet) and continuously circulated (Eheim 1262). Every day, temperature and salinity were adjusted at 09:00, based on the water temperature and salinity prevalent at the Tjärnö Marine Laboratory’s pier the previous day, considering the maximum temperature and minimum salinity recorded in the ambient treatment, maintaining natural environmental variability.

The experiment was maintained for 10 d, from July 19–29, 2021. The ambient treatment experienced a temperature of 22.5 ± 0.8°C and a salinity of 24.1 ± 0.8, while the climate change treatment experienced 26.6 ± 1.4°C and a salinity of 19.6 ± 1.7 (means of manual measurements carried out every other day at 13:00 using a WTW Multi 3630 IDS sonde connected with Tetra Con 925 a temperature and salinity probe).

Response traits assessed for eelgrass

Before *Z. marina* plants were placed in their experimental units, each shoot was photographed (NIKON 1 AW1) on a light table, its wet weight (Mettler PC 8800; 0.1 g) was measured, and the number of leaves was counted. Each plant was pierced with a hypodermic needle 1 cm above the meristem.

After the experimental period, plants were separated into belowground biomass (including rhizomes and roots) and aboveground biomass (leaves), weighed, and photographed. The number of leaves (original and newly developed) and newly developed shoots on each individual plant was documented. The rhizomes/roots and leaves were put into aluminum foil forms, dried for 48 h at 60°C, and weighed (Sartorius BP221 S; 0.0001 g). To minimize moisture absorption from the air, the samples were kept in a desiccator until measurement.

Photographs were analyzed using ImageJ (version 1.53n). The growth of individual leaves was measured from the hole to the meristem (Gaeckle and Short 2002). New leaves were measured similarly, but starting at the node of the leaf instead of the hole. The growth rate was calculated by dividing the sum of growth across all leaves by the number of experimental days. Additionally, the presence of visible *Labyrinthula zosterae* infections in the form of their characteristic blackened lesions on the leaf was analyzed from the pictures. Dead individuals and individuals whose pierced holes were not evident at the end of the experiment (not pierced or fouled in the area) were removed from the analysis.

Statistical procedures

Differences in plant traits (wet weight and leaf number) among meadows at the start of the experiment were analyzed using mixed effects models, including meadow as a fixed factor. Because we used a paired design (one of a pair of shoots from the same genetic individual was allocated to the “ambient” or the “climate change” treatment), we included individual ID as a random factor.

At the end of the experiment, the effects of treatment and microclimate of the meadow on the number of new leaves, growth rate, total dry weight, and dry weight of the roots were tested using mixed effects models. Treatment, meadow, and their interactions were treated as fixed factors. Individual ID and mesocosms (five in total, controlling for a tank effect; *see* Supporting Information Fig. S3) were included as random factors in the full model. As the random factor mesocosms did not improve the model fit, it was omitted from the final models. Careful model selection from the saturated model was carried out based on Bayesian information criterion and biological reasoning. Assumptions of all statistical tests were validated graphically. The final model outputs are reported as type II Wald F tests using Kenward–Roger degrees of freedom.

The presence of visible *L. zosterae* infections before and after the experiment and mortality data did not follow a normal distribution and were modeled with a generalized linear model (family = binomial), including the same fixed and random terms. The outcomes of the generalized linear mixed effects models are reported as type II Wald χ^2 tests.

The models were fitted in R using the *lme4* package and visualized using the *ggplot2* package (Douglas et al. 2015; Wickham 2016; v. 4.3.0; R Core Team 2023).

Results

Thermal microclimates

The microclimates of the *Z. marina* meadows in this study were characterized using high-resolution temporal temperature profiles (Fig. 1). Despite their close proximity to one another (1.5–14 km), temperature profiles differed clearly among *Z. marina* meadows, likely driven by local variations in the shoreline creating differences in exposure to waves and currents and thus water exchange (Fig. 1a; Supporting Information Fig. S4). Generally, more exposed meadows showed a higher frequency of lower temperatures and a narrower temperature range when compared to more sheltered meadows (Fig. 1b). This led to generally lower extremes and lower thermal variability (Fig. 1c–e), while the opposite patterns were observed for sheltered meadows. More precisely, the lowest daily maximum temperature was 21.4°C at Flatskär, which was 3°C lower than the highest daily maximum of 24.4°C at Tångeholmen (Fig. 1c). Diurnal fluctuations doubled from 1.4°C to 2.7°C in the two most diverging meadows (Flatskär vs. Tångeholmen, respectively; Fig. 1d). Further, we observed a difference of 2.5°C in daily mean summer temperature between the two most extreme meadows (20.5°C in Styrsö vs. 23.0 in Tjärnöbo; Fig. 1b,e).

Genetic differentiation

As for thermal variability, we also observed genetic differentiation among the meadows, and particularly for the exposed meadows Inre Vattenholmen (PC1 = 5.63% of the variance) and Flatskär (PC2 = 4.27% of the variance; Fig. 2a). Meadows experiencing higher mean temperatures and variability tended to be more genetically similar (Fig. 2a). As the principal component analysis (Fig. 2a) not only showed both site differentiations but also overlap in genetic differentiation among some sites, we further explored genetic structure among the sites with a LEA admixture analysis (Fig. 2b). When setting the maximum number of ancestral populations to two ($K = 2$), a pattern emerged where meadows exposed to higher temperatures and higher thermal variability were clustered separately (in yellow) from sites that showed lower mean temperature and lower extremes (more admixed between blue and yellow; Fig. 2b). Allowing separation into finer genetic clusters ($K = 5$) showed that among the exposed meadows Inre Vattenholmen and Flatskär exhibited the highest differentiation, while Koster, Kockholmen, and Styrsö were the most admixed (Fig. 2c). At an even finer scale ($K = 7$), a more pronounced genetic structure was observed with most meadows clustering into separate distinct genetic groups (Fig. 2d).

Phenotypic differences at the start of the experiment

The different microclimates contributed to the diverging phenotypes of the collected individuals (Fig. 3). However, these differences in phenotypes should not be seen as representative of the meadows' intraspecific trait variation as we, in order to increase growth potential and avoid differences between meadows solely driven by size or age, targeted equally sized, small plants for the experiment. Most individuals included in the experiment had three to four leaves at the start of the experiment across all meadows (Fig. 3a; $F_{9,37.4} = 2.09$, $p = 0.055$; Supporting Information Table S2). The wet weight at the start ranged from 0.47 to 2.40 g (in Tångeholmen and Koster, respectively; Fig. 3b). This resulted in significant differences in mean wet weight of meadows, with the lightest eelgrass individual being six times lighter than the heaviest ($F_{9,39.9} = 3.6$, $p = 0.002$; Supporting Information Table S2). Individuals of most meadows showed no to low signs of infection with *L. zosterae*. Only Koster and Inre Vattenholmen had up to 5 out of 10 visibly infected shoots (Fig. 3c; $W[1] = 1.1$, $p = 0.288$; Supporting Information Table S2).

Effect of the climate change treatment

Overall, the climate change treatment had a negative effect on *Z. marina*, although there were small overall differences among plants from different meadows. While the climate change treatment only led to a slight increase in deaths (Fig. 4a; $W[1] = 1.5$, $p = 0.213$; Supporting Information Table S3), it significantly increased the number of shoots that were visibly infected with *L. zosterae* (Fig. 4b; $W[1] = 5.9$, $p = 0.014$; Supporting Information Table S3). However, there was no significant difference in the number of infected plants among meadows (Fig. 4b; $W[1] = 0.6$, $p = 0.425$; Supporting Information Table S3). Further, new leaf growth was significantly reduced under the climate change treatment ($F_{1,45.6} = 6.8$, $p = 0.011$), but did not differ among meadows (Fig. 4c; Supporting Information Table S3). Comparably, significant negative effects were observed on the growth rate of eelgrass leaves (Fig. 4d). The individuals under the climate change treatment grew significantly less (on average 0.05 cm per day, 28%; Fig. 4d; $F_{1,39.2} = 13.2$, $p < 0.001$; Supporting Information Table S3) compared to ambient conditions (growth rates: ambient = 0.22 cm d^{-1}, treatment = 0.17 cm d^{-1}; Supporting Information Fig. S6). Again, there were no significant differences in growth rates among meadows. In contrast to growth-related immediate responses, the dry weights of the entire plant and their roots only were predominantly explained by meadow (Fig. 4e,f; $F_{9,35.1} = 7.2$, $p < 0.001$ and $F_{9,39.7} = 4.2$, $p < 0.001$; Supporting Information Table S3). Additionally, the dry weight of the roots was significantly (on average 10 mg, 12%) reduced under the climate change treatment compared to the ambient

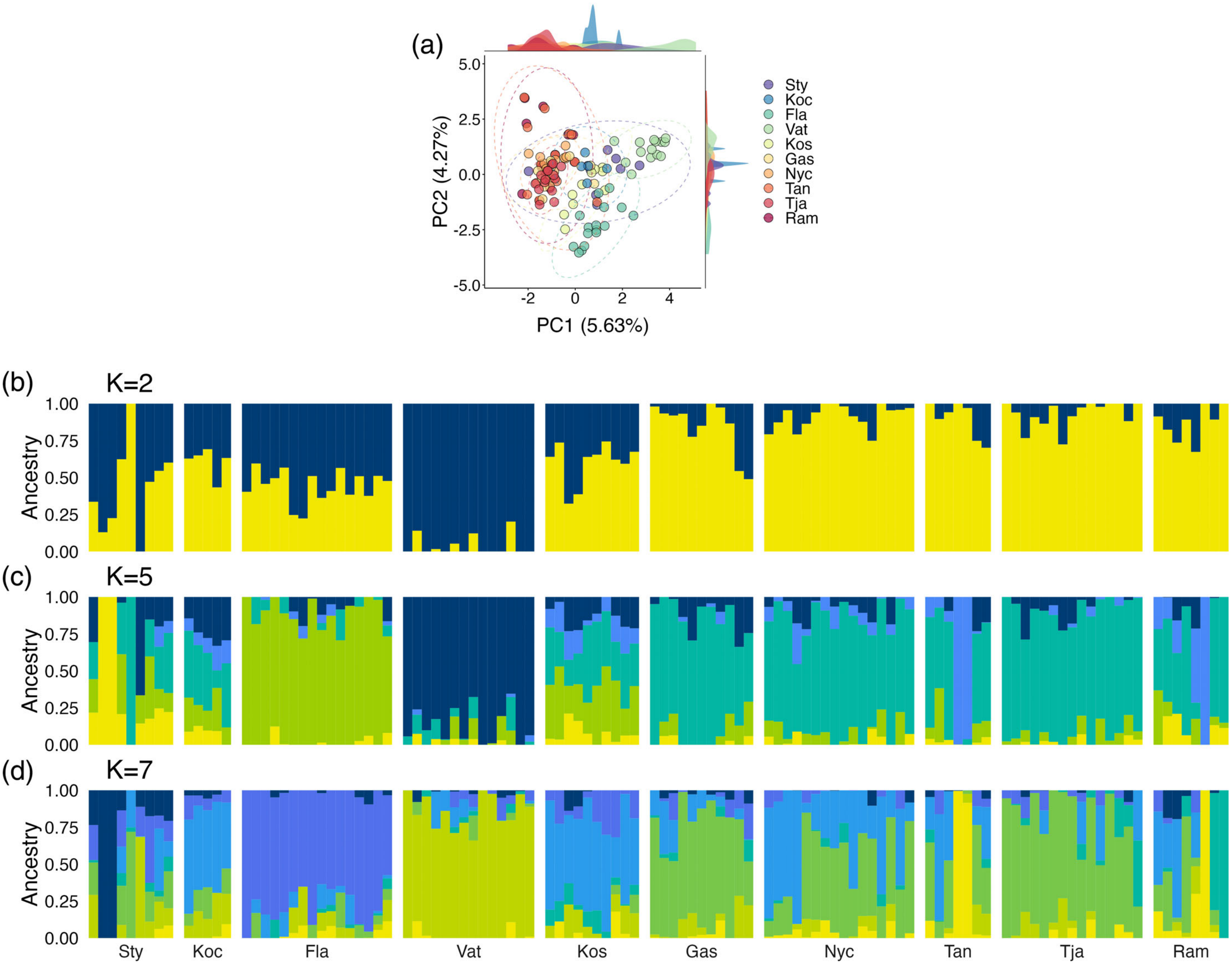

Fig. 2. (**a**) Principal component analysis of 111 multilocus lineages from the 10 eelgrass meadows sampled in the Kosterhavet Archipelago. Color coding (in **a**) is done following a gradient of thermal microclimates (*see* Fig. 1b–e). Each point represents the genotype of one individual from the site specified by color. The ellipses delineate groups of individuals from the same sampling site, illustrating some degree of population structure among the meadows. The 1st (PC1) and 2nd (PC2) components explained the largest amount of variation in the data. Eigenvalues can be found in Supporting Information Fig. S5. (**b–d**) landscape and ecological association analyses (LEA) of genetic structure analysis of the 10 *Zostera marina* meadows assessed. Each vertical line represents one individual within the meadow specified on the *x*-axis. The *y*-axis shows the proportion of each color-coded genetic ancestry in every individual. The maximum number of ancestral populations was set to $K = 2$, 5, and 7. Shared multilocus lineages between meadows were removed from the analysis. Fla, Flatskär; Gas, Gåsholmen; Koc, Kockholmen; Kos, Koster; Nyc, Nycklebykilen; Ram, Ramnekroken; Sty, Styrsö; Tan, Tångeholmen, Tja, Tjärnöbo; Vat, Inre Vattenholmen.

treatment (Fig. 4f; $F_{1,38.7} = 4.8$, $p = 0.033$). The total dry weight increased slightly (Ramnekroken) and decreased strongly (Inre Vattenholmen) under the climate change treatment across the meadows (Fig. 4e; Supporting Information Fig. S6D; $F_{9,31.6} = 0.01$, $p = 0.08$; Supporting Information Table S3). However, this treatment-meadow interaction was only visible as a trend and could not be linked to the microclimates present in the meadows (Figs. 1, 4e).

Discussion

This study demonstrates that fine-scale island characteristics across short distances (1.5–14 km) of the shoreline create a mosaic of habitats with distinct thermal microclimates and genetic differentiation of seagrasses inhabiting these microclimates. As a consequence, biomass (wet weight) and phenotype of eelgrass plants differed significantly across meadows at the

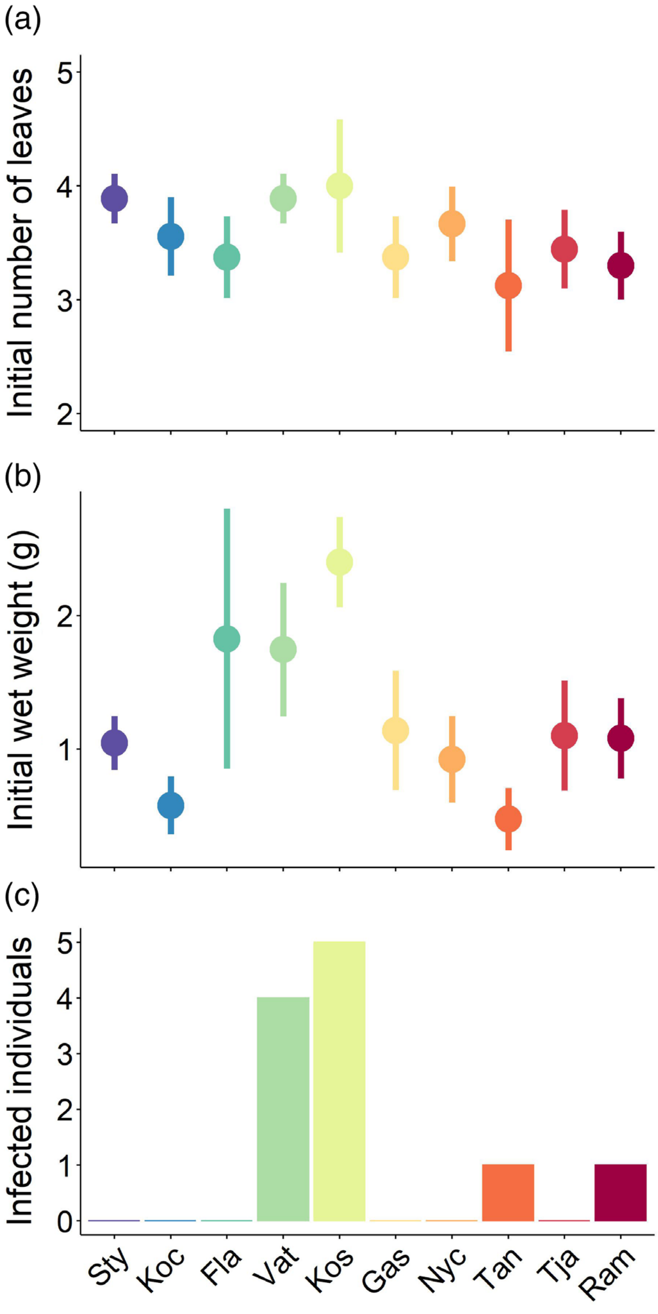

Fig. 3. *Zostera marina* intraspecific differences across the 10 meadows sampled in the Kosterhavet Archipelago, in the selected shoots at the start of the experiment in terms of (**a**) the initial number of leaves, (**b**) wet weight (means and 95% confidence interval [CIs]), and (**c**) the number of individuals visibly infected with *Labyrinthula zosterae* (presence/absence). Color coding is done following a gradient of thermal microclimates from lowest (left, purple) to highest (right, dark red) mean temperature (*see* Fig. 1b–e). Fla, Flatskär; Gas, Gåsholmen; Koc, Kockholmen; Kos, Koster; Nyc, Nycklebykilen; Ram, Ramnekroken; Sty, Styrsö; Tan, Tångeholmen; Tja, Tjärnöbo; Vat, Inre Vattenholmen.

start of the experiment, despite an effort to normalize the size of included individuals. Notwithstanding these small differences in starting conditions, we observed a strong effect of the climate change treatment (increased temperature + decreased salinity) on eelgrass, in the form of increased mortality, visible *Labyrinthula* infections, decreased numbers of new leaves, growth of leaves, and root biomass during the experiment. We also found variable responses to the climate change treatment among plants from different meadows. Yet, our initial hypothesis that meadows experiencing higher mean summer temperatures and thermal variability (i.e., sheltered meadows) would display greater resilience to the climate change treatment (i.e., reflected in a significant interactive effect of the climate change treatment and meadow) was not supported by the data.

The pronounced impact of the climate change treatment on growth, survival, and disease prevalence is in line with the previous work (Niu et al. 2012; Salo and Pedersen 2014; Hammer et al. 2018). Given our experimental design, it is not possible to draw conclusions on the relative importance of each driver (temperature and salinity) or the interaction between them. Other studies have demonstrated the potential of negative synergistic effects of salinity and temperature on eelgrass performance (Salo and Pedersen 2014). The increased temperature imposed here led to temperature fluctuations that reached a maximum of over 26.6°C during daytime, which is around the thermal limit of eelgrass (~ 26°C; Beca-Carretero et al. 2021; Nejrup and Pedersen 2008). In contrast, the salinity was only reduced to a minimum of about 19.6, while *Z. marina* has been suggested to exhibit comparable growth rates in salinities of 10–35 (Nejrup and Pedersen 2008). This suggests that elevated temperatures may dominate the effects, as indicated by previous studies showing that a single dominant driver can determine the combined effect of multiple stressors (Brennan and Collins 2015).

Surprisingly, the observed differences in microclimates among the meadows did not significantly impact the response to increased temperatures, contrary to the general notion that species exhibit thermal optima aligned with their natural habitat's mean maximum temperature (e.g., Thomas et al. 2012; Marbà et al. 2022). Initially, we hypothesized that mean temperature would be the primary driving factor behind the slight variations among meadows recorded at the start of the experiment as well as in response to the climate change treatment. However, testing this assumption proved challenging due to the complex correlations among various environmental variables (Supporting Information Fig. S7). When conducting a redundancy analysis including all traits, we found that, in addition to meadow identity, mean summer temperature emerged as a significant factor (Supporting Information Fig. S8). However, our ability to discern the impact of thermal microclimates on resilience in single traits may have been hindered by the mosaic of environmental drivers present across the meadows. The thermal microclimates across the studied meadows changed along a gradient and were not fully distinct. Additionally, other factors such as sediment structure and fetch (a measure of exposure) could vary significantly for individual meadows (as illustrated in the example of Inre Vattenholmen; Fig. 1;

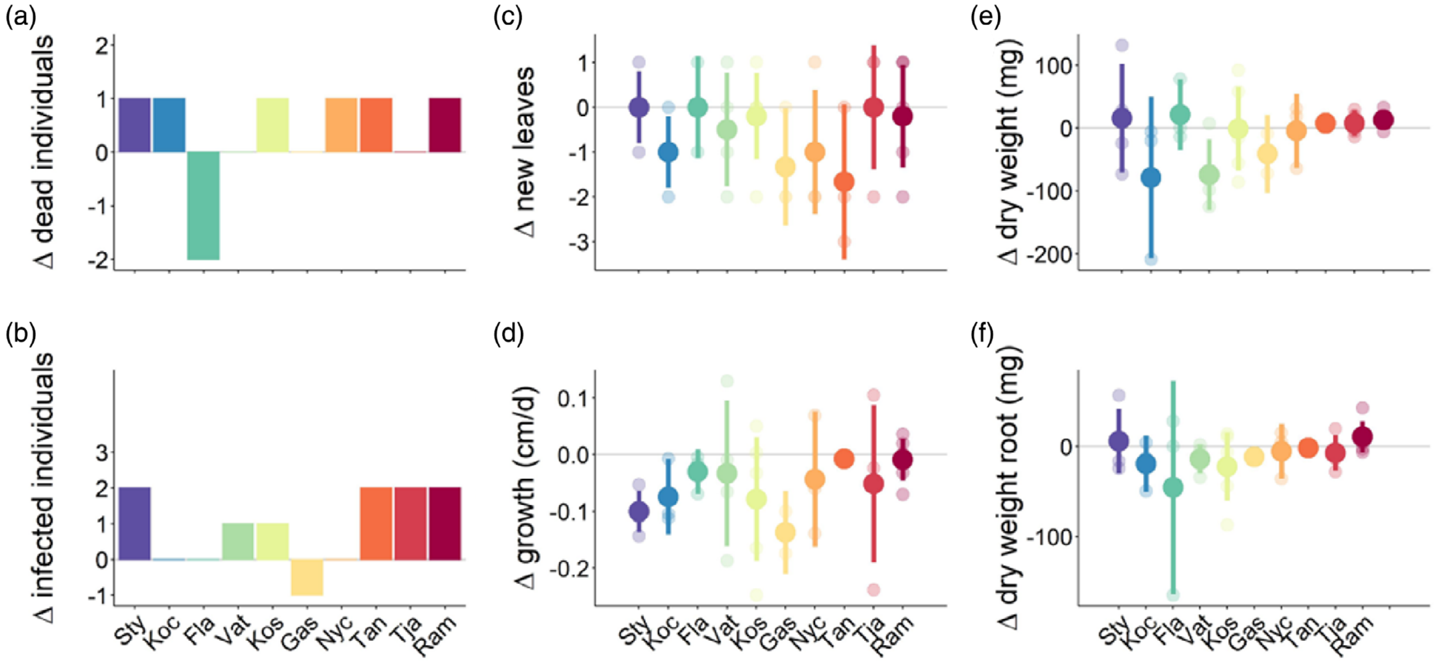

Fig. 4. Effect of the climate change treatment compared to the ambient treatment on (**a**) mortality (number of dead individuals), (**b**) the number of individuals infected with *Labyrinthula*, (**c**) the number of new leaves grown during the experiment, (**d**) growth rate (sum of the growth of all leaves together), (**e**) total dry weight, and (**f**) dry weight of the roots of *Zostera marina* plants following 13 d of incubation. The effect is calculated as the difference between the treatment minus the ambient group. In (**c–f**), the effect is calculated per pair of two shoots of one individual plant and shown as means and 95% CIs. Shoots were collected from 10 meadows sampled in the Kosterhavet Archipelago. Color coding is done following a gradient of thermal microclimates from lowest (left, purple) to highest (right, dark red) mean temperature (*see* Fig. 1b–e). Gas, Gåsholmen; Fla, Flatskär; Koc, Kockholmen; Kos, Koster; Nyc, Nycklebykilen; Ram, Ramnekroken; Sty, Styrsö; Tan, Tångeholmen; Tja, Tjärnöbo; Vat, Inre Vattenholmen.

Supporting Information Fig. S4). Consequently, intraspecific trait variation may not solely be influenced by thermal differences but may also depend partly on other strongly diverging environmental variables, and differences between summer and winter extremes. In contrast, a recent study focusing on distinct thermal habitats within a single bay demonstrated substantial intraspecific trait variation among *Z. marina* populations on a small regional scale (DuBois et al. 2022). These conflicting findings suggest that while differences in environmental conditions can indeed lead to intraspecific trait variation on a small regional scale, they may also be constrained by interacting environmental variables.

Short-term physiological responses can result in acclimation, allowing individuals to track shifts in environmental conditions. The acclimation capacity of *Z. marina* to temperature appears considerable. Staehr and Borum (2011) highlighted a 2°C shift in optimum temperature between winter- and summer-acclimated *Z. marina* exposed to 20°C in situ temperature differences. In our study, mean in situ temperature differed up to 2.5°C across meadows, which may not have triggered detectable intraspecific trait variations. In fact, the peak in summer temperature has the potential to enhance the productivity of temperate eelgrass, normally constrained by temperature (Beca-Carretero et al. 2021). Keeping the collected shoots in a common garden for about 20 d before the experimental start might additionally have reduced intraspecific trait variation caused by differences in acclimation. The timing of shoot collection is also crucial, given recent findings that temperate eelgrass responses to temperature and light stress are influenced by annual acclimatization cycles (Beca-Carretero et al. 2021; Sawall et al. 2021). In the present study, shoots were gathered from the end of June to early July, preceding the peak summer temperatures in the area (Supporting Information Fig. S2). Given the mild spring-to-summer temperatures and minimal heatwaves (Supporting Information Fig. S1), the collected individuals were likely to have been in a state of spring acclimation, potentially reducing meadow differences. Including the potential of acclimation to intraspecific trait variation thus requires careful consideration of how the time of sampling and handling can affect the experimental outcome.

The eelgrass meadows of this study were situated on the Swedish west coast and have relatively high genetic diversity and connectivity in the context of the North East Atlantic (Jahnke et al. 2018; Ries et al. 2023; Yu et al. 2023). Nevertheless, we observed genetic differentiation within the small spatial scale of the study area (≤ 14 km) centered around sheltered vs. exposed sites. This pattern of genetic differentiation could indicate that both connectivity and local adaptation play an important role in maintaining gene flow and genetic diversity (Harwell and Orth 2002; Olsen et al. 2013;

Christie and Knowles 2015). Connecting the genetic structure to the observed phenotypes is, however, limited. For example, some populations that cluster closely genetically, such as the sheltered meadows Tjärnöbo, Nycklebykilen, and Tångeholmen (Fig. 2a), exhibit very distinct growth responses (Fig. 4d). In contrast, the exposed meadows Flatskär and Inre Vattenholmen, which are more distinct from each other (Fig. 2a), show similar growth responses (Fig. 4d). Overall, we could not demonstrate an adaptation to microclimates across meadows. In contrast, *Z. marina* populations situated within approximately 10 km of each other in northern California have exhibited in situ adaptation to divergent temperature regimes (Dubois et al. 2022), a pattern that has also been observed in other geographic areas (Kamel et al. 2012). However, local adaptation might not be solely driven by differences in thermal microclimates, but also by the extent of temperature disparities, especially the extent of both the minimum and maximum extremes over annual and inter-annual cycles.

In natural settings, the interplay between shifts in mean temperature and overall variability can reshape intraspecific trait variation by impacting evolutionary processes. Variability can manifest through diurnal, semi-lunar, seasonal and annual fluctuations. Rapid fluctuations have been shown to accelerate evolutionary adaptation in planktonic autotrophs (Schaum et al. 2018). However, the fluctuation regime employed by (Schaum et al. 2018), oscillating between 22°C and 32°C every 3–4 generations, might yield distinct effects compared to those of diurnal fluctuations on long-lived eelgrass. To comprehend the impact of marine microclimates on intraspecific trait variation, it remains essential to consider how the relationships between drivers and their fluctuations align with the lifespans of the organisms studied (Jackson et al. 2021). In our study area, diurnal and likely annual fluctuations increase with greater shelter from open waters and wave exposure, which reduces water currents and not only elevates summer temperatures but potentially facilitates lower winter troughs and ice formation. This complex interdependence could impede directional selection (Fig. 5, "Evolution of elevated thermal tolerance"), observed elsewhere across latitudes (Marbà et al. 2022) as well as on local scales, when diverging summer temperatures do not coincide with different winter conditions among meadows (Bennett et al. 2022; DuBois et al. 2022). However, our approach may have overlooked the opposing effects of shelter on both summer and winter temperatures, which together could drive selection in long-lived eelgrass species and may not only restrict directional selection (Fig. 5, "No shift in thermal tolerance"), but also favor the selection of the most plastic genotypes (Fig. 5, "Evolution to generalist"), capable of coping with diverse and fluctuating environmental conditions. Increased plasticity has been demonstrated in *Z. marina* populations experiencing pronounced fluctuations in salinity (Salo et al. 2014). However, the limited range of temperatures tested in this study does not allow us to discern potential alterations in thermal performance curves (Fig. 5), which could have far-reaching consequences on eelgrass resilience. The comprehensive characterization of habitat differences across seasons, together with assessing thermal performance curves of seagrass, will thus be key to gaining a better understanding of how microclimates influence intraspecific trait variation in the future ocean.

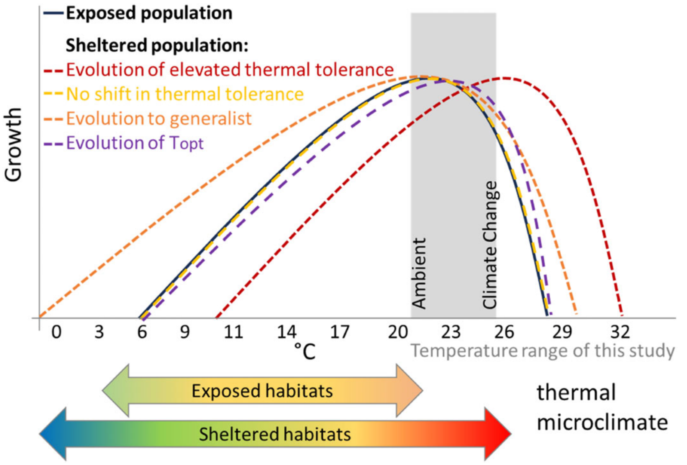

Fig. 5. Theoretical illustration depicting potential shifts in thermal performance curves in response to different thermal microclimate experiences in exposed and sheltered meadows. The proximate temperature range between the ambient and climate change treatment of this study is indicated by the vertical gray bar. The thermal performance curve of the (ancestral) exposed population is depicted as a solid line. Our study does not provide support for the evolution of elevated thermal tolerance (red dashed line) but cannot distinguish between other potential shifts in the thermal performance curve (yellow, orange, and purple dashed lines). Topt, thermal optimum.

Conclusion

In conclusion, the strong genetic differences we detected in the relatively small study area, combined with distinct thermal habitat variability, highlight the potential for, and need to, better understand intraspecific trait variation on small spatial scales. Yet, our study could not demonstrate that meadows experiencing higher mean summer temperatures and thermal variability display greater resilience to a simulated climate change. This potential absence of directional selection for more heat-resistant individuals in sheltered meadows may not be a general feature but could be specific to temperate regions with the potential for cold winter temperatures and sea ice formation. To fully address and understand how microclimates influence eelgrass' intraspecific trait variation, future studies should test broader temperature ranges to capture potential shifts in thermal performance, separate the effects of co-occurring environmental drivers (here salinity), and sample meadows at different times within the summer to account for potential seasonal acclimation effects. Understanding the complexities of microclimate–resilience interactions is crucial for devising targeted conservation and management strategies. In theory, donor meadows for eelgrass restoration should match the genotype required for the environmental conditions of the restoration site to maximize transplant survival. In practice, moderately exposed, shallow areas with good light are prioritized for faster recovery, while sheltered sites are avoided due to loose sediment causing high turbidity and poor visibility during harvesting (Moksnes et al. 2016). Considering the meadow-specific responses observed and assuming a lack of genetic data, it might be advisable for restoration efforts to aim to match the environmental conditions of the donor meadow with the restoration site, or include several donor meadows with varying conditions, to ensure the resilience of restored meadows in the face of changing environmental factors.

Author Contributions

All co-authors planned the experiment and were involved in setting up the mesocosm facilities, and in the collection of habitat environmental characteristics, the shoots, and the sediment. Niklas Niemi ran the experiment with help from Swantje Enge and Giannina S. I. Hattich. Giannina S. I. Hattich, and Christian Pansch conceptualized the manuscript. Maru Bernal-Gómez carried out the genetic analyses under the supervision of Marlene Jahnke. Giannina S. I. Hattich analyzed the environmental and experimental data and drafted the first version of the manuscript with input from Christian Pansch. All co-authors have revised the manuscript and commented during the revision process.

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Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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