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Rapid evolution of a coastal marsh ecosystem engineer in response to global change

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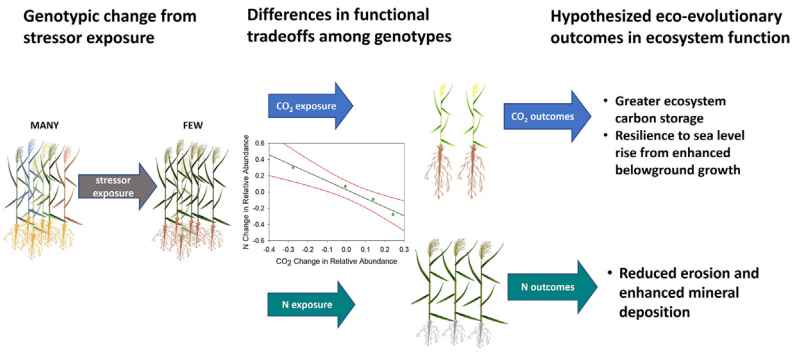
HIGHLIGHTS

- Aspects of global change, like rising concentrations of atmospheric carbon dioxide (CO_2) and nitrogen (N) enrichment, can potentially alter ecosystems by eliciting rapid evolution of ecologically important plants.
- We conducted a long-term field experiment to assess whether exposure to elevated CO_2 and N can alter genotypic variation in the common reed, *Phragmites australis*.
- Genotypic shifts were detectable after only three years of exposure, particularly to N enrichment.
- We found evidence that genotypes responded favorably to only one factor, rather than to multiple or combinations of different factors.
- By illustrating that global change can elicit rapid evolution, our findings suggest that organismal evolution can be an important determinant of how ecosystems function.

GRAPHICAL ABSTRACT



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ABSTRACT

There is increasing evidence that global change can alter ecosystems by eliciting rapid evolution of foundational plants capable of shaping vital attributes and processes. Here we describe results of a field-scale exposure experiment and multilocus assays illustrating that elevated CO_2 (eCO_2) and nitrogen (N) enrichment can result in rapid shifts in genetic and genotypic variation in *Phragmites australis*, an ecologically dominant plant that acts as an ecosystem engineer in coastal marshes worldwide. Compared to control treatments, genotypic diversity declined over three years of exposure, especially to N enrichment. The magnitude of loss also increased over time under conditions of N enrichment. Comparisons of genotype frequencies revealed that proportional abundances shifted with exposure to eCO_2 and N in a manner consistent with expected responses to selection. Comparisons also revealed evidence of tradeoffs that constrained exposure responses, where any particular genotype responded favorably to one factor rather than to different factors or to combinations of factors. These findings challenge the prevailing view that plant-mediated

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ecosystem outcomes of global change are governed primarily by differences in species responses to shifting environmental pressures and highlight the value of accounting for organismal evolution in predictive models to improve forecasts of ecosystem responses to global change.

1. Introduction

It is becoming increasingly evident that global change can alter ecosystems by eliciting evolutionary responses of foundational plants capable of governing vital attributes and processes (Schweitzer et al., 2004; Pauls et al., 2013; Fischer et al., 2014, Monroe et al., 2018). Assertions about the potential importance of rapid evolution are supported by studies demonstrating that a range of ecosystem properties are subject to the influence of intraspecific variation, particularly in ecosystem engineers inhabiting naturally species-poor ecosystems like coastal marshes (Hughes, 2014; Bernik et al., 2018a, Bernik et al., 2018b). Many plants also exhibit heritable variation in response to factors like elevated atmospheric carbon dioxide (eCO_2) (Ward et al., 2000; Mohan et al., 2004; Rae et al., 2007; Nakamura et al., 2011), nitrogen (N) enrichment (e.g., Kettenring et al., 2011; Bernik et al., 2018a) and drought (e.g., Franks et al., 2007). There is also evidence that conditions associated with global change – changes in CO_2 (Bazzaz et al., 1995; Stinson et al., 2011; Lohbeck et al., 2012; Grossman and Rice, 2014), salinity (Blum et al., 2021), N (Cleland and Harpole, 2010; Kelly, 2018) and precipitation (Avolio et al., 2013; Ravenscroft et al., 2015) – act as selective agents (i.e., forces, filters) that can alter genetic variation in plants. However, little is known about the pace of responses that may result in ecological change, especially to concurrent exposure to more than one potential selective agent.

Organismal evolution may exert greater influence on ecosystem processes if responses to selection unfold at a pace comparable to the rate of ecological change. There is a growing body of evidence that consequential evolutionary change can parallel ecological change (Hairston et al., 2005), with strong support coming from studies of selective responses to anthropogenic pressures (Palumbi, 2002), including pressures associated with global change (Franks et al., 2007; Grossman and Rice, 2014; Barton et al., 2020; Kelly and Griffiths, 2021; McGaughran et al., 2021; Zhong et al., 2021; Cheng et al., 2022). Field-scale experiments have shown, for instance, that exposure to elevated temperature and drought can lead to a rapid loss of genetic (i.e., allelic) diversity and divergence (e.g., Avolio et al., 2013; Ravenscroft et al., 2015), indicating that there is potential for selection-driven adaptation. Model simulations (Moran and Kubiske, 2013) and experimental studies also indicate that exposure can impose selective pressures on heritable traits (Franks et al., 2007; Stinson et al., 2011; Avolio et al., 2013; Grossman and Rice, 2014; Ravenscroft et al., 2015), with the nature of responses contingent on the potency of the pressure as well as ecological conditions like competition and genetic factors like trait covariance (Bazzaz et al., 1995; Etterson and Shaw, 2001; Lau et al., 2007; Moran and Kubiske, 2013; Lau et al., 2014; Schaum et al., 2018; García-Carreras et al., 2018; Barton et al., 2020; Limberger and Fussmann, 2021; Zhong et al., 2021; Jin et al., 2022).

Arguments for the relevance of evolutionary responses to global change remain tenuous, in part because few empirical studies have examined the relative magnitude and pace of responses elicited by exposure to different environmental pressures, particularly for species capable of governing the structure, function, and fate of ecosystems. To address these deficits, we conducted a fully crossed, field-scale exposure experiment and multilocus genetic assays to examine whether, and to what extent, eCO_2 and N enrichment elicit rapid shifts in genetic variation in the C_3 monocot grass *Phragmites australis* subs. *australis* (hereafter '*Phragmites*'), an ecologically dominant constituent of coastal wetlands worldwide. To gain perspective on underlying processes (i.e., differential survival, stochastic drift and gene flow), we evaluated trends of genetic variation over three years of treatment in experimental plots and drew comparisons to a second population located at a nearby reference site.

2. Methods

2.1. Study system and study site

Coastal marshes are an excellent setting to assess the nature and potential importance of evolutionary responses to global change. Coastal marshes are temperate grasslands with plant assemblages composed of distinct groups (e.g. C_3 grasses, C_4 grasses, and C_3 sedges) that have informed ecological theory about outcomes of global change (e.g., Langley and Megonigal, 2010; Kirwan and Megonigal, 2013). The plant assemblages found in coastal marshes are often dominated by ecosystem engineers, which increases the potential ecological significance of plant evolution, where even small shifts in variation can alter meaningful ecosystem attributes like shoreline stability (Bernik et al., 2018a; Bernik et al., 2018b; Bernik et al., 2021) and processes like carbon cycling (Hines et al., 2014; Mozdzer et al., 2016; Mozdzer and Caplan, 2018; Mozdzer and Megonigal, 2013).

Our field-scale exposure study was conducted at the Smithsonian Global Change Research Wetland (GCReW) on the Rhode River sub-estuary of Chesapeake Bay. GCReW (38.8742° N, 76.5474°W) consists of a brackish high-marsh (40–60 cm above mean low water), that experiences a mean salinity of 10 PSU (range 4–15) and a mean tidal range of 44 cm. Besides *Phragmites*, the plant assemblages at the site includes the C_3 sedge *Schoenoplectus americanus* and the C_4 grasses *Spartina patens* and *Distichlis spicata* (Holmquist et al., 2021).

2.2. Study species

Phragmites, also known as the common reed, is one of the most widespread angiosperms and it is an ecologically dominant constituent of coastal wetlands worldwide (Holm et al., 1977). *Phragmites* has recently been identified as an emerging model organism in plant sciences and invasion biology (Meyerson et al., 2016; Cesarino et al., 2020), and it has become a focal organism of global networks (Packer et al., 2017) used to evaluate ecophysiological responses to global change (Eller et al., 2017). It also is a well-recognized ecosystem engineer with the ability to store C, quickly build soils, raise surface elevation, and alter hydrology (Rooth et al., 2003; Teal and Peterson, 2005; Caplan et al., 2015). *Phragmites* is monoecious and genetically self-incompatible, and thus it is an obligately outcrossing species. It can become sexually reproductive after one growing season (McCormick et al., 2010), with local seedling recruitment contributing to within-marsh genetic diversity (Kettenring and Mock, 2012). However, gene flow appears to be limited, even among nearby embayments (Lambertini et al., 2008; McCormick et al., 2010; Stabile et al., 2016). Only Eurasian *Phragmites* is known to occur at our study site; there are no records of the native lineage, hybrids, or the other subspecies at or near GCReW.

2.3. Global change manipulation

As described in Caplan et al. (2015), our in-situ field-scale $eCO_2 \times N$ enrichment experiment was established in 2011 at GCReW to assess whether and how *Phragmites* responds to global change. Briefly, we installed twelve 1.25 × 2.5 m (3.125 m^2) open top chambers (OTCs) at the leading edge of a *Phragmites* monoculture progressing into a high marsh community dominated by the C4 grass *Spartina patens* and C3 sedge *Schoenoplectus americanus* (Fig. 1). OTCs were assigned to one of four treatments ($n = 3$ per treatment) representative of realistic global change scenarios known to alter the productivity of coastal marsh ecosystems: (1) ambient CO_2 + ambient N (A), (2) ambient CO_2 + N enrichment

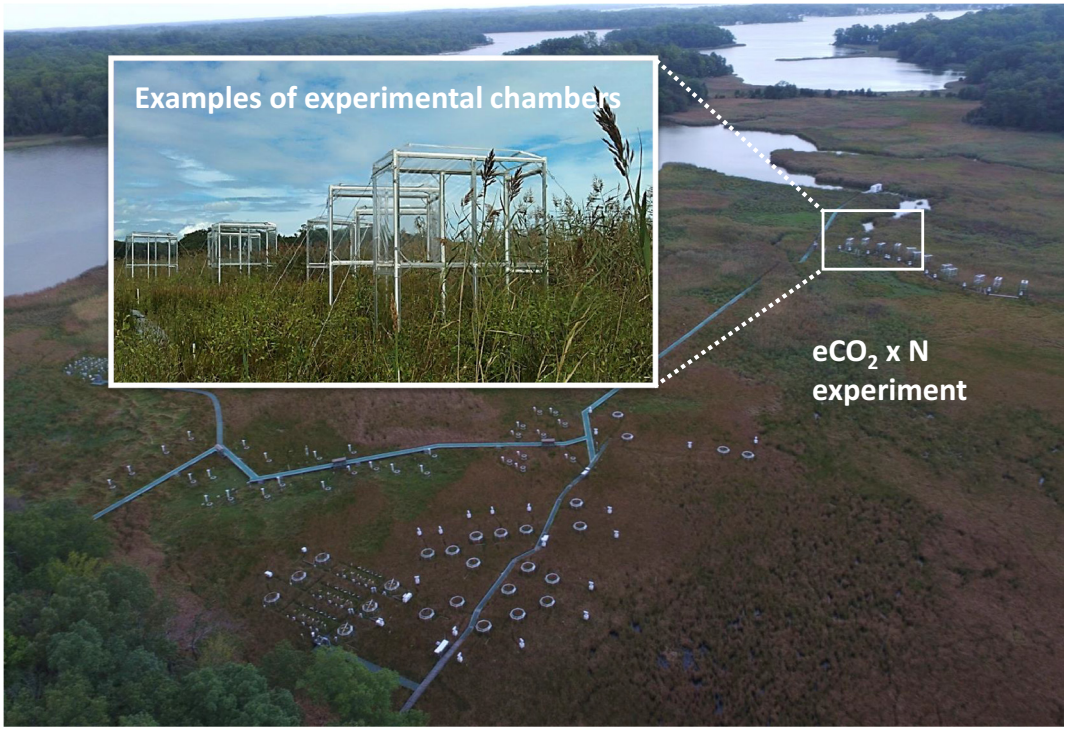

Fig. 1. Picture of the Smithsonian Global Change Research Wetland, with inset photo of the *Phragmites* global change experiment. Photo credit: David Klinges & Thomas J. Mozdzer.

(25 g N m^{-2} yr^{-1} added as NH_4Cl) (N), (3) eCO_2 (ambient + 300 ppm), and (4) eCO_2 + N enrichment. The treatment parameters are representative of predicted near-future concentrations of CO_2 and moderate levels of N enrichment in coastal wetlands. The conditions also parallel those examined in other long-term global change experiments at the study site (Curtis et al., 1989; Langley et al., 2009; Noyce et al., 2019). Notably, open top chambers produce a small increase in air temperatures (Curtis et al. 1997, Caplan et al., 2015), but since all chambers experience warming, the effect should not impact comparisons across chambers (i.e., among treatments, between treatments and controls, etc.). Here we focus on changes observed during the first three years of the experiment to characterize the nature of responses over time.

2.4. Sampling and multilocus microsatellite assays

We inventoried and collected leaf tissue from each *Phragmites* ramet in each OTC during 2011, 2012 and 2013. Cumulatively, we genotyped nearly 75 % of all *Phragmites* ramets in the chambers (n = 1494 total, with 384, 384, and 726 samples collected in 2011, 2012, and 2013 respectively) at a suite of putatively neutral microsatellite (μ_{sat}) loci to measure field-scale outcomes of eCO_2 and N exposure. We did not genotype every ramet because ramets can be clonal propagules. Rather, leaves for genotyping were chosen randomly within each chamber, with the stipulation that a minimum of 20 leaves were analyzed, or all stems if fewer than 20 were available, and the number of samples from the denser chambers reduced to yield the total number of samples in each year of the study. Notably, sample sizes increased to account for the increased abundance of *Phragmites* in the chambers over time (Mozdzer and Caplan, 2018). Owing to the polyploid nature of *Phragmites*, we identified polyploid genetic phenotypes (Becher et al., 2000; Saltonstall, 2003) to map and track variation in genetic phenotype identity (hereafter "genotype") in each experimental chamber in each year of the study. Doing so allowed us to assess whether the identity, richness, and relative abundance of genotypes differed according to exposure treatment and whether differences reflected exposure duration. We also calculated a standard panel of metrics including allelic richness and observed heterozygosity to determine whether exposure resulted in a loss or gain of genetic variation (Saltonstall, 2003). We drew comparisons to μ_{sat} variation in a second population located at a nearby site of similar size on the Severn River to better infer whether observed changes reflect underlying processes such as differential survival, stochastic drift, and gene flow. The Severn River site is 0.5 km long, approximately 2/3 of the wetland has been invaded by *P. australis*, which is invading the remaining native marsh. The Severn River site is approximately 17.5 km away (39.031823, −76.579943) from the GCREW site. A total of 39 samples (n_{2011} = 20; n_{2013} = 19) were taken at the Severn River reference site across a 50 m transect, comparable to the distance over which the experimental chambers are distributed at the GCReW site.

2.5. Genetic analysis and statistical tests

Following McCormick et al. (2010), we calculated genotypic richness, mean number of alleles, and observed heterozygosity using GenAlEx v. 6.5.03 (Peakall and Smouse, 2006, 2012). We tested for differences in genotypic richness across treatments and time by conducting generalized linear modeling using the glmmTMB (Brooks et al., 2017) package in R (R Core Team, 2013). The models included N treatment, CO_2 treatment, and Year as fixed main effects and Chamber as a random effect within each N and CO_2 treatment. A Poisson distribution was used to account for the discrete nature of genotypic richness. We also examined differential responses by genotypes that were detected in multiple years by comparing the number of stems attributed to each genotype in 2013 versus 2011 for each chamber. Because we sampled nearly twice as many stems in 2013 as in 2011, we first calculated the proportional representation of each genotype in each chamber by dividing the number of stems belonging to each genotype by the total number of stems that were sampled in the chamber. We tested for trade-offs in response to eCO_2 and N exposure by first calculating the change in representation of each of the four genotypes that were detected in chambers spanning all four treatments from 2011 to 2013. We then examined the correlation between changing representation in response to elevated N with that in response to eCO_2 using Pearson correlation analysis

in Systat v. 12. Because genotypes of polyploid organisms violate the assumptions of most measures of genetic variation, we first conducted a principal components analysis (PCA) using the Adegenet (Jombart, 2008) package in R (R Core Team, 2013). We then determined the centroid for the area occupied by individuals from each chamber each year and calculated the mean distance from individuals to the centroid mean to characterize the extent of genetic variation within each experimental plot per year and for each study site. We estimated pairwise F_{st} values using Adegenet (Jombart, 2008) to compare genetic distinctiveness among treatments and across time at the GCReW site, as well as between the GCReW and Severn River sites. We also plotted the results of the PCA to visualize the nature of genetic variation within and among the GCReW and Severn River sites.

3. Results

3.1. Genetic and genotypic variation

We detected evidence of extensive genetic and genotypic variation within *Phragmites* at the GCReW and Severn River sites. We detected 64 genotypes in the 1494 ramets sampled from the 12 OTCs at the GCReW site (Table 1). The distribution of genotypic richness ranged from 1 to 17 genotypes per chamber per year (Table 1), and 7 to 39 genotypes per treatment per year. A total of 22 alleles and an average of 3.42 alleles per locus were recovered, with per locus allelic richness varying from 1.25 to 2.75 across the chambers, from 3.5 to 3.75 across treatments, and from 2.375 to 3.25 across years (Table 1). H_o values ranged from 0.125 to 0.522 among the 12 OTCs, from 0.367 to 0.463 among treatments, and from 0.119 to 0.528 across the sample years (Table 1). Estimates of F_{st} ranged from 0 to 0.707 among chambers within a year, 0.201 to 0.24 across years across all chambers, and 0.009 to 0.199 among treatments. A pairwise comparison of genetic differentiation recovered an F_{st} estimate of 0.214 between the GCReW and Severn River sites. Visualization of genetic variation further illustrated the distinctiveness of *Phragmites* growing at the two sites (Fig. 1).

3.2. Comparisons by treatment and time

Genotypic richness declined as a result of exposure to eCO_2 and N enrichment over the course of the first three years of our experiment (Fig. 3A), but only N enrichment resulted in a statistically significant reduction of genotypic richness. Consistent with this, pairwise comparisons by treatment over time revealed that there was greater decline in other measures of genetic variation (e.g., the distance to the centroid median) from 2011 to 2013 in the elevated N treatment and the elevated CO_2 treatment compared to the control treatment (Fig. 3B). We detected a significant decline in genotypic richness in N treatment plots from 2011 to 2013 ($p = 0.02$); while eCO_2 exposure also tended to reduce genotypic richness (Fig. 3a), the effect was not statistically significant ($p = 0.45$). There was no significant interaction of eCO_2 and N treatment on genotypic richness ($CO_2 \times N$; $p = 0.50$). Notably, the magnitude of loss increased over time in the N treatment plots (year × N, $p = 0.032$; Fig. 3). Comparisons of *Phragmites* genotype frequencies revealed that proportional abundances shifted with exposure to eCO_2 and N ($p < 0.001$) (Fig. 4A, B). Because four of the genotypes were exposed to all four treatments, we were able to detect evidence of tradeoffs in exposure responses, where any particular genotype responded favorably to one factor rather than to different factors or to combinations of factors (Fig. 4A, B). A statistically significant relationship was recovered between the change in relative abundance of these genotypes with N enrichment versus the change in relative abundance with eCO_2 exposure ($r = 0.986$; $p = 0.014$) (Fig. 4C).

4. Discussion

We found that in situ exposure to elevated N and eCO_2 elicited marked changes in genotypic variation over a three-year period, illustrating that natural populations of *Phragmites* can rapidly evolve in response to global change. *Phragmites* populations appear to exhibit sufficient genetic variation upon which selection may act (Saltonstall, 2003; Lambertini et al., 2008; McCormick et al., 2010) (Fig. 1), with exposure resulting in rapid shifts consistent with the expected outcome of natural selection. These observations align with those of previous studies indicating that global change factors like eCO_2 can act as selective agents (Bazzaz et al., 1995; Ward et al., 2000; Grossman and Rice, 2014; Sandrini et al., 2016; Jin et al., 2022), further challenging the long-standing notion (e.g., Arp et al., 1993; Rasse et al., 2005; Drake, 2014) that exposure elicits phenotypic acclimation (i.e., plasticity) rather than evolution of coastal marsh plants like *Phragmites*.

Our study offers further evidence that selection-driven evolution can unfold over ecologically relevant time scales (Hairston et al., 2005; Post and Palkovacs, 2009; Hoffmann and Flatt, 2022; Rudman et al., 2022). Rapid evolution can be due to a variety of mechanisms, including selection leading to differential survival, stochastic variation caused by genetic drift, and the influx of alleles via gene flow. We can infer that selection is the most likely mechanism eliciting rapid evolution, in part because the observed shifts are consistent with expected outcomes of selection like declining genotypic variation over time (Fig. 3). Additionally, comparisons presented here (Fig. 2) and elsewhere (McCormick et al., 2010) indicate

Table 1
Estimates of genetic and genotypic variation by study site (GCReW, Severn River), experimental treatment (Ambient, eCO_2, N, eCO_2 + N) and time (2011, 2012, 2013), and overall (Total). N = number of ramets genotyped; N_G = number of unique genotypes; A_R = mean allelic richness; H_o = observed heterozygosity.

GCREW		2011				2012				2013				Total			
Treatment	Chamber	N	N_G	A_R	H_o	N	N_G	A_R	H_o	N	N_G	A_R	H_o	N	N_G	A_R	H_o
Ambient		68	11	2.5	0.349	49	15	3.125	0.372	62	9	2.625	0.381	179	33	3.625	0.367
	1	21	4	1.250	0.119	13	4	1.375	0.125	17	3	1.250	0.132	51	7	1.625	0.125
	8	26	4	2.000	0.404	17	7	2.500	0.390	18	5	2.250	0.396	61	15	2.750	0.398
	11	21	3	1.750	0.512	19	5	2.250	0.526	27	2	1.750	0.528	67	7	2.375	0.522
eCO_2		107	19	3.25	0.382	106	14	2.875	0.400	243	9	2.375	0.349	456	39	3.750	0.372
	2	37	8	1.625	0.139	28	4	1.625	0.143	62	5	1.375	0.139	127	11	1.875	0.140
	5	35	4	7.750	0.476	41	7	2.125	0.469	53	3	1.625	0.439	129	9	2.375	0.438
	10	35	8	2.125	0.554	36	4	1.875	0.514	52	2	1.625	0.507	123	10	2.250	0.522
N		112	15	3.125	0.423	125	14	2.75	0.45	167	7	2.375	0.459	404	33	3.500	0.448
	3	33	6	2.000	0.413	41	6	2.000	0.393	64	4	1.750	0.398	138	10	2.125	0.400
	6	53	5	1.875	0.432	54	6	2.500	0.468	115	3	1.625	0.471	222	10	2.875	0.461
	12	26	4	1.750	0.418	30	2	1.500	0.496	64	1	1.500	0.500	120	6	1.750	0.481
eCO2 + N		97	18	2.875	0.465	104	21	2.625	0.442	254	11	2.625	0.47	455	44	3.500	0.463
	4	38	9	2.000	0.475	43	11	2.000	0.390	72	5	1.625	0.457	153	17	2.375	0.438
	7	38	5	1.750	0.457	41	5	2.250	0.460	121	4	1.750	0.464	200	10	2.500	0.462
	9	21	4	1.750	0.494	21	4	2.250	0.512	61	4	2.375	0.500	103	12	2.750	0.501
Severn R		20	16	2.000	0.500	0	na	na	na	19	16	2	0.513	39	22	2.000	0.506

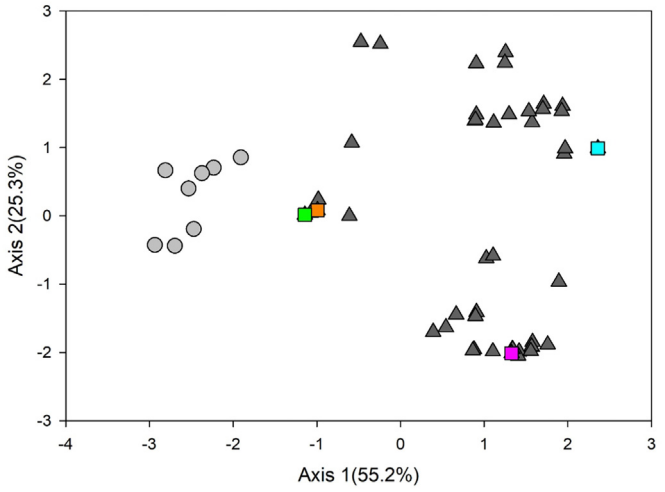

Fig. 2. PCA of variation among all 64 *Phragmites* genotypes detected in the exposure experiment at the GCReW site (grey triangles) with reference to four genotypes found in all treatments (colored squares, blue = genotype 11, purple = genotype 24, orange = genotype 45, green = genotype 50), and relative to genotypes detected at the Severn River site (light grey circles).

that gene flow is negligible among nearby stands of *Phragmites*. The consistency in directional change over time and treatments (Fig. 3) also indicates that the observed shifts are not attributable to genetic drift. Extending comparisons to capture trends over a longer time period (e.g., Blum et al., 2021) would, however, better determine the relative strength of deterministic and stochastic forces acting on local populations of *Phragmites*.

Notably, we found indications that tradeoffs to concurrent pressures may regulate responses to global change. We detected evidence of tradeoffs in response to eCO_2 and N, with genotypes exhibiting sub-optimal responses when exposed to both factors. While the comparison was limited, we recovered a negative correlation between individual genotype responses to eCO_2 and N enrichment. Thus it appears that some genotypes respond favorably to C versus N availability (and vice-versa), which could reflect variation in resource acquisition driven by intraspecific competition. It also appears that, like constraints that can arise due to factors like genetic correlations among functional traits (Etterson and Shaw, 2001; Walworth et al., 2021), concurrent exposure to multiple global change factors can dampen rather than amplify responses (e.g., nitrogen and warming, nitrogen and eCO_2, temperature and acidification) (Lau et al., 2008; Hines et al., 2014; Zhong et al., 2021). Exposure might therefore result in apparent stasis (i.e., dynamic equilibrium), which highlights the dual possibilities that evolutionary responses to global change are much more common than presently imagined and that evolutionary responses to multiple stressors may help maintain rather than alter ecological functionality. Our results also suggest that genetic by environment (G × E) interactions are a plausible explanation for why global change can have inconsistent effects (Langley et al., 2018) on C cycling and other ecosystem processes.

Evolutionary responses to global change can have cascading consequences on ecosystem processes if heritable trait variation aligns with genotypic variation. Our findings suggest environmental pressures may alter ecosystems by causing the loss or gain of heritable trait variation, even in the absence of direct effects. It is well understood that *Phragmites* exhibits heritable trait variation that influences several key aspects of C cycling, including decomposition (Hines et al., 2014), primary production (Mozdzer et al., 2016), nutrient uptake (Mozdzer et al., 2010), photosynthetic rate (Mozdzer and Zieman, 2010, Mozdzer et al., 2016), and methane emissions (Mozdzer and Megonigal, 2013). For example, reciprocal common garden experiments on *Phragmites* sampled across a broad latitudinal range showed that heritable variation in litter chemistry influenced rates of leaf mass loss and microbial respiration under current and expected warming and nutrient conditions (Hines et al., 2014). It is thus likely that eCO_2 and N enrichment exert selection on traits that alter ecosystem outcomes, particularly considering that the magnitude of effects arising from trait variation among *Phragmites* genotypes can be equal to, or greater than, the influence of variation reported for different species (e.g., Cornwell et al., 2008) and from variation in environmental pressures (e.g., Reich and Oleksyn, 2004; Wright et al., 2004; Santiago, 2007). For example, *Phragmites* responses to eCO_2 and N increase GPP by 44 % and 60 % (respectively), which is two- to three-fold greater in magnitude, and proportionally greater than the response of other plant species grown under the same conditions (Mudd et al., 2009; Kirwan and Megonigal, 2013; Caplan et al., 2015). *Phragmites*-driven increases in GPP manifest as enhanced belowground productivity and surface elevation gain, consistent with well-known relationships between plant exposure responses and geophysical attributes of coastal marshes (Langley et al., 2009; Cott et al., 2018). It also reflects changes in morphological (e.g., height, biomass,

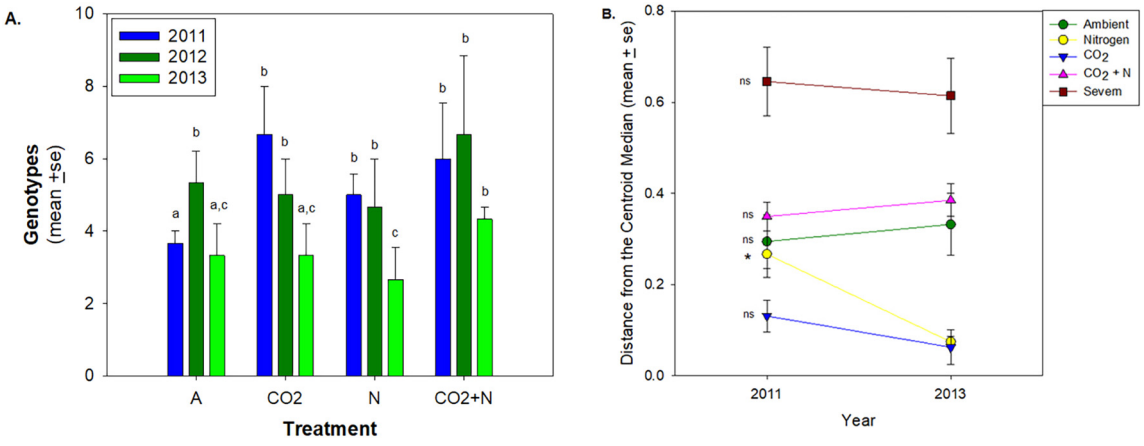

Fig. 3. A. Mean ± SE richness of genotypes within experimental chambers (n = 12; 3 per treatment) at GCReW over time. A = ambient; eCO_2 = elevated CO_2; N = Nitrogen enrichment. Genotypic richness significantly declined in N experimental chambers (p = 0.02), over time (N × time; p = 0.032). Significantly different values are indicated by different letters above the bars.

B. Changes in genetic variation, as indicated by mean ± SE distance to the centroid median, from 2011 to 2013. Ambient = green circles, elevated CO_2 = blue inverted triangles, N enrichment = yellow circles, elevated CO_2 + N enrichment = pink triangles, Severn River site = dark red squares. Treatments with significantly different values among years are indicated with asterisks to the left of the line.

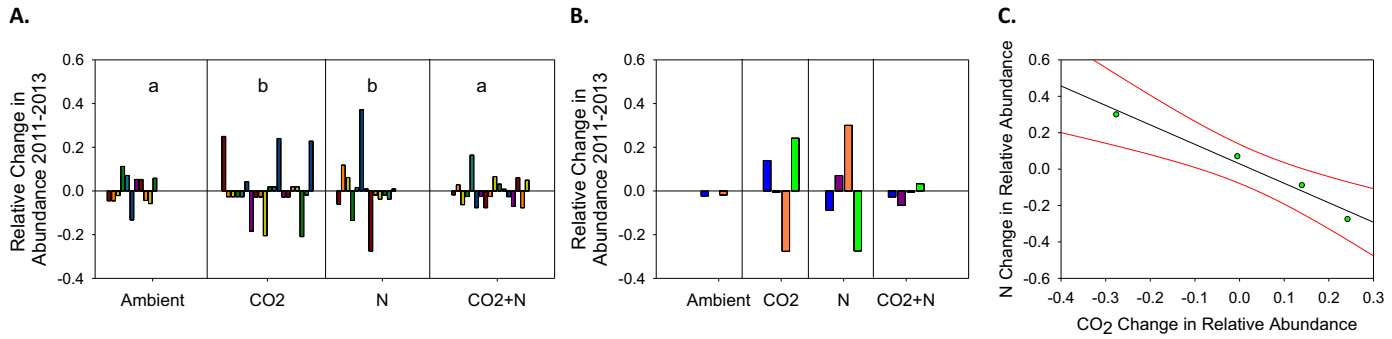

Fig. 4. A. Relative change in genotype abundance of 64 *Phragmites* genotypes in the GCReW experiment detected in 2011–2013. Each genotype is represented by a unique color. Both eCO_2 (CO_2) and nitrogen enrichment (N) induced a strong and statistically significant response, whereas ambient and eCO_2 + N conditions did not. **B**. Proportional change in relative abundance of four *Phragmites* genotypes present in all four treatments (blue = genotype 11, purple = genotype 24, orange = genotype 45, green = genotype 50) of the GCReW experiment. **C**. The tradeoff in the relative response of the same four genotypes to eCO_2 and N.

leaf area) and physiological (e.g., light saturated rate of photosynthesis) attributes (Mozdzer and Caplan, 2018) that influence belowground C cycling through changes in C inputs (i.e., C quantity) (Fischer et al., 2014; Bernal et al., 2017).

5. Conclusions

While our findings point to the plausibility that ecosystem attributes are subject to the outcomes of evolutionary responses to global change, testing this hypothesis will require coordinated measurement of genetic and genomic variation, functional trait variation, and ecosystem properties over time. By providing perspective on whether ecosystem attributes and processes constitute 'extended phenotypic' attributes sensu Whitham et al. (2003), an integrative eco-evolutionary investigation would help reveal the functional linkages that couple plant evolution to ecosystem processes (Monroe et al., 2018), and thus offer a novel basis for predicting the near-term future and long-term fate of coastal marsh ecosystems. Next steps might include further study of geographic variation among marshes and extending the period of observation in field-scale common garden experiments to better determine the balance of influence of different factors and clarify what processes (e.g., differential survival, differences in sexual or asexual reproductive success, stochastic variation, immigration of favored alleles or genotypes via pollen and seed dispersal) contribute to changes in genotypic composition over time. Analysis of quantitative genetic variation and assays of other regions of the genome would also shed light on the nature of phenotypic responses (i.e., heritable versus plastic, deterministic versus stochastic) to eCO_2 and N enrichment. Subsequent studies might then focus on heritable traits that influence marsh platform elevation and erodibility (Bernik et al., 2018a; Bernik et al., 2021) to elucidate whether rapid evolution deters the loss of marshes under conditions of accelerating rates of sea level rise. It has been shown that greater belowground growth and changes in root distribution can translate into large vertical shifts at the marsh surface (Turner et al., 2004). Greater aboveground growth due to shifts in traits such as stem density and height can also reduce erosion and facilitate mineral deposition by dissipating wave energy (Leonard and Luther, 1995; Christiansen et al., 2000; Neumeier and Ciavola, 2004). The sum of these effects can be large, considering that vegetation can increase platform elevation by as much as 13 mm per year (Baustian et al., 2012) and alter shoreline erosion rates by >10 % (Bernik et al., 2018b). Accordingly, even small evolutionary changes in plant performance could determine whether marshes are resilient to sea level rise and other aspects of global change.

CRediT authorship contribution statement

TJM, MKM, and JPM designed the study; TJM, MKM, JPM, and IS contributed to data collection; TJM, MKM, IS, and MJB contributed to data analysis; TJM, MKM and MJB wrote the manuscript; all authors contributed to editing the manuscript.

Data accessibility

All data will be publicly available on a Smithsonian Institution server, as part of the long-term Smithsonian Global Change Research Wetland long-term data sets (https://serc.si.edu/gcrew/data).

Data availability

Data will be made available on request.

Declaration of competing interest

The authors have no competing interests to declare.

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