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ORIGINAL PAPER

Impact of invasive *Carex kobomugi* on the native dune community in a US mid-Atlantic coastal system

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Abstract Dunes provide numerous ecosystem services including habitat for flora and fauna, coastal protection through mitigation of wind and wave energy, and as a barrier to storm flooding. Dune vegetation that inhabits these systems plays a vital role in building dunes and resisting erosion. In the United States, the Virginia coast is a transitional temperature zone for several dominant dune grasses, where the northern species, *Ammophila breviligulata* (C3) and the southern species, *Uniola paniculata* and *Panicum amarum* (both C4) overlap. At Back Bay National Wildlife Refuge (NWR), Virginia, warming temperatures are resulting in native species range shifts altering biotic interactions. Additionally, the invasive sedge, *Carex kobomugi* (C3) has become more prevalent in the region with unknown effects on the landscape. To understand the impact of *Carex* on the native plant community, we quantified species distribution and morphological traits of three dominant native species, *A. breviligulata*, *Panicum*, and *Uniola* as well as invasive *Carex*. We found that *Carex* was most dominant and exhibited similar individual traits when compared to native species. The suite of plant traits was unique in *Carex*, with less variation than in native species allowing for rapid nutrient acquisition and growth. These traits, combined with species distribution data suggest that *Carex* may limit *Ammophila* abundance. Similarly, presence of *Carex* had a negative effect on *Panicum* growth, but no discernible effect on *Uniola*. Success of *Carex* at Back Bay NWR may be indicative of the future spread of the species due to above and belowground morphological traits, which may give the invasive an advantage with climate warming.

Keywords Plant distribution · Root traits · Tensile strength · Aboveground · Belowground

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Introduction

Biotic invasions have been an increasing problem with climate change (McKinney and Lockwood 1999; Dukes and Mooney 1999) affecting growth and persistence of endemic species (Reviewed In: Hughes 2000; Walther et al. 2002). These biotic shifts occur in most ecosystems, including coastal systems (Grabherr et al. 1994; Walther et al. 2002; Wang et al. 2019; Henry and Sorte 2022), where sea-level rise and oceanic storms exacerbate climate change influences. Perhaps most important, is the mitigation of invasive species effects within coastal dune systems. Dunes provide a multitude of ecosystem services, such as habitat for shore birds, water purification, carbon sequestration, and recreation (Reviewed In: Barbier et al. 2011), but also protect economically valuable coastal infrastructure from wind and wave action, as well as rising sea levels (Ruggiero et al. 2001; Hesp 2002; Mullins et al. 2019). An additional concern is that low elevation coastal zones include 10% of the world's population (McGranahan et al. 2007). Predicting responses of coastal dunes to a range of climate change scenarios and potential biotic invasions is limited by a critical lack of knowledge of morphological plant traits (above and belowground) for native and invasive species that influence resource acquisition and dune dynamics (i.e., dune building, erosion).

Dunes are formed through the feedback of vegetation and sediment deposition (Hesp 2002; van IJzendoorn et al. 2021). Dune vegetation is limited to species that can withstand high abiotic stress such as salt spray, blowing sand, heat, drought, frequent flooding, and nutrient limited soils (Ehrenfeld 1990; Young et al. 1994). Within a dune system, species composition (due to associated morphological traits) can determine the size, shape, and erosion resistance of a particular dune (Feagin et al. 2015; Hacker et al. 2019; Mullins et al. 2019). Many of these traits including height, stem density, burial response, and aboveground plant cover determine dune shape and size (Woodhouse et al. 1977; Hacker et al. 2012; Zarnetske et al. 2012; Reviewed In: Feagin et al. 2015). Knowledge of these aboveground metrics are incorporated into dune management plans; however, belowground characteristics are less understood, especially the influence of species-specific belowground traits on dune building and erosion resistance (Reijers et al. 2020; Walker and Zinnert 2022). Belowground traits influence resource capture for plant growth, propagation throughout the dune system, and dune erosion resistance (Reubens et al. 2007; de Battisti and Griffin 2020). These traits are of equal importance to aboveground characteristics when assessing dune stability, and they may be altered by plant invasions, but belowground traits have not been thoroughly investigated.

Grasses play a vital role in dune building and the introduction of non-natives may have many unintended impacts. An example of these potential impacts can be seen in the introduction of *Ammophila arenaria* and *Ammophila breviligulata* along the US Pacific Northwest coast. Expansion of these species has led to significantly taller and wider dunes than those built by native species (Hacker et al. 2012; Zarnetske et al. 2012). Along the US Atlantic coast, *Carex kobomugi* (Asiatic sand sedge, hereafter referred to by genus) is expanding from Massachusetts to North Carolina, dominating habitat previously occupied by native dune grasses (Charbonneau et al. 2020). *Carex* proliferates via clonal propagation, which facilitates rapid expansion (Hilton et al. 2006; Hacker et al. 2012). The dense root structure of *Carex* may enhance dune building and providing protection from storm induced erosion (Wootton et al. 2005; Charbonneau et al. 2016). However, it is important to consider all ecological impacts (positive and negative) when evaluating an invasive species. Due to the dune building function of non-natives along with expanding infrastructure in the North American Pacific Coast, where monitoring the establishment and expansion has been the primary focus (Hacker et al. 2012). In comparison, along the Atlantic Coast efforts are focused on *Carex* removal (Wootton et al. 2005) as protection of native dune grasses is important for wildlife habitat, including threatened and endangered species.

Carex invasion has the potential to alter native plant community structure and traits but has not been evaluated in North American dunes. The Virginia, USA coastline represents the northernmost range for southern species and the southernmost range for northern species (Goldstein et al. 2018), with increasing temperatures causing latitudinal range shifts in coastal (Huang et al 2018; Goldstein et al. 2018). Above and belowground traits provide a mechanistic understanding of resource use for the growth of dominant species. Quantifying the interactions of invasive species, such as *Carex*, with native counterparts is essential for long-term restoration projects and navigating predicting future species range shifts. Our objective is to quantify the influence of invasive *Carex kobomugi* on the native community for a climatically transitional dune system and determine the plant traits that enhance resource acquisition relative to native species. To achieve this goal, we (1) quantified species distributions and abundance across the dune to identify relationships relative to dune position, (2) evaluated morphological traits of *Carex* relative to native species, and (3) quantified the effect of

Carex on the community through changes in species richness, traits, and species composition.

Methods

Study site

This study was conducted at Back Bay National Wildlife Refuge (NWR), Virginia Beach, VA, USA (36.6880° N, 75.9218° W) along the northernmost portion (1.6 km) of dune ridge (Fig. 1). The area of Back Bay NWR was home to multiple tribes within the Powhatan chiefdom. They were either forcibly removed by the English colonizers or died during the smallpox epidemic by the early 1700s (Rountree 1990). The land this research was completed on was stolen from these Indigenous communities and needs to be respected in accordance with their ideals of land preservation and returned to the remaining modern-day tribes.

The northern section of the site is currently closed to the public and has not been the focus of active management; the *Carex* population remains intact. Throughout the southern portion, *Carex* has been removed through yearly targeted spraying of glyphosate along with the planting of native dune grasses including *Ammophila breviligulata* (American beach grass), *Panicum amarum* (bitter switchgrass), *Uniola paniculata* (sea oats), and *Spartina patens* (salt-meadow cordgrass).

Carex is native to eastern Asia and was introduced in New Jersey, US in the 1920s (Small 1954). The invasion of *Carex* in the US has primarily been studied along the New Jersey coast, but the species has spread further south causing concern for land managers. The three focal natives here are *Ammophila breviligulata*, *Uniola paniculata*, and *Panicum*

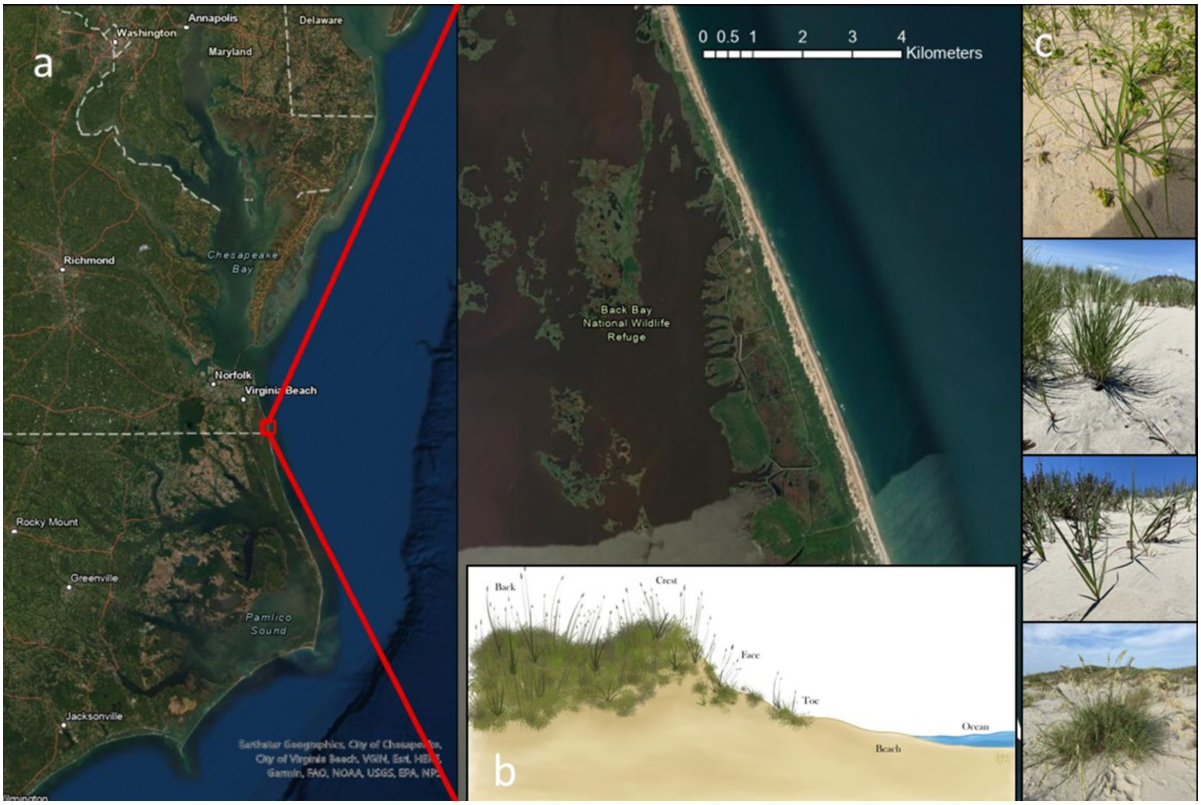

Fig. 1 **a** Map of site; Back Bay NWR; Virginia Beach, VA, USA. Created by Alexander Sabo **b** Labeled dune schematic. Created by Julia Yee **c** Species used for trait measurements (from top to bottom): *Carex kobomugi*, *Ammophila breviligulata*, *Panicum amarum*, and *Uniola paniculata*

amarum (hereafter referred to by genus). *Ammophila* is a C3 grass (cool-season) that has dominated much of the northern US east coast, with limited distribution in North Carolina and farther south (Goldstein et al. 2018). *Ammophila* is often used in restoration projects but is sensitive to high temperatures (Woodhouse 1978) that occur with climate warming. *Uniola* is a C4 grass (warm-season) and dominates the southern Atlantic and Gulf coasts. This species has expanded northward due to warming temperatures (Goldstein et al. 2018). *Panicum* is a C4 grass that exists along the entire east coast and is typically used in tandem with *Ammophila* for dune grass planting projects. *Panicum* is a moderate dune builder that is less studied (Woodhouse 1978; Hodel and Gonzalez 2013). It is unclear how *Carex* invasion is influencing interactions between native dune grasses as warming induced range shifts occur.

Field sampling

Plant community composition and aboveground traits

To assess dune composition and potential species interactions, transects were established from the dune toe to the back dune (Fig. 1b) and spaced ~ 120 m apart (n = 15) throughout June 2020. Plots (0.25 m^2) were positioned 5 m apart and included the toe, face, crest, and back dune (Fig. 1b) with 5 plots per transect. Within each plot, percent cover, number of shoots, and maximum height of each species were recorded. Percent cover of individual species and bare sand were ocularly estimated with a quadrat, rounded to the nearest 5% and totaling 100%. Relative importance was calculated for each species present, using relative cover, relative frequency, and relative stem densities (Eq. 1). This calculation ranges from 0 to 300 with higher numbers being of higher importance at the site.

Equation 1 Calculation for relative importance values by species

$$\text{Relative Importance} = \left(\frac{\text{Species Frequency}}{\text{Total Frequency}} \times 100\right) + \left(\frac{\text{Species Stem Counts}}{\text{Total Stem Counts}} \times 100\right) + \left(\frac{\text{Species Cover}}{\text{Total Cover}} \times 100\right) \tag{1}$$

Biomass and belowground trait measurements Based on species composition from community composition plots, monocultures (within a minimum 0.25 m^2 plot) of dominant species (*Ammophila*, *Panicum*, *Uniola*, and *Carex*, Fig. 1) were selected for further above and belowground morphological measurements (n = 10 per species) from the dune face. Additional cores were selected from mixed species plots where *Carex* was present with native species and absent (mixed native species only, n = 10).

All cores were collected in June 2020, except for monocultures of *Panicum* which were collected in June 2021. Following modified methods of Charbonneau et al. (2016), cores were collected to 60 cm depth using a slide hammer (AMS, Inc.; American Falls, ID), bagged, and placed in a cooler for further processing. Aboveground biomass within the core was cut at the soil surface and placed in a bag for later processing. Cores were processed by wet-sieving using the #6 (3.35 mm), #18 (1.00 mm), and #35 (500 µm) standard sieves to remove all belowground material. Roots were scanned using Epson Perfection V800 picture scanner (Epson America Inc., Long Beach, California, USA) and WinRHIZO software (Regent Instruments Inc, Québec, Canada) to quantify total root length and surface area for different root diameter classes. After scanning, the total below and aboveground material was dried at 60℃ for 72 h to determine biomass. Root tissue density (RTD) was calculated as the ratio of dried root material to volume of the roots. Dried material (both above and belowground) was analyzed by Cornell Isotope Laboratory for % carbon (C), % nitrogen (N), $\delta^{15}N$, and $\delta^{13}C$. Isotope analysis of $\delta^{15}N$ aided in the determination of N source, and to give an indication of nitrogen fixation (Unkovich 2013), while analysis of $\delta^{13}C$ is a proxy for water use efficiency (Bacon 2004).

For each species, additional roots were collected (n = 10) for tensile strength measurements. Roots were washed and stored in 15% ethanol until processing. For measurements, roots were rehydrated in water for at least 30 min (Böhm 1979; Bischetti et al. 2003). Clamping of roots followed a modified procedure, similar to De Baets et al. (2008), using sandpaper (3 M, 220 grit) and foam (Walker and Zinnert 2022). Tensile strength was quantified with an MTS Insight 30 Universal Testing Machine (UTM) and MTS Advantage Wedge Action Grips (MTS Systems Corporation; Eden Prairie, MN) with a 50N load cell and connected to the software, Testworks 4. The software calculates peak stress required to break the root (i.e., tensile strength).

Statistical analysis

Plant community composition and aboveground traits

Due to non-normality, cover was log + 1 transformed to account for 0's in data across the dune profile; plant height and stem density were log transformed. Two-way mixed model analysis of variance (ANOVA) identified differences in cover by location and species with plot as a random variable. Analysis of covariance (ANCOVA) determined species differences in plant height and stem density with species cover as the covariate. Tukey tests were used to examine post-hoc significant differences among groups.

Biomass and belowground trait measurements

All biomass and belowground trait variables were log transformed. Analysis of covariance (ANCOVA) identified species differences in biomass and belowground trait variables (i.e., above and belowground biomass, root:shoot, root diameter, root surface area, fine root surface area, root tissue density) with species cover as the covariate. ANCOVA quantified species differences in peak stress with root diameter as a covariate for the tensile strength. Species differences in aboveground and belowground nutrient and isotope data were determined with ANOVA. Tukey tests were used to examine post-hoc significant differences among groups.

The multiple above and belowground variables (i.e., cover, stem density, height, biomass, root traits, nutrients and isotopes) for each species from coring plots along the face, were analyzed with Multiple Response Permutation Procedure (MRPP) with Euclidean distance to detect significant differences among species. Multivariate results were visualized with Nonmetric Multidimensional Scaling (NMS) using Euclidean distance.

Effects of Carex

Differences in percent cover, height, and stem density for *Ammophila*, *Panicum,* and *Uniola* were assessed in plots with and without *Carex* (data from full community plots) using multi-factor ANOVA (location, *Carex* presence/absence). We used a Bonferroni p-value adjustment accounted for multiple tests ($\alpha = 0.017$). Total above and belowground biomass differences among mixed species coring plots where *Carex* was present and absent were determined with two-factor ANCOVA (*Carex* presence/absence, native species identity, and native cover as a covariate). All statistics were completed in R version 4.1.0.

Results

Distribution of species on the dune

Carex had the highest percent cover of all species across the dune profile, decreasing from the back to the dune toe (Fig. 2, Fig. S1). In comparison to the dominant native grasses (*Ammophila*, *Panicum*, *Uniola*), *Carex* had higher cover at every dune location except the toe where it was rarely found (species × location: $F = 2.67$, $p < 0.01$); Fig. 2). *Ammophila* was dominant at the dune toe and decreased in cover at the crest and back dune. In order of relative importance at the site the species from highest to lowest importance were: *Carex*, *Ammophila*, *Panicum*, *Uniola*, and *Spartina patens* (Table S1). The most frequent species in order were *Carex*, *Panicum*, *Uniola*, and *Ammophila* (Table S1). Other species present on the dunes in low quantities included: *Spartina patens*, and the forbs *Gamochaeta purpurea*, *Hydrocotyle bonariensis*, and *Krigia virginica* (Table S1).

Species plant traits

Stem density was lowest in *Panicum* (6 ± 1) compared to the other natives ($F = 13.41$, $p < 0.01$). The tallest species were *Uniola* and *Ammophila* (~ 70 cm), while *Carex* and *Panicum* were shorter (~ 29 cm) ($F = 108.7$, $p < 0.0001$; Table 1). Aboveground biomass was highest for *Uniola* (> 300%, $F = 29.92$, $p < 0.0001$, Table 1). *Carex* belowground biomass was > 2 times more than *Panicum* ($F = 3.98$, $p = 0.02$). Root:shoot was relatively low with *Uniola* and *Panicum* significantly lower than *Carex* ($F = 7.65$, $p < 0.001$). *Ammophila* and *Carex* had smaller average root diameter (0.33 mm, $F = 14.44$, $p < 0.0001$) than *Uniola* and *Panicum*, which was reflected in higher tensile strength for both species

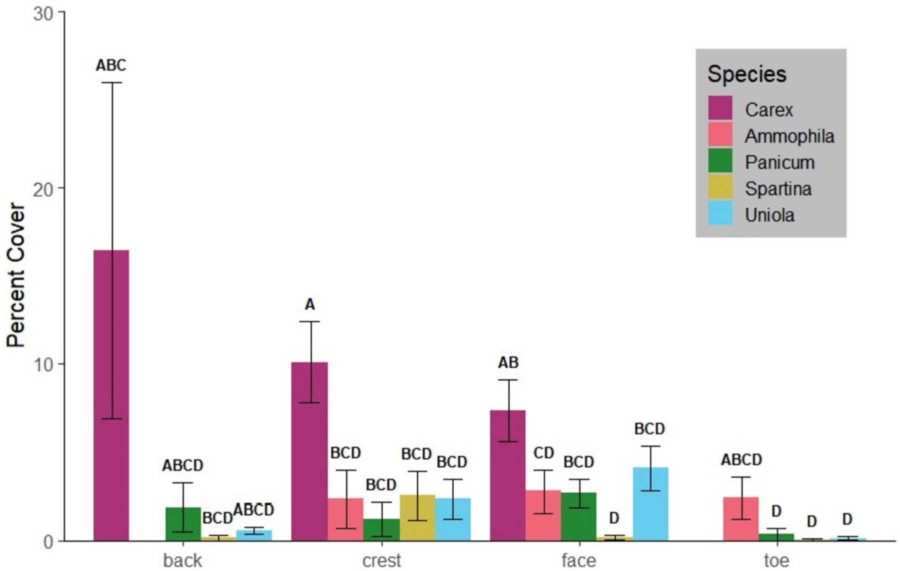

Fig. 2 Percent cover ± SE along the dune profile of each of the dominant dune species. Letter codes indicate significant species × location differences ($\alpha \leq 0.05$) based two-way mixed model ANOVA

Table 1 Species differences for dominant dune grasses. Letter codes indicate significant differences among species for each plant trait ($\alpha \leq 0.05$) from Tukey post-hoc tests

Traits	Carex	*Ammophila*	*Panicum*	*Uniola*
Height (cm)	27.1 ± 1.1^{a}	63.6 ± 4.1^{b}	30.2 ± 1.7^{a}	75.7 ± 3.2^{b}
Stem Density (0.25 m^2)	9 ± 1^{a}	15 ± 5^{a}	6 ± 1^{b}	6 ± 1^{ab}
Aboveground Biomass (g 0.25 m^{-2})	320 ± 33^{a}	309 ± 30^{a}	307 ± 46^{a}	1007 ± 71^{b}
Belowground Biomass (g 0.25 m^{-2})	43 ± 6^{a}	33 ± 8^{ab}	17 ± 4^{b}	34 ± 10^{ab}
Root:Shoot	0.14 ± 0.02^{a}	0.12 ± 0.03^{ab}	0.07 ± 0.02^{bc}	0.04 ± 0.01^{c}
Root Diameter (mm)	0.35 ± 0.03^{a}	0.31 ± 0.02^{a}	0.61 ± 0.04^{b}	0.60 ± 0.07^{b}
Root Tissue Density (g cm^{-3})	0.19 ± 0.01^{a}	0.27 ± 0.02^{b}	0.15 ± 0.02^{a}	0.15 ± 0.02^{a}
Root Surface Area (cm^2)	57.9 ± 7.27^{a}	34.5 ± 2.94^{ab}	20.1 ± 4.32^{b}	36.5 ± 8.41^{ab}
Fine root surface area (cm^2)	36.4 ± 5.68^{a}	22.3 ± 1.06^{ab}	10.6 ± 2.38^{c}	16.9 ± 4.63^{bc}

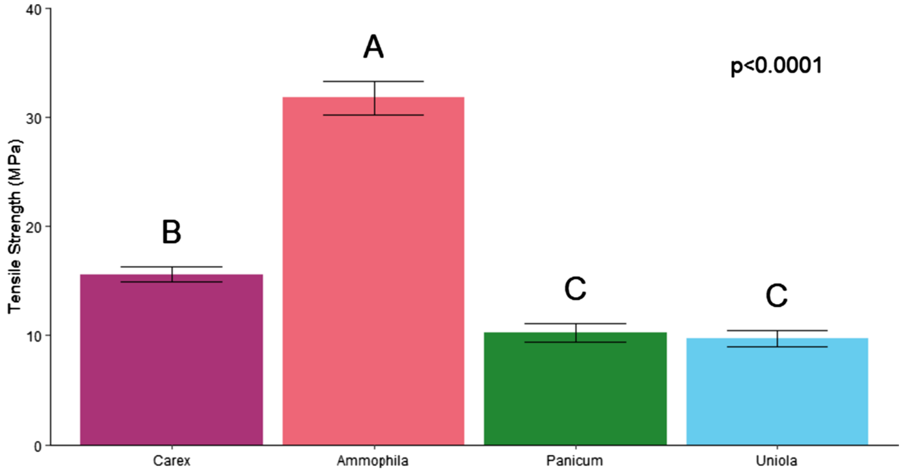

Fig. 3 Tensile strength differences for the main species, before log transformation. Letter codes indicate significant differences ($\alpha \leq 0.05$) from Tukey post-hoc test

($F = 16.53$, $p < 0.0001$; Fig. 3). *Ammophila* had the highest RTD ($F = 11.26$, $p < 0.0001$) and highest tensile strength ($p < 0.0001$). *Ammophila* tensile strength was > 2 times higher than that of all other species.

Carex had higher %N in the aboveground biomass than all other species ($F = 26.5$, $p < 0.001$) but lower %N than *Uniola* in belowground material ($F = 5.0$, $p < 0.01$, Figure S2). *Carex* had significantly less aboveground %C than all other species ($F = 12.8$, $p < 0.0001$) with no differences found belowground ($F = 3.5$, $p = 0.03$, Figure S2). These differences in *Carex* led to the same patterns for C:N, lower aboveground ($F = 19.1$, $p < 0.0001$) and higher belowground ($F = 8.7$, $p < 0.001$, Figure S2) compared to the natives. *Panicum* had lower $\delta^{15}N$ aboveground ($F = 6.5$, $p = 0.001$) whereas *Carex* had lower belowground $\delta^{15}N$ ($F = 8.7$, $p < 0.001$, Figure S3). Belowground $\delta^{15}N$ values were close to 0 in *Carex*, an indication of possible nitrogen fixation. Species separated out by C3 (*Carex* and *Ammophila*) and C4 (*Panicum* and *Uniola*) for $\delta^{13}C$ values aboveground ($F = 282.4$, $p < 0.0001$) and belowground ($F = 224.2$, $p < 0.0001$, Figure S3).

Multivariate analysis based on the aforementioned traits revealed that species differed significantly from each other (MRPP: $t = -12.9$, $p < 0.0001$). When visualized using NMS (stress = 5.52; variance explained: Axis 1 = 64.9%, Axis 2 = 21.9%), *Carex* exhibited lower variability and did not overlap with native species (Fig. 4). Above and belowground %C, belowground C:N, height and aboveground biomass were correlated with axis 1 (Table S2) contributing to the majority of *Carex* separation from other species occurred.

Effects of *Carex* on plant community

Across the dune profile at Back Bay NWR, *Carex* grew predominantly in mixed plots, most frequently with *Panicum* and *Uniola* (Table 2). All native species were more commonly found in mixed plots

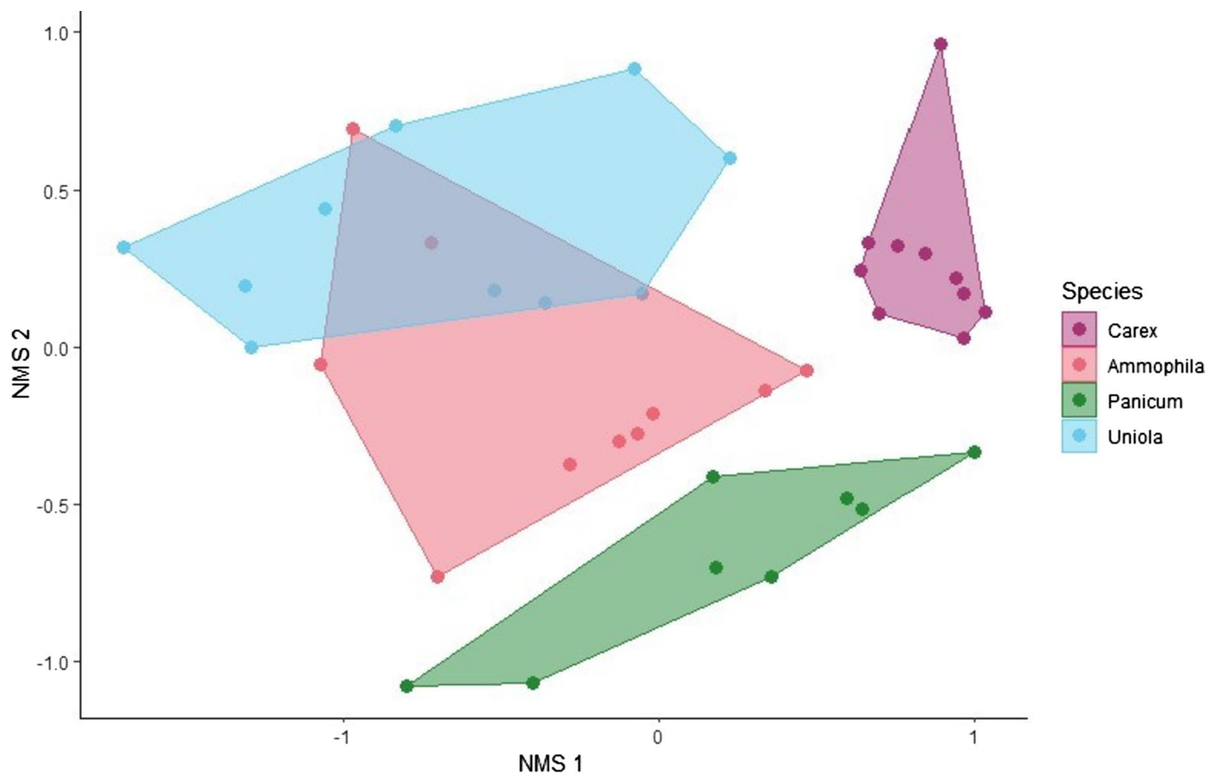

Fig. 4 Nonmetric Multidimensional Scaling (NMS) visualization of plant trait differences of dominant dune grasses. All species significantly differ ($\alpha \leq 0.05$) from one another based on MRPP analysis

Table 2 Species relative frequency found in mixed and monoculture plots, as well as relative frequency with *Carex* and without *Carex*

Species	Mixed	Monoculture	With *Carex*	Without *Carex*
Carex	0.89	0.11	–	–
Ammophila	0.61	0.39	0.39	0.61
Panicum	0.73	0.27	0.47	0.53
Uniola	0.79	0.21	0.63	0.37

than monoculture. Species richness increased for plots with *Carex* (2.3 ± 0.14) relative to those without (1.4 ± 0.10), with *Carex* included in the count when present. *Carex* did not appear to inhibit growth of *Uniola* or *Ammophila*, but a decline in *Panicum* cover ($F = 14.2$, $p < 0.01$) and stem density ($F = 5.9$. $p = 0.013$) was observed when *Carex* was present. (Fig. 5). When comparing biomass from mixed species core plots, aboveground biomass was not affected by the presence of *Carex*, but belowground biomass was significantly higher with *Carex* present ($F = -10.09$, $p = 0.02$; Fig. 6).

Discussion

Coastal communities are impacted significantly from climate change, especially sea-level rise and increasing storms, both strength and frequency (Suursaar et al. 2015). Climate change also contributes to increased plant invasions and altered native species distributions, leading to novel species interactions and potential loss of native species (Bradley et al. 2010; Dukes and Mooney 1999). Our objective was to identify traits that contribute to the

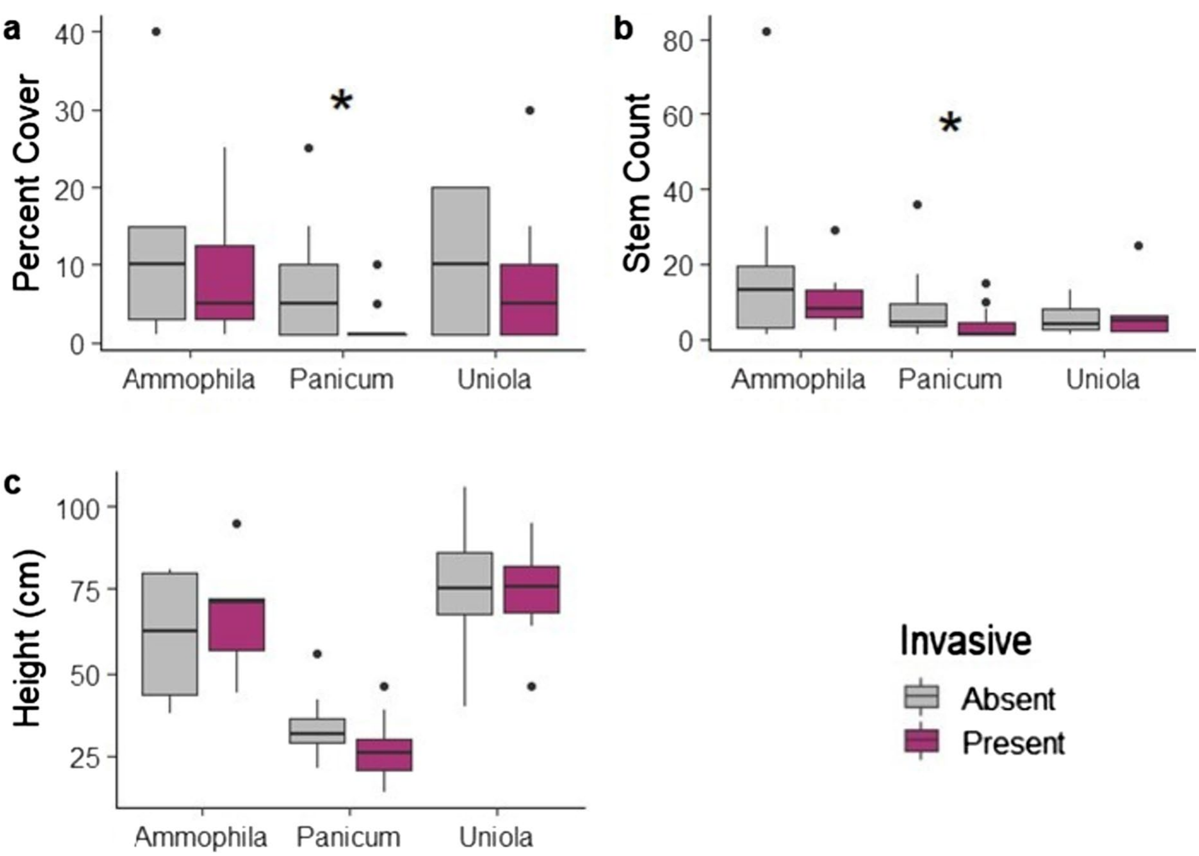

Fig. 5 Boxplots of species-specific response to the presence of *Carex* in mixed community composition plots. Asterisks indicate significant difference results of multi-factor ANOVA (location, *Carex* presence/absence) with Bonferroni adjustment ($\alpha = 0.0125$). Points indicate outliers. **a** Percent Cover and **b** Stem Counts in 0.25 m^2 plots. **c** Height in each plot

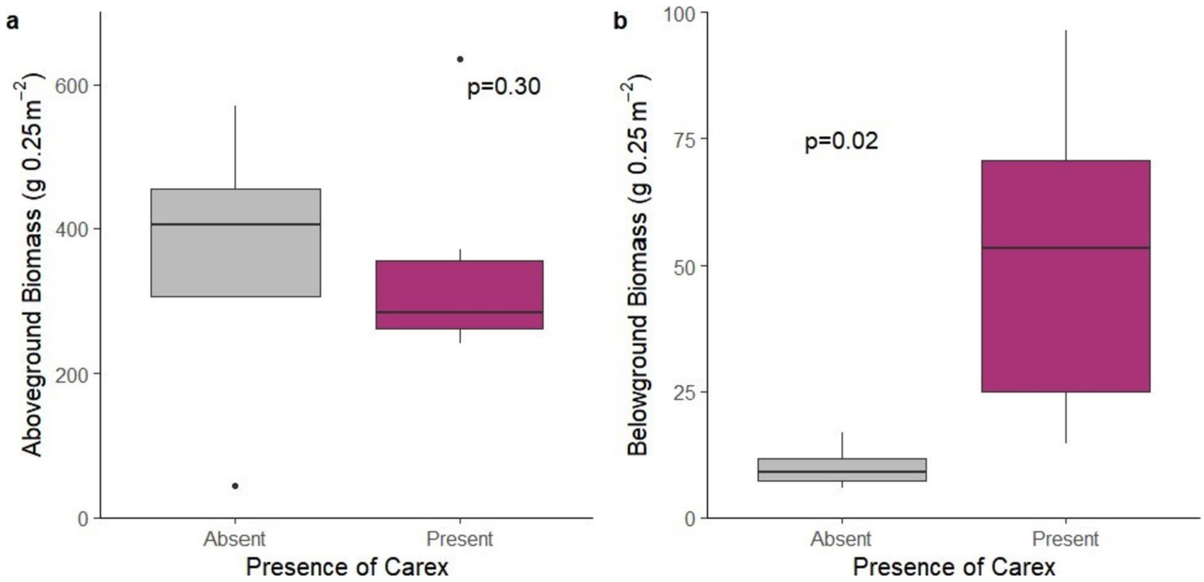

Fig. 6 Boxplots of differences in biomass totals from mixed coring plots with and without *Carex kobomugi*. Points indicate outliers. **a** Aboveground biomass **b** belowground biomass

success of the invasive sedge, *Carex*, on a coastal dune with overlapping distributions of northern and southern native species. We defined success as expanding populations and relative declines in native populations. Community composition of Back Bay NWR dunes differed from northern study sites where *Carex* has been more closely monitored (Small 1954; Charbonneau et al. 2020). We demonstrated that *Carex* is the most dominant species at this site, co-occurring with native species. As a C3 species, *Carex* exhibits overlapping individual traits (e.g., aboveground biomass, root diameter, root tissue density) of both C3 (*Ammophila*) and C4 species (*Panicum*). But when considering the entire suite of plant traits, *Carex* exhibited unique traits that promote resource acquisition and had less variability relative to native species. In mixed plots, there was greater belowground biomass with *Carex* present than in mixed plots of that were composed only of native species. *Carex* was found to have a negative impact on the growth of *Panicum* although no impacts were observed with other species. The limited occurrence of *Ammophila* with *Carex* along with reduced cover across the dune relative to *Panicum* suggests that both species may be impacted by *Carex* expansion.

Community composition and species interactions

Dunes of the US mid-Atlantic region are heavily dominated by *Ammophila*, *Uniola*, *Panicum*, and *Spartina patens* (Hacker et al. 2019). These species co-occur and disperse at different elevations and dune positions (Hacker et al. 2019; Woods et al. 2023). The dunes at Back Bay NWR have different levels of management activity. In the northern portion of our study site, *Carex* was not actively managed and was the most dominant species based on cover and relative importance values. *Ammophila*, *Panicum,* and *Uniola* were the dominant native species, but with less overall abundance and frequency relative to *Carex*. *Carex* had highest abundance on the dune face, crest, and back, but was absent at the dune toe where *Ammophila* was most abundant. *Ammophila* was less likely to co-occur with *Carex* and was less abundant on the dune face, differing from dunes at Back Bay NWR that have been actively managed for *Carex* removal (Woods et al. 2023). Both species are C3 and likely to compete for space and resources due to timing of active growth (Bossuyt et al. 2005;

Charbonneau et al. 2020), but extended phenology of *Carex* may provide a competitive advantage (personal observation; Hess et al. 2019). Based on findings in New Jersey (Charbonneau et al. 2020) and Back Bay NWR (our study and Woods et al. 2023), *Ammophila* growth and distribution is likely constrained by *Carex*.

Phenological timing of growth and response to warming temperatures (both minimum and maximum) may be key determinants of growth for species and provide opportunities for further research. In higher latitudes along the Atlantic coast, *Ammophila* dominates entire dunes (Burk 1968; Emery and Rudgers 2009; Goldstein et al. 2018). Summer temperature constraints on *Ammophila* growth and known competitive effects with *Uniola* may be additional factors limiting the distribution and abundance at our site (Seneca and Cooper 1971; Harris et al 2017; Brown et al. 2018; Woods et al 2023). *Uniola* was most abundant on the face and crest, frequently co-occurring with *Carex. Panicum* was dominant on the dune face and back, but less is known about the recent distribution in this region despite use in restoration projects (Seneca et al. 1976; Long et al. 2013). High abundance of *Panicum* at Back Bay NWR and other Virginia dunes relative to earlier reports (Conn and Day 1993; Sabo 2023) may indicate climatically driven shifts in species composition. Our study did not examine the phenology and growth over time of species, but *Ammophila* may be most impacted by warming temperatures and *Carex* invasion in the region. Quantifying temperature limitations to growth across the dune profile will enable future species dominance predictions with climate warming.

Morphological differences in graminoids

Graminoids were the dominant life form of the Back Bay NWR dunes but exhibited distinct differences in morphological traits (Walker and Zinnert 2022). *Carex* and *Panicum* were > 50% shorter than *Ammophila* and *Uniola*. *Carex* had high stem density (similar to *Ammophila*) relative to *Panicum* and *Uniola*. The short stature and high stem density of *Carex* creates unique growth relative to the native species and may impede germination or growth of other species (Silvertown 1980). In addition, it spreads multiple leaves along the soil surface (compared to upright growth of native grasses) which may provide an aboveground competitive advantage by increasing local soil moisture (Wetzel and van der Valk 1998; Deutsch et al. 2010) in the dune system, although not measured in our study.

Carex exhibited individual traits similar to *Ammophila* (i.e. above and belowground biomass, root:shoot, stem density, and root diameter) and *Panicum* (i.e. above and belowground biomass, root:shoot, height, and root tissue density). Although *Carex* and *Ammophila* had similar root diameters, tensile strength was > 2 times higher in *Ammophila,* indicating higher erosion resistance (Davidson et al. 2020; Walker and Zinnert 2022; Figlus 2022). *Ammophila* root traits (smaller diameter and high root tissue density) may contribute to drought tolerance with lower relative growth rates (Wahl and Ryser 2000; Fort et al. 2013). Leaf and root $\delta^{13}C$ showed species differences based on photosynthetic pathways (C3, C4), indicating lower water use efficiency in *Ammophila* and *Carex* (Ellsworth and Cousins 2016). Most interesting, *Carex* exhibited several traits that may provide a competitive advantage relative to native species: higher leaf %N, more N allocated per unit C in leaves (lower C:N), thus possibly enhancing photosynthetic rates for faster growth (Leuning et al. 1995). *Carex* was the only species with evidence suggesting symbiotically fixed N_2 ($\delta^{15}N$ values close to 0, Robinson 2001). Rhizosheath fixation through symbiotic rhizosphere relationships has been suggested in other non-N_2 fixing coastal species as a way to acquire N in an N-limited system (Brown and Zinnert 2021). Root C:N was highest in *Carex* and coupled with low RTD indicates a more rapid root growth strategy compared with native species, further contributing to success as an invasive species (Wahl and Ryser 2000).

Effects of *Carex* on the landscape

Vegetation along dunes exist more frequently in community with other species than in monoculture as we found in our analysis. Of the native species, *Uniola* was most frequently found co-occurring with *Carex* and was unaffected in growth metrics by the presence of *Carex*. *Carex* and *Uniola* differed in most traits, indicating potentially different spatial–temporal niches, and providing opportunities to determine if niche differentiation allows for co-existence. Conversely, *Panicum* and *Carex* were similar in aboveground biomass and stature, yet *Carex* presence was detrimental to *Panicum* growth (i.e., lower cover and stem density). *Carex* ability to acquire higher leaf N has the potential to outcompete *Panicum* due to similar aboveground niche space and faster growth. Although *Carex* belowground biomass was similar to native species when examined in monoculture, when co-occurring with other species, presence of *Carex* with native species increased belowground biomass compared to mixed plots with native species only. The mechanism for this increased biomass cannot be determined from our study design but implies an effect of *Carex* to the plant community.

Belowground biomass, proportion of fine roots, and high tensile strength are indicators of erosion resistance, but it is unclear how these traits are distributed throughout the dune (de Battisti and Griffin 2020; Walker and Zinnert 2022; White 2022). Increased belowground material provides more surface area for sand to bind, but the belowground components are more complex than just gathering biomass (i.e., Feagin et al. 2015). Extensive belowground structures also aid in nutrient and water uptake in these low nutrient soils (Klimešová et al. 2023). Although *Ammophila* has traits associated with erosion resistance (e.g., small root diameter, high tensile strength), the long, linear dunes formed by *Ammophila* could be lost due to *Carex* invasion (Charbonneau et al. 2020) and known temperature constraints on *Ammophila* growth (Seneca and Cooper 1971; Woods et al. 2023). Changes in species composition could have a major impact on dune building and coastal erosion (Zarnetske et al. 2012). The effect of *Carex* invasion remains to be determined for locations with higher temperatures where C4 species are expected to thrive.

Conclusions

Success of *Carex* at Back Bay NWR, Virginia is indicative of future spread of the species due to specific morphological traits that create a competitive advantage relative to native species. *Carex* has previously been documented to displace native grasses (specifically *Ammophila*) farther north along the Atlantic coast. Our research documents potential competition with *Ammophila* and *Panicum* in a climatically transitional dune system. Although there are few studies of *Panicum* in this region, it was the second most frequent species after *Carex*, a possible indication of climatically induced range shift by the C4 species. We found that native species more frequently co-occur, which may benefit wildlife habitat and coastal erosion through increased biodiversity. The invasion of *Carex* may lead to a monoculture dune system over time if left unmanaged. Future research should evaluate the impacts to ecosystem services resulting from monocultural spread of the invasive sedge compared to the functional role of multi-species communities. Regardless, removing invasive species and revegetating dunes with native species provides a suite of traits able to provide broader habitat for multiple native species while providing erosion resistance. Understanding climate change impacts to native species, including effects of non-native species, will enhance predictions of dune composition in future climate scenarios.

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Declarations

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