Climate Change Alters The Interaction of Two Invasive Beachgrasses With Implications For Range Shifts And Coastal Dune Functions

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Abstract

Forecasting the effects of climate change on the distribution of invasive species can be difficult because invaders often thrive under novel physical conditions and biotic interactions that differ from those in their native range. In this study, we experimentally examined how rising temperatures and sand burial could alter the abundance and biotic interactions of two invasive beachgrasses, *Ammophila arenaria* and *A. breviligulata*, along the U.S. Pacific Northwest coast. We asked whether the current geographic ranges of the two congeners, and thus their effects on dune morphology and coastal ecosystem services, might shift as a consequence of climate driven changes in warming and sand supply. Our results show that *A. breviligulata* had lower biomass and tiller production when exposed to warming and high rates of sand burial, while *A. arenaria* showed neutral or positive responses to those treatments. Nevertheless, under all experimental combinations, *A. breviligulata* had strong negative effects on *A. arenaria*, while *A. arenaria* had weaker effects on *A. breviligulata*. Our models predict that although *A. breviligulata* mostly excludes *A. arenaria*, elevated temperatures and high rates of sand burial also increase the likelihood of species coexistence. We suggest that under climate change, the differences in physiological tolerance and the mediation of species interactions could expand the northern distributional limit of *A. arenaria* but restrict the southern limit of *A. breviligulata*. Moreover, because beachgrass abundance has direct effects on biophysical functions of dunes, reductions in vigor from warming could alter coastal protection, biodiversity, and carbon sequestration.

Introduction

By the end of the twenty first century, climate warming is predicted to increase average annual temperatures by 2°C to 5°C across North America, resulting in a 500-800 km northward shift in comparable average temperatures (IPCC 2014). As such, ecologists are grappling with how climate change could alter species distributions, including those of invasive species, and the potential consequences for ecosystem structure, function, and services (e.g., Walther et al. 2002; Parmesan and Yohe 2003; Pearson and Dawson 2003; Chen et al. 2011). The present-day distributions of species, and their potential responses to climate change, depend on numerous attributes, including historical ranges, modes of dispersal, environmental conditions, and species interactions (Urban et al. 2016). Thus, forecasting potential climate change effects on invasive species requires an understanding of multiple invasion processes, including dispersal and colonization abilities and responses to abiotic and biotic factors within the new range (Dukes and Mooney 1999; Hobbs et al. 2006; Broennimann et al. 2007; Hellmann et al. 2008; Walther et al. 2009; Bradley et al. 2010; Gallagher et al. 2010; Václavík and Meentemeyer 2012; Parker et al. 2013). For example, climate change may benefit non-native species through changes in abiotic barriers to colonization and/or changes in the biotic resistance of communities, both of which could produce range shifts in species invasion (Bradley et al. 2009; Allen and Bradley 2016; Merow et al. 2017). Depending on their nature, species interactions may also contract or expand non-native species ranges, thus accelerating or slowing climate tracking, either of which could significantly influence management efforts (HilleRisLambers et al. 2013; Urban et al. 2013).

Here, using the U.S. Pacific Northwest (PNW) coastal dune ecosystem as a case study, we examined how rising temperatures alter the abundance and competitive interactions of two invasive beachgrasses with implications for range shifts and dune functions and services. Foredunes (i.e., the seaward-most sand ridges running parallel to the shoreline) in the PNW are dominated by two congeneric, non-native invasive beachgrasses, *Ammophila arenaria* and *Ammophila breviligulata*. Their introduction and spread throughout the PNW has caused significant changes to the geomorphology, ecology, and ecosystem services of these systems (Zarnetske et al. 2010, 2012, 2015; Hacker et al. 2012; Seabloom et al. 2013; Biel et al. 2017, 2019a). The two beachgrasses have transformed the PNW dune system from a hummocky system of open sand and sparse vegetation cover to one dominated by tall, well-vegetated foredunes dominated by near *Ammophila* monocultures (Wiedemann and Pickart 1996). The bioengineering of foredunes has displaced numerous endemic plants and animals and has resulted in significant population declines of numerous plants, insects, and shore-nesting birds (Slobodchikoff and Doyen 1977; Wiedemann 1984; USFWS 1993, 2013). Moreover, the two congeners differ in the changes they create to coastal dune ecosystems. *Ammophila arenaria* creates taller and narrower foredunes than *A. breviligulata* (Seabloom and Wiedemann 1994; Hacker et al. 2012; Zarnetske et al. 2012; Biel et al. 2019a), providing superior protection against winter coastal storms (Seabloom et al. 2013) and promoting greater endemic plant diversity (Hacker et al. 2012; David et al. 2015).

The present-day range of the two non-native *Ammophila* species, and forecasts for the future, hinge on knowing how a combination of historical introduction events, dispersal abilities, abiotic tolerances, and biotic interactions affect their distribution and abundance. *Ammophila arenaria* and *A. breviligulata* were introduced to the U.S. Pacific coast for sand stabilization in the early 20th century, but the spatial extent of plantings differed between species. Between the 1870s and 1960s, *A. arenaria* plantings occurred extensively throughout the U.S. Pacific coast and it subsequently colonized dunes between Los Angeles, CA, USA (34°N) and the Queen Charlotte Islands, BC, Canada (54°N) (Green 1965; Breckon and Barbour 1974; Wiedemann and Pickart 2008). *Ammophila arenaria* was pervasive throughout this range but is presently restricted in its dominance on dunes from central Oregon to southern California (Seabloom and Wiedemann 1994; Buell et al. 1995; Hacker et al. 2012). In contrast, *A. breviligulata* plantings were primarily relegated to northern Oregon and southern Washington in the 1930s. Since its introduction, *A. breviligulata* has expanded predominantly northward to Vancouver Island, BC, Canada (49°N), but also southward into northern Oregon, displacing *A. arenaria* as the dominant beachgrass as far south as Seaside (46°N) (Fig. 1) (Seabloom and Wiedemann 1994; Page 2001; Hacker et al. 2012). There are also small extant *A. breviligulata* populations on beaches, including Seaside to Cascade Head (45°N), Siltcoos (44°N), Coos Bay (43°N), OR, and San Francisco, CA (38°N) (Hickman 1993; Hacker et al. 2012). Although the *Ammophila* congeners have spread since their initial introductions (Seabloom and Wiedemann 1994; Hacker et al. 2012; David et al. 2015), their present-day distributions in part simply reflect their respective planting histories.

However, the mostly segregated distribution of the two congeners is also a consequence of several interacting factors including species interactions, dispersal limitation, and temperature. Based on

multidecadal field surveys, *A. breviligulata* has gradually replaced *A. arenaria* as the dominant vegetation on foredunes in regions where the two species co-occur (Fig. 1) (Seabloom and Wiedemann 1994; Hacker et al. 2012; David et al. 2015; Zarnetske et al. 2015). Manipulative experiments show that *A. breviligulata* is competitively dominant to *A. arenaria*, especially under lower sand deposition regimes characteristic of the northern coast (Baye 1990; Zarnetske et al. 2013). Thus, though *A. arenaria* is present in northern Oregon and southwest Washington, *A. breviligulata* has largely displaced *A. arenaria*, effectively limiting its northern extent (Fig. 1). Moreover, the present-day southerly range of *A. breviligulata* is partly a consequence of dispersal limitation. *Ammophila* primarily invades new territory via establishment of rhizome fragments, and to a lesser extent via seed recruitment (Maun 1984; van der Putten 1990), which can be carried offshore and transported hundreds of kilometers via ocean currents (Baye 1990; Aptekar and Rajmanek 2000). The PNW coastal climate is conducive to this mode of long-distance dispersal, with harsh winter storms that erode foredunes (Ruggiero et al. 2010), leading to rhizome fragmentation and spreading when sprouting is at its peak (Pavlik 1983; Konlechner et al. 2016). However, prevailing winds and currents during winter months are directed northerly (Komar 1998), limiting beach grass dispersal southward. Additionally, the Pacific Northwest is divided into many discrete littoral cells separated by large, rocky headlands (Komar 1985). These headlands redirect alongshore currents offshore, limiting transportation of sediment and propagules between adjacent littoral cells (Bray et al. 1995). Consequently, while *A. breviligulata* has rapidly expanded its range northward, geographic barriers and ocean currents have likely slowed its southern expansion and limited its potential range (Fig. 1) (Hacker et al. 2012).

Finally, evidence suggests that the two congeners differ in their temperature tolerances with *A. arenaria* showing better tolerance to warmer temperatures. In its native range, the optimal temperature for *A. breviligulata* varies between 15°C and 30°C, depending on environmental as well as population genetic variability, with reductions in primary production as temperatures approach 20°C (Seneca and Cooper 1971; Yuan et al. 1993; Emery and Rudgers 2013). In contrast, *A. arenaria* grows in regions where temperatures regularly exceed 40°C and is known to survive and grow when exposed to temperatures of 50°C or more (Huiskes 1979). Along the PNW coast where both species co-occur, mean maximum daily temperatures range from 14°C to 18°C and average monthly rainfall ranges from 15 mm to 55 mm between June and September, depending upon the month and location (Table S1). At the southern range limit of *A. arenaria* (34°N at Los Angeles, CA; Breckon and Barbour 1974), temperatures range from 18°C to 21°C and average monthly rainfall ranges from 0.25 mm to 5.3 mm (Table S1). With climate change, PNW annual air temperatures are expected to increase by 2.5-3.4°C by 2080 relative to a 1980s baseline, depending upon the climate scenario (Mote and Salathé 2010; Salathé et al. 2010), creating temperature conditions similar to the present-day climate at the southern distribution of *A. arenaria* in California.

Therefore, although multidecadal observational surveys and manipulative experiments demonstrate that *A. breviligulata* effectively constrains the northern limit of *A. arenaria* by competitive displacement, and dispersal limitation constrains the southern limit of *A. breviligulata*, it is unknown whether these range limits are sensitive to temperature. As a result, forecasting the response of the two *Ammophila* species to climate warming is essential because changes to their distribution and abundance could influence

foredune ecology, morphology, and ecosystem services (Hacker et al. 2012; Seabloom et al. 2013; Biel et al. 2017, 2019a).

In this study, we report the effects of warming and sand burial on the abundance, morphology, and competitive interactions of the two *Ammophila* congeners. We used large sand-filled planters to manipulated temperature, sand burial, and the relative abundances of *A. arenaria* and *A. breviligulata* to address the following questions. (1) Does warming and sand burial alter plant growth and morphological traits for each of the *Ammophila* species? We hypothesized that *A. breviligulata* would exhibit higher sensitivity to warming via reductions in biomass, while *A. arenaria* would show little response. (2) Does warming and sand burial alter the direction and/or magnitude of the competitive interaction between the congeners? If so, do they exert density-independent or density-dependent effects on *Ammophila* growth? Given that competitive displacement of *A. arenaria* by *A. breviligulata* presently limits the distribution and abundance of *A. arenaria*, if *A. breviligulata* exhibits a negative response to warming and/or sand burial, then we hypothesize that such changes might foster coexistence or even a reversal of competitive dominance. By extension, latitudinal gradients in temperature and rising temperatures from climate change would impede southerly range expansion of *A. breviligulata*. However, if neither species is sensitive to rising temperatures, then climate is unlikely to prevent further *A. breviligulata* invasion and displacement of *A. arenaria*.

Methods

Warming and sand burial experiments

We assessed the growth responses and species interactions of *Ammophila arenaria* and *A. breviligulata* under varying temperature, sand burial, and species composition and density using a split-split-plot common garden experiment that consisted of one whole plot treatment (ambient vs. heated; $n=8$), one split-plot treatment (low vs. high sand burial; $n=64$), and two split-split plot treatments (low vs. high plant densities for each species; $n=256$). In September 2013, we placed 64 1 m² (base) x 2 m (height) permeable geotextile bags (Flexible Intermediate Bulk Container; Bag Corp, Richardson, TX) in an 8 x 8 grid on a sandy area outside of the Hatfield Marine Science Center (HMSC), Newport, OR (Fig. S1). Each bag was then subdivided into four equal sized 0.25 m² quadrants (256 total) using clear greenhouse film (6 mil, 91% light transmission), mounted to a wood frame and secured to the interior of the bag to function as a barrier between the quadrants (Fig. S2).

We collected *A. arenaria* and *A. breviligulata* plants from Clatsop Plains, Oregon, USA, a site where both species co-occur (Fig. 1). We set aside 100 haphazardly chosen plants of each species to establish the initial biomass, tiller density, and morphology of the plantings. We then planted four combinations of each species at varying densities in the four quadrants of each bag: a monoculture of 6 *A. arenaria* plants (A6), a monoculture of 6 *A. breviligulata* plants (B6), a polyculture of 3 *A. arenaria* and 3 *A. breviligulata* plants (AB3), and a polyculture of 6 *A. arenaria* and 6 *A. breviligulata* plants (AB6)(Figs. S1, S2). A single plant had one rhizome with multiple tillers that varied from 1–8 for *A. arenaria* and 1–6 for

A. breviligulata. AB3 quadrants had mean ($\pm$ SE) tiller densities of 12.5 ± 0.6 for *A. arenaria* and 8.1 ± 0.5 for *A. breviligulata* (Fig. S3). A6, AB6, and B6 quadrants had mean ($\pm$ SE) tiller densities that were roughly twice those of AB3: 25.2 ± 0.9 tillers for *A. arenaria* and 14.3 ± 0.4 tillers for *A. breviligulata*. Plants established for 8 months before applying warming and sand treatments in May 2014 and the experiment was terminated in September 2015.

Given that the annual air temperatures of the PNW are expected to increase by 2.5–3.4°C by 2080 (Mote and Salathé 2010; Salathé et al. 2010), our warming treatment was designed to maintain a temperature differential of 2.5–3°C between the heated and ambient bags. We divided the 8 x 8 common garden grid into eight blocks, four with heat and four without heat (Fig. S1). For the heated bags, we wove heat resistive cables (LT210 Self-Regulating Heater Cable, Nelson Heat Trace Systems, Tulsa, OK) through wire mesh that was placed 4 cm below the sand surface (Figs. S1, S2). We similarly placed wire mesh within ambient temperature bags as a control. For each block, differential temperature controllers (N321S controller, NOVUS, Miami, FL) with NTS thermistors were used to maintain the 2.5–3°C temperature differential. Independent measurements from HOBO temperature loggers (Onset Computer Corporation, Bourne, MA), placed centrally in each bag, indicated that heating maintained a median temperature differential of 2.0°C to 3.1°C between paired bags, depending on month and year (Table S2).

We also established a low and high sand addition treatment. The low deposition bags received 4 cm of sand at the start of the experiment. The high deposition bags received 4 cm of sand roughly every 5 weeks, resulting in ~60 cm of sand per bag by the end of the experiment. The high sand deposition rate reflects a high range for sand accretion at the face of the foredune in the field (median 18 cm/yr, min. – 52, max. 65; Biel et al. 2019a, b). As the bags grew in height from the sand additions, we attached additional dividers to maintain quadrant separation and we adjusted the wire mesh so that it stayed within 4 cm of the sand surface.

Grass species response variables

At the end of the experiment, we counted the tillers in each quadrant, harvested the plant material, and then air dried the plants. For both the initial and final plants, we counted the number of tillers and measured the dry biomass [aboveground (tillers above the primary root node), belowground (rhizomes below the primary node), total] of each plant. We used the initial biomass measurements of the plants along with the initial observed plant densities (Fig. S3) to estimate the initial biomass per species per quadrant in the bag.

To measure plant morphology, we haphazardly chose five plants per species per quadrant and measured the length of the longest tiller (from the primary root node to the longest leaf tip), the width of the widest part of the leaf, and the number of leaves. We also calculated total leaf area for each plant by multiplying half the tiller length x leaf width x leaf number.

Statistical analyses

We analyzed our data using R (R Development Core Team 2017). We first calculated log response ratios [LRR; $\log(\text{final response variable} / \text{initial response variable})$] for beachgrass biomass (total, aboveground, and belowground) and tiller density and we also log transformed the plant morphology (tiller length, leaf width, and total leaf area) metrics. We then performed linear mixed effects models (lme4 package) to assess changes in grass biomass, tiller density, and morphology as a result of warming, sand burial, and species interaction treatments. For quadrant scale measurements of biomass and tiller density, we included a nested random intercept term (1|whole plot/subplot) to account for the nested structure of our experimental design. For plant morphological metrics, we included a nested random intercept term (1|whole plot/subplot/sub-subplot) to account for intra-quadrant non-independence.

To predict how warming and sand burial affects tiller density change under intraspecific and interspecific interactions of the two beachgrass species, we used linear mixed models to parameterize the Ricker model, a density dependent species interaction model, written as:

$$\log\left(\frac{N_{A, \text{Final}}}{N_{A, \text{Init}}}\right) = r_A - \left(\frac{r_A}{K_A}\right) N_A - \left(\frac{\alpha_{AB}}{K_A}\right) N_B$$

$$\log\left(\frac{N_{B, \text{Final}}}{N_{B, \text{Init}}}\right) = r_B - \left(\frac{r_B}{K_B}\right) N_B - \left(\frac{\alpha_{BA}}{K_B}\right) N_A$$

where N_A and N_B represent *A. arenaria* and *A. breviligulata* tiller density, respectively. The intercept term (r) represents the intrinsic growth rate, K represents the carrying capacity, and α represents the competition coefficient, where the subscript A is *A. arenaria* and B is *A. breviligulata*. We incorporated environmental factors into the model using the following equations for each species:

$$\log\left(\frac{N_{A, \text{Final}}}{N_{A, \text{Init}}}\right) = (r_A + \beta_1 \cdot \text{Temp} + \beta_2 \cdot \text{Sand}) - \left(\frac{r_A}{K_A} + \beta_3 \cdot \text{Temp} + \beta_4 \cdot \text{Sand}\right) N_A - \left(\frac{\alpha_{AB}}{K_A}\right) N_B$$

$$\log\left(\frac{N_{B, \text{Final}}}{N_{B, \text{Init}}}\right) = (r_B + \beta_1 \cdot \text{Temp} + \beta_2 \cdot \text{Sand}) - \left(\frac{r_B}{K_B} + \beta_3 \cdot \text{Temp} + \beta_4 \cdot \text{Sand}\right) N_B - \left(\frac{\alpha_{BA}}{K_B}\right) N_A$$

In this model, heat and sand burial treatments each exerted both density-independent effects (β_1, β_2) and density-dependent effects (β_3, β_4) on growth. When depicted in linear mixed model form, each regression equation followed the form:

$$\log(N_{1, \text{Final}} / N_{1, \text{Init}}) \sim \beta_0 + \beta_1 \cdot N_{1, \text{Init}} + \beta_2 \cdot N_{2, \text{Init}} + \beta_3 \cdot \text{Temp} + \beta_4 \cdot \text{Sand} + \beta_5 \cdot \text{Temp} \cdot N_{1, \text{Init}} + \beta_6 \cdot \text{Sand} \cdot N_{1, \text{Init}} + (1 | \text{Wholeplot} / \text{Subplot}) + \varepsilon$$

For all statistical analyses, we used an information theoretic approach to model comparisons by examining the relative degree of support for multiple a-priori hypothesized models using sample size corrected Akaike Information Criterion (AIC_c) methods (Table S3). For each set of models, we report which explanatory variables were included in substantially supported models ($\Delta\text{AIC}_c < 2$) and the restricted

maximum likelihood parameter (RMLP) estimates of the response variables, and their 95% confident intervals (CI), as well as back-transformed percent change [i.e., $(e^{RMLP}-1) \times 100$] for these estimates.

Results

Treatment effects on beachgrass biomass

Ammophila arenaria and *A. breviligulata* differed in their biomass response to species interactions, warming treatment, and sand deposition (Fig. 2, Tables S4, S5). For *A. arenaria*, the best supported model ($\Delta AIC_c = 0$) shows that *A. breviligulata* had a negative effect on the total biomass of this species but there was no effect of warming or sand burial treatment (Fig. 2A, Tables S4A, S5A). Mean total biomass of *A. arenaria* increased by 52% in monoculture but decreased by 2.0% with each additional *A. breviligulata* tiller in polyculture. For *A. breviligulata*, the best supported model ($\Delta AIC_c = 0$) shows that *A. arenaria* had a negative effect on the total biomass on this species but there was also an additional negative effect of sand burial (Fig. 2B, Tables S4A, S5A). Mean total biomass of *A. breviligulata* increased by 302% in monoculture but decreased by 1% with each *A. arenaria* tiller, or by 15% under high sand burial. Another supported model ($\Delta AIC_c = 0.9$) shows that warming also had a negative effect (Table S4A), reducing *A. breviligulata* total biomass by 19%.

When aboveground biomass is considered separately, the best supported models show that both species are affected by interspecific competition, similar to the total biomass models (Fig. 2C, D, Tables S4B, S5B). However, when belowground biomass is considered, both species had more complex responses to the three experimental treatments (Fig. 2E, F, Table S4C). For *A. arenaria*, the best supported model ($\Delta AIC_c = 0$) shows a negative relationship with increasing *A. breviligulata* tiller density (2% decline with each tiller) but a positive effect of warming (21% increase) and sand burial (67% increase) (Fig. 2E, Tables S4C, S5C). However, when *A. arenaria* was exposed to both warming and high sand burial, mean belowground biomass decreased by 45%. For *A. breviligulata*, the best supported model ($\Delta AIC_c = 0$) shows a negative relationship with increasing *A. arenaria* tiller density (2% decline with each tiller) and is further reduced by warming (36%; Fig. 2F, Tables S4C, S5C). Sand burial had no effect.

Treatment effects on beachgrass tiller density

The tiller density results for the two beachgrass species were similar to those of total biomass. The Ricker logistic model showed that *A. breviligulata* exerted a strong negative effect on *A. arenaria*, regardless of treatment (Tables S6, S7). *A. arenaria* tiller production decreased with increasing initial *A. arenaria* and *A. breviligulata* tiller density (by 2% and 1% per tiller, respectively). Other supported models ($\Delta AIC_c = 1.7$) showed that besides *A. breviligulata*, sand burial decreased *A. arenaria* tiller production but warming had no effect (Table S6). *Ammophila breviligulata* tiller production also decreased with increasing *A. breviligulata* and *A. arenaria* tiller densities (by 6% and 1% per tiller, respectively) and high sand burial (60% decrease) (Tables S6, S7). However, there was a sand burial and tiller density interaction such that, at high sand burial, high initial *A. breviligulata* tiller density was associated with increased tiller

production. Additionally, one supported model ($\Delta AIC_c = 1.1$) showed a negative effect of warming on *A. breviligulata* but our power to detect a warming effect was limited (Table S6).

Overall, even though warming decreased the intrinsic growth rate (r) of *A. breviligulata*, it still had a higher intrinsic growth rate and carrying capacity (K) when compared to *A. arenaria*, and was competitively dominant (a) under all heat and sand burial combinations (Fig. 3, Table S8). Our models predict that under ambient temperatures and low sand burial conditions, *A. arenaria* infrequently coexists with *A. breviligulata* (3/16 or 19% of bags; Fig. 3). In contrast, under warming temperatures (low burial: 6/16 or 38% of bags, high burial: 5/16 or 31% of bags) or ambient temperatures with high sand burial (7/16 or 44% of bags), *A. arenaria* is predicted to coexist with *A. breviligulata* more often (Fig. 3).

Treatment effects on plant morphology

The morphology of the two beachgrasses were influenced by species interactions, sand burial, and to a lesser extent, by temperature (Figs. 4, 5; Tables S9, S10). For *A. arenaria*, tiller length, leaf width, and leaf area were independent of both *A. arenaria* and *A. breviligulata* initial tiller densities (Fig. 4; Tables S9, S10). Although sand burial did not influence *A. arenaria* tiller length, it increased leaf width (23%), and leaf area (14%), except under high monoculture densities ($N_{AMAR} \times$ sand burial interaction for leaf width). Additionally, warming increased *A. arenaria* tiller length (8%), but not leaf width or leaf area, and high *A. breviligulata* density lessened (-0.2%) the effect ($N_{AMBR} \times$ heat interaction). For *A. breviligulata*, tiller length, leaf width, and leaf area were relatively unaffected by either *A. arenaria* or *A. breviligulata* initial tiller density (Fig. 5, Tables S9, S10). Sand burial increased *A. breviligulata* tiller length slightly (3%), and leaf width (13%) and leaf area (14%) moderately. Finally, warming had no effect on *A. breviligulata* tiller length and leaf area, but decreased leaf width (13%), especially at increasing *A. breviligulata* tiller densities, where there was a $N_{AMBR} \times$ heat interaction (-26%).

Discussion

The goal of this study was to examine whether the current distributional ranges of two invasive beachgrasses (*Ammophila arenaria* and *A. breviligulata*) on the U.S. Pacific Northwest coast have the potential to shift as a consequence of their physiological tolerances and species interactions in response to climate change. We asked whether warming, and its interaction with sand deposition, could decrease the production of *A. breviligulata*, thereby mediating or potentially reversing its competitive dominance over *A. arenaria*. We hypothesized that such a competitive reversal under warming could result in the extension of the northern distribution of *A. arenaria* and the restriction of the southern distribution of *A. breviligulata*, thereby shifting the range of overlap of the two species and influencing dune ecosystem functions and services.

We found that the two congeners had opposite responses to warming and sand burial, but *A. breviligulata* still remained competitively dominant across the full range of experimental conditions. *Ammophila arenaria* either did not change, or responded positively, to warming and high rates of sand

burial. In contrast, *A. breviligulata* declined under the same conditions but this was somewhat mediated by intraspecific density, as suggested by the positive density-dependent effects of sand burial on some metrics. However, under all four combinations of warming and sand burial, *A. breviligulata* exerted a comparatively strong negative effect on *A. arenaria*, while *A. arenaria* exerted a weaker negative effect on *A. breviligulata*. Based on the fitted Ricker interaction models, we predict that *A. breviligulata* would exclude *A. arenaria* under nearly all experimental conditions. Because warming and high sand burial disproportionately reduced *A. breviligulata* growth rates, our models show that there is an increased but relatively moderate likelihood of stable coexistence. For example, ~30-45% of the heated and high sand burial bags were predicted to maintain a stable coexistence of both species, while ~20% of the ambient temperature and low sand burial bags were predicted to maintain such coexistence. Thus, reductions in *A. breviligulata* performance under warming and high rates of sand burial may allow *A. arenaria* to stably coexist, or at least reduce its rate of displacement.

Species-specific growth and morphological responses to warming temperatures

Although we found that *A. breviligulata* is less tolerant of warming than *A. arenaria*, the observed differences were generally small with some uncertainty likely associated with a small sample size ($n = 8$). One exception was the belowground biomass of *A. breviligulata*, which declined by 36% under warming conditions. Nonetheless, our findings are consistent with previous observations and single-species warming experiments for *Ammophila*. For example, using a literature survey, Goldstein et al. (2018) found suggestive but inconclusive support for a northern range shift in naturally occurring populations of *A. breviligulata* on the U.S. Atlantic coast. Warming experiments conducted on *A. breviligulata* in its native range (U.S. Atlantic coast and Laurentian Great Lakes) showed parallel results to ours, in which air and soil temperatures as high as 26°C–30°C resulted in decreased aboveground and belowground production (Seneca and Cooper 1971; Emery and Rudgers 2013). Likewise, Huiskes (1979) found that *A. arenaria* appeared to be insensitive to high temperatures, even when temperatures frequently exceeded 50°C under greenhouse conditions.

It is important to note, however, that the limited aboveground biomass responses of both *Ammophila* species in our experiment may be related to how our methods differed from the other studies. We manipulated soil temperature by 2.5–3°C to match the predicted regional warming of the Pacific Northwest over a century time period and we warmed the sand itself by using heating cables buried in outdoor planters. In contrast, Seneca and Cooper (1971) and Emery and Rudgers (2013) manipulated warming by 5°C or more and by using growth chambers (controlled, uniform heating throughout soil and canopy). Consequently, we likely observed a lower magnitude response to warming given that, even though summer soil temperatures varied between 26–30°C in our study, summer air temperatures did not exceed 21°C. Thus, based on our results and similar studies, it appears that *A. breviligulata* experiences greater heat stress than *A. arenaria*, but the milder predicted regional temperatures of the PNW may allow *A. breviligulata* and its congener to continue to be successful invaders despite rising temperatures.

Species-specific growth and morphological responses to sand burial

In this study, we found key differences between the congeners in their response to sand burial. High rates of sand burial caused little change in *A. arenaria* tiller production or biomass, and increased belowground biomass production and total leaf area. In contrast, sand burial reduced *A. breviligulata* production of total biomass, aboveground biomass, and tiller production. Previous studies have also shown similar species-specific growth patterns across sand burial gradients: in *A. arenaria*, sand burial has repeatedly been shown to stimulate tiller production, even at sand burial rates in excess of 50 cm/yr (Huiskes and Harper 1979; Baye 1990; Zarnetske et al. 2013), compared to *A. breviligulata*, for which sand burial either did not alter tiller production (Maun and Lapierre 1984), did not increase tiller production as much as *A. arenaria* (Baye 1990; Zarnetske et al. 2013), or showed a decline in aboveground biomass (Brown and Zinnert 2018). Multiple hypotheses have been proposed to explain why sand burial often stimulates tiller production, including increased nutrient availability (Marshall 1965; Wahab and Wareing 1980; Constant 2019), changes in species interactions (Huiskes 1980, Zarnetske et al. 2013; Brown et al. 2018; Brown and Zinnert 2018), and escape from predation (van der Putten et al. 1988; Little and Maun 1996). In this experiment, we found that sand burial was also associated with positive-density dependent increases in *A. breviligulata*, which might arise from increased resource use efficiency with sand burial and/or increased facilitative interactions among conspecifics (e.g., structural support may enable higher survival).

Invasive beachgrass range shifts and changes in dune functions under a warming climate

Even though *A. breviligulata* mostly displaces *A. arenaria* under present-day conditions, our experiments and models project that warming and high sand burial will increase the likelihood for coexistence of the two species. Currently *A. breviligulata* is dominant in the Columbia River Littoral Cell, a region of open coastline near the mouth of the Columbia River (Fig. 1), which has an expanding shoreline and cooler temperatures than the coastlines of southern Oregon and California (Table S1). This extremely high rate of beach building in the north is associated with low vertical sand dune accretion, whereas more stable shorelines that are common in central to southern Oregon exhibit higher rates of accretion (Hacker et al. 2012; Ruggiero et al. 2018; Biel et al. 2017, 2019a). Because *A. breviligulata* dominance coincides with cooler temperatures and lower sand burial conditions compared to those for most southern dunes, and given our results, we hypothesize that the physiological response of *A. breviligulata* under climate change may hinder its ability to maintain its current dominance over *A. arenaria*, and/or invade southern dunes. On the other hand, under warming and varying sediment supply, our experiments suggest that *A. arenaria* might benefit, resulting in increased abundance and coexistence with *A. breviligulata* on dunes in its northern range.

Changes to the distribution and abundance of either *Ammophila* congener could have important consequences for foredune ecology, morphology, and coastal protection. Ecologically, *A. breviligulata* is not only dominant to *A. arenaria*, but to many native and endemic beach and foredune plant species as well (Hacker et al. 2012). For example, *A. breviligulata* was used for sand stabilization, in part because of “its ability to withstand competition from other plants, particularly weeds common to coastal sand areas” (MacLaughlin and Brown 1942). When *A. breviligulata* displaced *A. arenaria* as the dominant grass in

northern dunes, native plant richness and cover also declined (Seabloom and Wiedemann 1994; Hacker et al. 2012; David et al. 2015). Moreover, the removal of *A. breviligulata* for the habitat restoration of Western snowy plover has resulted in increased native plant species richness at these locations (Zarnetske et al. 2010; Biel et al. 2017). Thus, a shift in the distribution and abundance of either *Ammophila* species could have positive or negative consequences for native dune plant communities, depending on the nature of the change to beachgrass distributions.

Finally, both *Ammophila* species are important to dune-building and their ability to capture aeolian sediment is proportional to beachgrass tiller density (Zarnetske et al. 2012), such that denser beachgrasses form taller and narrower foredunes (Hesp 1989; Biel et al. 2019a). Thus, changes in tiller density could result in differences in sand capture and ultimately foredune morphology. Because foredune morphology strongly influences the risk of coastal flooding and erosion during storm events (Ruggiero et al. 1996; Sallenger 2000; Stockdon et al. 2006), changes in species composition or abundance could substantially influence coastal hazard exposure particularly with rising sea-level and changes in storminess (Seabloom et al. 2013). Other ecosystem services such as carbon sequestration could also be impacted.

In conclusion, we suggest that under climate change, differences in the physiological tolerances and response to competition of two invasive beachgrass species could expand the northern distributional limit of one species (*A. arenaria*) but restrict the southern limit of the other species (*A. breviligulata*). Because beachgrass species identity and abundance have direct effects on the biophysical functions of dunes, changes in beachgrass vigor from warming or sand deposition could alter coastal protection, biodiversity, and carbon sequestration.

Declarations

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Figures

Figure 1

Distribution and relative percent cover of *Ammophila arenaria* (AMAR; white fill) and *A. breviligulata* (AMBR; black fill) for US Pacific Northwest coast foredune sites [Grays Harbor (GH), Leadbetter Point (LBP), Long Beach (LB), Clatsop Plains (CP), Nehalem Bay (NB), Cape Lookout (CP), Sand Lake (SL)), Pacific City (PC), SB (South Beach), Governor Patterson State Recreation Site (GP), Siuslaw Jetty (SJ), SI (Siltcoos River), DO (Dunes Overlook) TK (Tahkenitch Creek), Umpqua Dunes (UD), Tenmile Creek (TM),

Bandon State Natural Area (BAN), and Elk River (ER)]. (Percent cover data from Biel et al. 2019a, b). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Log response ratios [i.e., $\log(\text{final}/\text{initial})$; LRR] for beachgrass biomass metrics (total biomass, aboveground biomass, and belowground biomass) as a function of conspecific tiller density, warming, and sand burial treatments. (A, C, E) *A. arenaria* (AMAR) biomass metrics versus *A. breviligulata* (AMBR) tiller density, and (B, D, F) AMBR biomass metrics versus AMAR tiller density. LRR > 0 indicates biomass gain. Lines and bands represent LRR predictions and 95% confidence intervals based on linear mixed models.

Figure 3

State space diagrams showing the zero-net growth isoclines (ZNGI) of *A. arenaria* (N_{AMAR}; blue) and *A. breviligulata* (N_{AMBR}; black) tiller density under varying warming and sand burial conditions. The thick

lines depict the mean ZNGI among all bags and thin lines depict the estimated ZNGI for each bag (random intercept, corresponding to variation in species-specific intrinsic growth rates among bags). The large black points show the stable equilibrium point among bags and the small black points show the stable equilibrium points for each bag.

Figure 4

Ammophila arenaria (AMAR) morphological responses (total leaf area, tiller length, and leaf width) to conspecific initial tiller density (A, C, E), *A. breviligulata* (AMBR) initial tiller density (B, D, F), and sand burial (all panels). Points represent partial residuals of morphometrics (excluding initial tiller density and sand burial effects; orange = low sand burial treatment; brown = high sand burial treatment). Lines and bands represent predictions of morphometrics based on linear mixed models and associated 95% confidence intervals.

Figure 5

Ammophila breviligulata (AMBR) morphological responses (total leaf area, tiller length, and leaf width) to conspecific initial tiller density (A, C, E), *A. arenaria* (AMAR) initial tiller density (B, D, F), and sand burial (all panels). Points represent partial residuals of morphometrics (excluding initial tiller density and sand burial effects; orange = low sand burial treatment; brown = high sand burial treatment). Lines and bands represent predictions of morphometrics based on linear mixed models and associated 95% confidence intervals.

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