

ARTICLE

Coastal and Marine Ecology

A novel hybrid beachgrass is invading U.S. Pacific Northwest dunes with potential ecosystem consequences

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Abstract

Invasive plants formed via hybridization, especially those that modify the structure and function of their ecosystems, are of particular concern given the potential for hybrid vigor. In the U.S. Pacific Northwest, two invasive, dune-building beachgrasses, *Ammophila arenaria* (European beachgrass) and *A. breviligulata* (American beachgrass), have hybridized and formed a new beachgrass taxa (*Ammophila arenaria* × *A. breviligulata*), but little is known about its distribution, spread, and ecological consequences. Here, we report on surveys of the hybrid beachgrass conducted across a 250-km range from Moclips, Washington to Pacific City, Oregon, in 2021 and 2022. We detected nearly 300 hybrid individuals, or an average of 8–14 hybrid individuals per km of surveyed foredune. The hybrid was more common at sites within southern Washington and northern Oregon where *A. breviligulata* is abundant (75%–90% cover) and *A. arenaria* is sparse and patchy. The hybrid displayed morphological traits such as shoot density and height that typically exceeded its parent species suggesting hybrid vigor. We measured an average growth rate of 30% over one year, with individuals growing faster at the leading edge of the foredune, nearest to the beach. We also found a positive relationship between hybrid abundance and *A. arenaria* abundance, suggesting that *A. arenaria* density may be a controlling factor for hybridization rate. The hybrid showed similar sand deposition and associated plant species richness patterns compared with its parent species, although longer term studies are needed. Finally, we found hybrid individuals within and near conservation habitat of two Endangered Species Act-listed, threatened bird species, the western snowy plover (*Charadrius alexandrinus nivosus*) and the streaked horned lark (*Eremophila alpestris strigata*), a concern for conservation management. Documenting this emerging hybrid beachgrass provides insights into how hybridization affects the spread of novel species and the consequences for communities in which they invade.

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KEYWORDS

beachgrass spread and growth, Endangered Species Act-listed western snowy plover (*Charadrius alexandrinus nivosus*) and streaked horned lark (*Eremophila alpestris strigata*), grass functional morphology, hybridization, native dune plant richness
U.S. Pacific Northwest dunes

INTRODUCTION

Species invasions are ever increasing (Seebens et al., 2021) and, as one of the leading drivers of global environmental change, they can be a pressing and costly concern (Diagne et al., 2021; Pyšek et al., 2020). Invasive species may also be ecosystem engineers, modifying ecosystem structure and functioning by altering biogeochemical cycling (Barot et al., 2007; Vitousek et al., 1987), disturbance regimes (e.g., Mack & D'Antonio, 1998), species interactions (e.g., Gribben et al., 2009), and/or physical characteristics of the environment (Crooks, 2002; Gutiérrez et al., 2011). Research has typically focused on the negative effects of biological invasions, but invaders may also increase ecosystem services, posing management trade-offs. Understanding the role of invader-mediated ecosystem functions is needed to optimize ecosystem services and management (Bennett et al., 2009; Funk et al., 2014).

One factor that can improve the invasion success of species is hybridization (Ellstrand & Schierenbeck, 2000; Schierenbeck & Ellstrand, 2009), as a result of new genotype combinations and greater genetic diversity (Hovick & Whitney, 2014; Lee, 2002; Vilà et al., 2000). Hybridization may also produce first-generation offspring (F_1 hybrids) with exceptional traits or greater fitness compared with both parent taxa, a phenomenon known as hybrid vigor (Arnold & Hodges, 1995). For instance, the cordgrass hybrid *Spartina anglica* has enhanced physiological functions that allows it to grow in a variety of habitats, contributing to its fast spread and dominance (Dethier & Hacker, 2005; Hacker & Dethier, 2006; Lee, 2003).

We explore for the first time the distribution, abundance, growth, and ecological effects of a newly discovered non-native beachgrass hybrid found on U.S. Pacific Northwest dunes (Figure 1; Appendix S1: Figure S1). This dune-building ecosystem engineer is the hybrid offspring of two invasive congeners, *Ammophila arenaria* (European beachgrass, native to Europe) and *A. breviligulata* (American beachgrass, native to the U.S. East Coast and Great Lakes), which were intentionally planted in the early 1900s for sand stabilization. The hybrid was first detected in 2012 and verified as a hybrid in 2021 (Mostow et al., 2021). As of 2019, 21 hybrid individuals had been detected from southern Washington to northern Oregon (Figure 1).

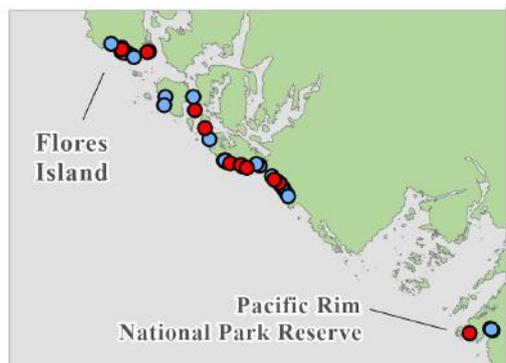
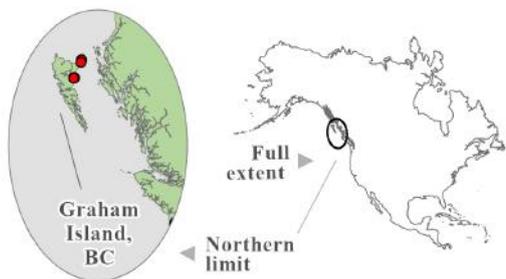
Ammophila arenaria was first introduced to California in 1869 (Cooper, 1967) and then to Oregon in 1910 (McLaughlin, 1942); it subsequently spread widely along the Pacific coast and now occupies a range from Los Angeles, California (34° N), to Haida Gwaii (54° N), British Columbia, Canada (Breckon & Barbour, 1974; Wiedemann & Pickart, 2004) (Figure 1). In the mid-1930s, *A. breviligulata* was planted in northern Oregon and southern Washington (McLaughlin, 1942) where it spread rapidly north of the Columbia River and invaded dunes previously dominated by *A. arenaria* (Seabloom & Wiedemann, 1994). The two congeners currently overlap in their geographic ranges between northern Oregon and British Columbia (Figure 1). The native dune grass species on the Pacific coast, *Leymus mollis* (American dune grass), continues to occupy a broad distribution in this range but occurs at lower densities than the *Ammophila* grasses (Hacker et al., 2012; Pickart, 2021).

The *Ammophila* beachgrasses are well known for their species specific ability to capture windblown sediment, forming differently shaped foredunes (Biel et al., 2019; Hacker et al., 2012, 2019; Zarnetske et al., 2012). On the Pacific coast, the dense vertical growth form of *A. arenaria* leads to deeper sand deposition and taller, narrower dunes, while the comparatively sparse and lateral growth habit of *A. breviligulata* results in shorter, wider dunes, even after controlling for sediment supply (Biel et al., 2019; Hacker et al., 2012). This variability in dune shape differentially affects coastal vulnerability (Ruggiero et al., 2018), with dunes formed by *A. breviligulata* projected to provide less coastal protection than *A. arenaria* as a result of overtopping by extreme waves and sea level rise (Seabloom et al., 2013).

The two beachgrass species are linked to decreased native plant dune species diversity (Biel et al., 2017; Pickart, 2021; Zarnetske et al., 2010), including the endangered pink sand verbena (*Abronia umbellata* ssp. *breviflora*) (Breckon & Barbour, 1974). Although both congeners pose threats to native species, *A. breviligulata* is associated with lower plant species richness, indicating that it may be a superior competitor (Hacker et al., 2012). Populations of the federally listed western snowy plover (*Charadrius alexandrinus nivosus*) and streaked horned lark (*Eremophila alpestris strigata*), which require open, sparsely vegetated habitat (Muir & Colwell, 2010; Pearson et al., 2005), have also declined due to the beachgrasses.

Distribution and abundance of *Ammophila arenaria*, *A. breviligulata*, and their hybrid

Ranging from Graham Island, British Columbia, Canada to southern California, US



- *Ammophila breviligulata*
- *Ammophila arenaria*

Data source	Relative abundance where species co-occur	
	Common	Rare
iNaturalist	○	○
Hybrid surveys: Rebecca Mostow	☆	☆
Sally Hacker	△	△

Layout: Risa Askerooth



FIGURE 1 Legend on next page.

Given the co-occurrence pattern of the two *Ammophila* parent species (Figure 1), and the detection of 21 hybrid individuals without a systematic search, we suspected that the hybrid was more common. Genomic analyses confirmed the presence of first-generation (F_1) and late-generation (F_2) hybrid individuals, as well as a single backcross between the hybrid and *A. arenaria*, confirming a hybrid swarm (population of hybrids beyond the first generation) (Mostow, 2022). These analyses showed that either species can serve as the maternal parent, indicating little to no reproductive barriers to hybridization. We also anticipated the hybrid would have a high growth rate and enhanced competitive ability given its morphology (high shoot density and shoot height) (Mostow et al., 2021; Mostow et al., in press) and its ability to outcompete its parents in a common garden experiment (Mostow et al., in press). These traits may enable the hybrid to capture more sand and build larger dunes than its parents, enhancing coastal protection and carbon storage (Stepanek, 2023). However, there could be negative effects on native species, especially if the hybrid spreads and establishes in areas where endemic plant species are common.

To address knowledge gaps surrounding the distribution and abundance, growth rate, and ecological consequences of the novel *Ammophila* hybrid, we surveyed dunes over a 250-km stretch of the U.S. Washington and Oregon coastline over a three-year period. We hypothesized the following:

1. The hybrid would be found over a larger range and at much higher abundances than previously known, including on designated habitat for Endangered Species Act-listed shorebirds. We also surmised that *A. arenaria* abundance may be a factor in hybridization rate, given the dominance of *A. breviligulata* and the sparse patchiness of *A. arenaria* at most locations in the hybrid's range.
2. Hybrid individuals would demonstrate significant growth over a year and that the hybrid would exceed its parents in functional morphology in a field setting, consistent with results from a common garden experiment (Mostow et al., in press).
3. We would observe greater sand deposition and lower plant species richness under hybrid plants than under

parent plants due to hybrid functional morphology and competitive ability.

METHODS

Distribution and abundance of the beachgrass hybrid and its parent species

To determine the distribution and abundance of the hybrid beachgrass *Ammophila arenaria* \times *A. breviligulata* and its parent species, we conducted ground-based field surveys in the summers of 2019, 2021, and 2022 across a 250-km stretch from Moclips, Washington to Neskowin, Oregon, at sites in which we had either found the hybrid in the past (Mostow et al., 2021) or suspected we would find the hybrid because of the presence of both parent species (Figure 1; Appendix S1: Tables S1 and S2). These surveys were in five distinct dune locations roughly corresponding to different littoral or sublittoral cells (i.e., areas along the coast containing the same sediment sources, transport pathways, and sinks), including from north to south: (1) North Beach, Washington, from Moclips to the Grays Harbor North Jetty; (2) Grayland Plains, Washington, from the Grays Harbor South Jetty to Tokeland; (3) Long Beach, Washington, from Leadbetter Point to Cape Disappointment (4) Clatsop Plains, Oregon, from the Columbia River North Jetty to Gearhart; and (5) Pacific City, Oregon, from Cape Kiwanda to Nestucca Spit (Figure 2; Appendix S1: Table S1). We additionally searched for the hybrid along a 9 km distance from Seaside to Neskowin, Oregon (just south of the hybrid's southern limit at Pacific City), but found none within these surveys (Figure 2; Appendix S1: Table S2).

From North Beach, Washington, to Clatsop Plains, Oregon, *A. breviligulata* has an average proportional abundance of 75%–90% whereas *A. arenaria* is sparse and patchy or is in relict populations on the back dune (Figure 1; Hacker et al., 2012). In contrast, the dune region south of Clatsop Plains but north of the Pacific City sub-cell shows an opposite pattern with *A. arenaria* as the dominant beachgrass and *A. breviligulata* in sparse patches.

We established transects in the alongshore direction to search for hybrid and *A. arenaria* individuals (or “patches”),

FIGURE 1 The distribution and relative abundance of *Ammophila arenaria* (red) and *Ammophila breviligulata* (blue) on the US Pacific Coast. The known range of the hybrid beachgrass *Ammophila arenaria* \times *A. breviligulata* is given between the arrows (see Figure 2). Observations range from Graham Island, British Columbia, Canada, to San Nicolas Island, off the coast of southern California, USA. Most observations (circles) were sourced from the iNaturalist project *Hybrid beachgrass mapping in the Pacific Northwest* (<https://www.inaturalist.org/projects/hybrid-beachgrass-mapping-in-the-pacific-northwest>) as of December 2022 ($N = 1202$ from 725 observers). Observations were “Research-grade,” meaning there was a consensus among at least two of three identifiers on iNaturalist as well as our independent visual assessment. Additional observations are from Hacker et al. (2012) (triangles) and R. Mostow (star). Photo by S. Hacker.

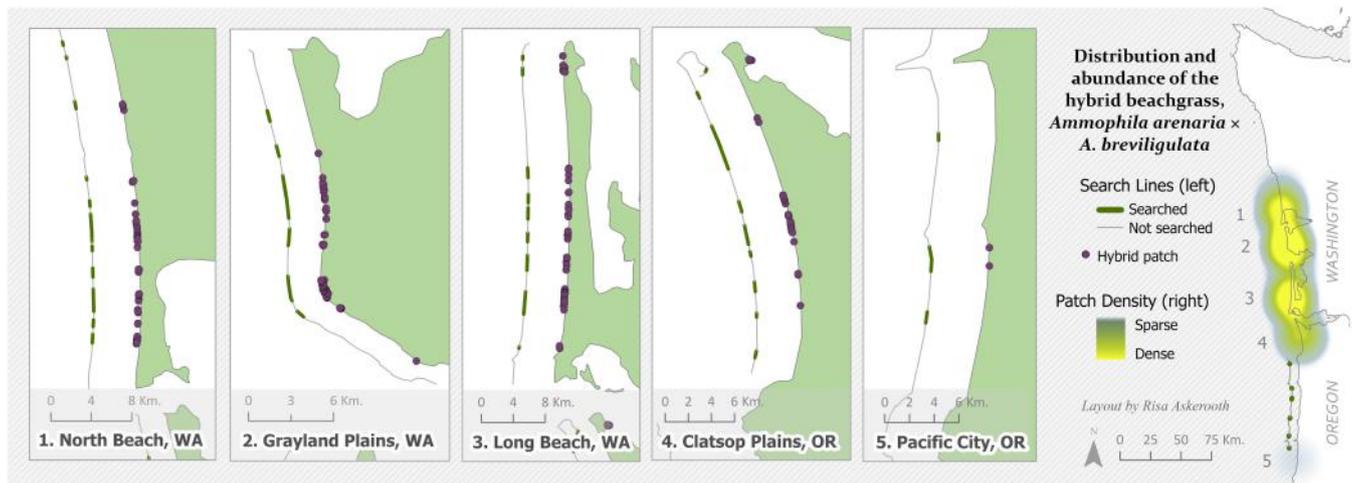


FIGURE 2 The distribution and abundance of the hybrid beachgrass *Ammophila arenaria* × *A. breviligulata* using heat map symbology, across a 250-km range from North Beach, Washington, to Pacific City, Oregon. The inset maps include hybrid patches and foredune search locations at five sites including North Beach, Grayland Plains, and Long Beach, Washington, and Clatsop Plains and Pacific City, Oregon. Foredunes searched along the coastline are represented as offset lines along the coast (green for searched, gray for not searched).

moving in a zigzag pattern in teams of three or four observers across the foredune profile (53 transects total, among sites: North Beach, 9 transects; Grayland Plains, 6 transects; Long Beach, 10 transects; Clatsop Plains, 10 transects; Pacific City, 2 transects; Other Oregon, 16 transects) (Appendix S1: Table S2). The abundance of *Ammophila breviligulata* was not quantified in our surveys given that this species is in such high abundance at all locations (except Pacific City) that it does not occur in patches (Hacker et al., 2012). Hybrids and *A. arenaria* were distinguished from *A. breviligulata* by visually comparing flowering shoots, shoot height, shoot length, and/or shoot color (hybrid has dark red shoots, Appendix S1: Figure S1). We used ligule length to confirm identification of each patch (average ligule length of 7.7 mm for the hybrid, 25.7 mm for *A. arenaria*, and 1.4 mm for *A. breviligulata*) and marked its location (Garmin GPSMap unit; accuracy $\pm\sim 3.7$ m). For Pacific City and a few other Central Oregon locations where *A. arenaria* is dominant and *A. breviligulata* is rarer, we conducted similar surveys for hybrids, but only found two patches at Pacific City (Appendix S1: Table S2).

Cartography and spatial analysis for the hybrid beachgrass surveys were conducted using ArcGIS Pro 3.0 with projection NAD1983 UTM Zone 10N. Distance for each alongshore search transect was calculated by measuring the distance between start and end latitudes, not accounting for longitudinal distance (Appendix S1: Table S2). To account for variation in length of each search transect (which ranged from 0.08 to 3.2 km), we divided the transect into equal intervals of approximately

0.2 km. We then standardized density by dividing the total number of individuals found within each transect segment by the total length (in kilometers) of the segment, and multiplied by 0.2 km.

In addition to ground-based field surveys, we mapped the occurrence of *A. arenaria*, *A. breviligulata*, and the hybrid on the Pacific coast using research-grade iNaturalist occurrence records (iNaturalist.org, 2023) of the two parent species housed on The Global Biodiversity Information Facility (GBIF, 2023a, 2023b). Inaccurate observations for each species were removed after assessing all records ($n = 467$ for *A. arenaria* and $n = 111$ for *A. breviligulata*).

Hybrid beachgrass growth and morphology compared with its parent species

To determine the size of hybrid individuals and their growth over time, the perimeter of a subset of patches ($n = 68$, among sites: North Beach, 18 patches; Grayland Plains, 19 patches; Long Beach, 23 patches; Clatsop Plains, 6 patches; Pacific City, 2 patches) was measured using a Real-Time Kinematic (RTK) GPS Global Positioning System (R7 and R9 models, Trimble, Westminster, CO, USA), which was programmed to collect GPS positions every 0.1 m. A further subset of 26 patches among sites was measured in both 2021 and again in 2022 to determine patch growth, which is the change in patch size over time.

We also measured the shoot density and morphology of the hybrid and its parent species using two methods.

First, depending on the patch size, we haphazardly placed one to many 0.25-m² quadrats in each hybrid patch ($n = 49$ patches) and in the nearest occurrence of *A. arenaria* ($n = 39$ patches) and *A. breviligulata* ($n = 48$ patches) and measured beachgrass shoot density (number of shoots per 0.25-m² quadrat), shoot height (in centimeters), and plant species percent cover. Shoot height was measured by randomly selecting three shoots of each beachgrass taxa in each quadrat and measuring their height from the base of the sand to the leaf tip. Second, we measured beachgrass morphology by first collecting three grass plant individuals (i.e., shoots attached to a single rhizome) of each taxon from the immediate vicinity of 30 hybrid patches (the same 26 patches measured for perimeters above, as well as one additional patch from North Beach and three patches from Clatsop Plains). Samples were air dried at room temperature (21°C) and each plant was measured for (1) shoots per plant, (2) shoot height, (3) leaf number per shoot, (4) ligule length (of the primary shoot), (5) blade width (second leaf on the primary shoot), and (6) above- and belowground mass separately. We then calculated several standardized metrics, including aboveground biomass per shoot (aboveground biomass [in grams]/shoots per plant), belowground biomass per rhizome length (belowground biomass [in grams]/rhizome length [in centimeters]), leaf area ($0.5 \times$ shoot length [in centimeters] \times leaf width [in centimeters] \times leaf number), and beachgrass biomass per quadrat (aboveground biomass per shoot [in grams per shoot] \times shoot density [shoots/0.25 m²]).

Sand deposition and plant community structure with the hybrid beachgrass

To examine sand deposition and plant community structure in areas with and without the hybrid beachgrass, we established a pair of shore-perpendicular transects at a subset of 20 locations on or near where hybrid patch growth measurements were made. For each pair, one transect intersected with a hybrid patch while the other transect was placed parallel to the first transect (spaced an average of 14.1 ± 1.7 m apart) but without hybrid (Appendix S2: Figure S1). To consider sand deposition, we measured the elevation of the transects using RTK GPS units (vertical uncertainty of ± 8 -cm elevation) from the mid-beach to the heel of the foredune in 2021 and again in 2022 (Appendix S2: Figure S2). To consider plant community structure, we used a point-intercept method to document all plant taxa that intersected each designated point every 2 m along the transect.

Sand deposition along the transects was calculated using MATLAB version R2022b (9.13.0) to compare the change in elevation (2021–2022) of paired cross-shore

transects with and without the hybrid present (hereafter referred to as transect type) and among sections along transects that were at pre-, within-, and post-hybrid patch locations (Appendix S2: Figures S1 and S3). We first transformed the horizontal units of the topographic survey from Universe Transverse Mercator (UTM) x - and y -coordinates to alongline distance (in meters; interpolated every 0.1 m) using the Euclidean distance formula $\text{Alongline distance} = \sqrt{(y_2 - y_1)^2 + (x_2 - x_1)^2}$, where y_n = the UTM y -coordinates of a point, x_n = the UTM x -coordinates of a point, and the subscript denoting the next point in the dataset. Then, we determined average elevation change (in meters) of the foredune pre-, within-, and post-patch interval for both transect types by computing the average difference between the 2022 and 2021 elevations at the interpolated points (Appendix S2: Figure S3).

Hybrid occurrence on threatened bird habitat

We mapped the occurrence of hybrid patch locations, from beachgrass search transects described above, and their proximity to the habitat conservation areas of two Endangered Species Act-listed birds. Hybrid locations were plotted on a map with GIS shapefiles of Snowy Plover Management Areas (Oregon State Parks, 2019), as well as Critical Habitat Areas of the western snowy plover (*Charadrius alexandrinus nivosus*) and streaked horned lark (*Eremophila alpestris strigata*) (US Fish and Wildlife Service, 2012, 2013).

Data and statistical analyses

All statistical analyses were conducted in R v.4.3.0 (R Development Core Team, 2019). Data were examined for normality and homogeneity of variance using visual inspection of histograms and residual plots, respectively, followed by Shapiro–Wilk tests and Levene’s tests for further confirmation as needed. Data of hybrid and *A. arenaria* abundance among sites (patches per 0.2 km) did not meet assumptions of normality and homoscedasticity, even after transformation. We therefore used a PERMANOVA with Bray–Curtis dissimilarity (adonis2 function in vegan package; Oksanen et al., 2013) to analyze abundance of both beachgrass taxa among sites (excluding Pacific City with only two hybrid individuals) and transects, nested within site. Even though the model allows post hoc comparisons with nesting, we repeated the analysis without the nested factor (transect) so that we could test for differences among

sites. The analysis showed no difference in the two models, so we proceeded without nesting using multiple pairwise comparisons among sites with a Bonferroni adjustment.

The relationship between hybrid and *A. arenaria* abundance (measured in patches per 0.2 km) was shown to be nonlinear through visual inspection and was thus examined using a generalized additive model (GAM; mgcv package; Wood, 2015) with Restricted Maximum Likelihood as the smoothing parameter. Following comparison to an intercept-only model using the Akaike information criterion (AIC), the predictors we included were site as a fixed effect (increasing the amount of deviance explained in the model by 10%) and *A. arenaria* abundance as a smoothing term.

After confirming data met assumptions of normality and homoscedasticity, we analyzed hybrid patch area (natural log transformation) among sites (excluding Pacific City) using a one-factor ANOVA. For hybrid patch growth data, we first calculated the log response ratio (LRR) of change in patch area across sites and profile locations, given by the equation: $LRR = \ln(2022 \text{ patch size [m}^2\text{]}/2021 \text{ patch size [m}^2\text{]})$. We then performed one-sided *t* tests to assess whether LRR was greater than zero. We also analyzed whether LRR varied among sites and profile locations using one-factor ANOVAs.

We conducted linear mixed-effects models (lme4 package; Bates et al., 2015) on field measured grass shoot density (natural log transformation) and shoot height (square root transformation) for the three beachgrass taxa to test for differences among sites (fixed; excluding Pacific City), patch nested within site (random), taxa (fixed), and profile location (fixed). We conducted Tukey honestly significant difference (HSD) post hoc tests (emmeans package; Lenth et al., 2019) on significant factors, unless interactions were found, in which case post hoc analyses were performed between levels of each factor (Underwood, 1996). We did not conduct post hoc tests on significant three-way interactions.

To determine the relationship between beachgrass taxa and plant species richness and abundance, we used two methods. First, we used our point-intercept transect surveys to consider the relationship between beachgrass taxa and plant species abundance. Proportional occurrence of each plant taxon along a transect was calculated as number of taxa observations/number of points along transect/transect length (in centimeters), where the number of taxa is the total number of points a plant taxon occurred along a transect, number of points is the total number of points along a transect that were surveyed, and transect length (in meters) is the total length of the transect from the vegetation line to the heel of the dune. We then used a linear mixed-effects model (Bates

et al., 2015) to test for differences in proportional occurrence of plant taxa (square root transformation) among dune grass taxa (fixed), site (fixed), and transect location (random, nested within site) and their interactions. Tukey HSD post hoc tests were conducted in the same manner as above (Lenth et al., 2019) on significant factors or their interactions. Second, we compared plant species richness of non-*Ammophila* species among quadrats ($n \leq 3$, randomly selected nonzero quadrats to control for sample size) dominated by the three beachgrass taxa. The dominant *Ammophila* beachgrass was determined by the taxon with the greatest number of beachgrass shoots in the quadrat, and a Kruskal–Wallis test was then used to analyze species richness among the three groups because data did not meet assumptions of normality and homoscedasticity.

Following inspection of normality and variance assumptions, we conducted a three-factor ANOVA to examine differences in transect elevation change among transect type (with- and without hybrid), transect section (pre-, within-, and post-hybrid patch), and profile location (toe/face or crest/heel). Tukey HSD post hoc tests were conducted on significant factors.

RESULTS

Distribution and abundance of the beachgrass hybrid and its parent species

Consistent with Mostow et al. (2021), iNaturalist observations and our ground-based surveys confirmed the presence of the hybrid beachgrass from Moclips, Washington in the north to Pacific City, Oregon in the south, a stretch of roughly 250 km (Figure 2) and a region where both parent species are common (Hacker et al., 2012). In addition, the iNaturalist observations showed that *A. arenaria* occurs from Graham Island, British Columbia, Canada, in the north, to San Nicolas Island, California, whereas *A. breviligulata* occurs at only a handful of locations outside of the main region of co-occurrence (Figure 1). These sites included, to the north, the western shore of Vancouver Island, British Columbia, Canada, and along Puget Sound near Seattle, Washington, and, to the south, Neskowin, Newport, Oregon and Eureka and San Francisco, California.

Within the detected range of the hybrid, we found 299 hybrid individuals by Spring 2023 at five sites, from north to south, including three sites in Washington and two sites in Oregon (Figure 2; Appendix S1: Tables S1 and S2). A PERMANOVA revealed a difference in hybrid and *A. arenaria* density among sites and transects in Clatsop Plains compared with more northern Washington

sites. Transect explained a much greater amount of variance than site in the model, although site was still significant when transect was removed (Figure 3A; Appendix S3: Table S1). We did find hybrid individuals across all foredune profile locations with the highest number at the dune toe ($n = 78$), dune crest ($n = 68$), and dune heel ($n = 65$) and the lowest number at the

dune face ($n = 40$) (Appendix S3: Figure S1). The size of hybrid beachgrass patches, which were 70.1 m^2 on average, was smaller at Grayland Plains, the second northernmost site, than at all others (Figure 3B; Appendix S3: Table S1).

We observed that hybrid patch abundance is highest among the three northernmost Washington sites, while *A. arenaria* generally increases in abundance from

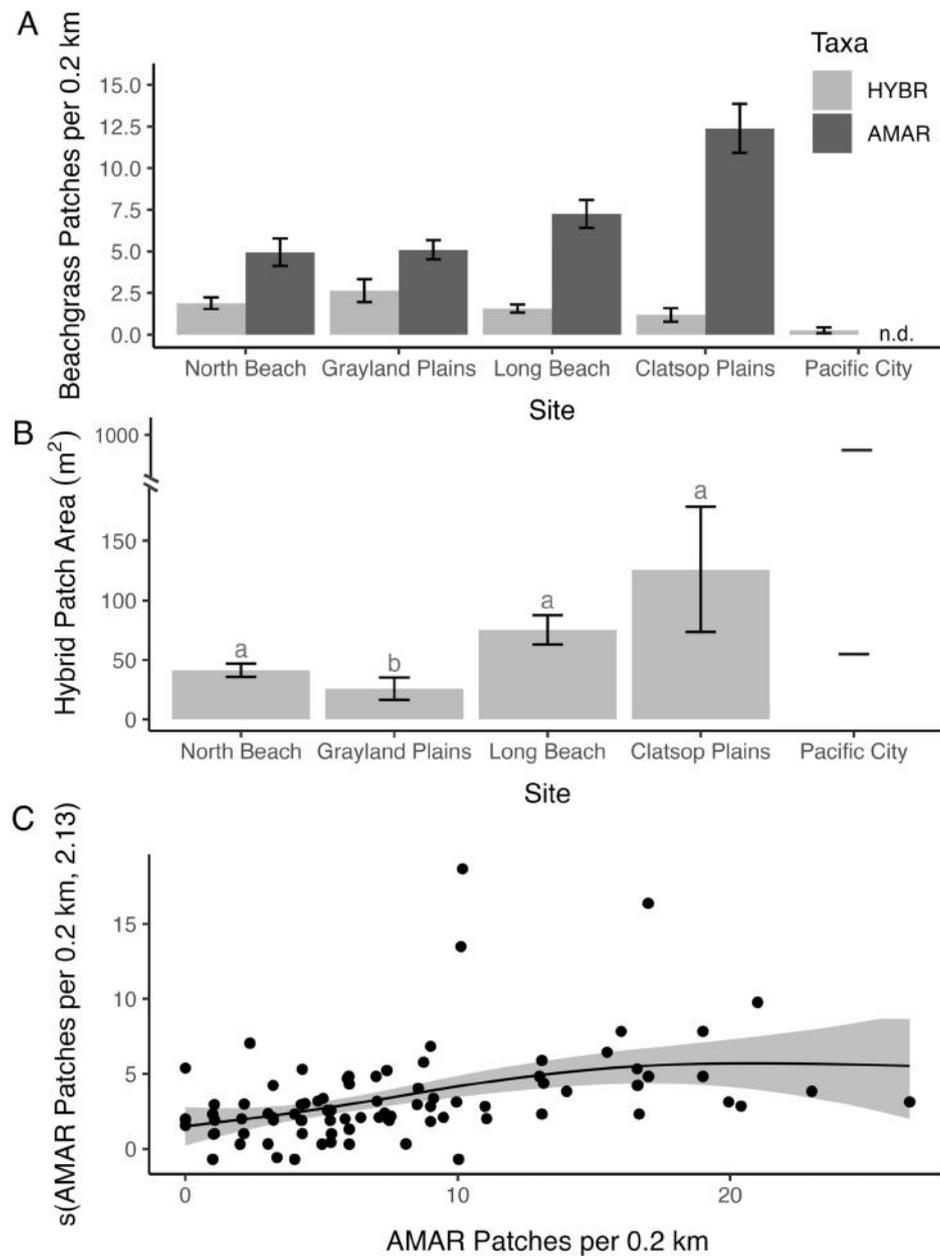


FIGURE 3 Mean (\pm SE) (A) *Ammophila* hybrid (HYBR) and *Ammophila arenaria* (AMAR) individual density and (B) hybrid patch area at five dune sites in Washington (North Beach, Grayland Plains, and Long Beach) and Oregon (Clatsop Plains and Pacific City) (Figure 2). Letters represent significant differences in hybrid patch density with site ($p \leq 0.05$, Tukey post hoc test). See Appendix S3: Table S1 for statistical results. n.d., no data. (C) The relationship between hybrid patch density (given as the smooth terms [AMAR patches per 0.2 km, df]) and AMAR patch density (solid line; shifted by the value of the intercept), with $\pm 95\%$ CI (shaded region), and residuals (points) from a generalized additive model. Data are excluded from Pacific City, Oregon, and from alongshore transects where no hybrid individuals were found. See Appendix S3: Table S2 for statistical results.

northern to southern sites (Figure 3A). An analysis at the sub-transect scale showed a positive trend between hybrid and *A. arenaria* densities (patches per 0.2 km) (Figure 3C), with a peak in hybrid individuals at *A. arenaria* densities greater than 10 patches per 0.2 km, although this relationship was not site-dependent (Appendix S3: Table S2).

The proportional abundance of dune grass taxa varied among taxa and site, and there was an interaction between the two (Figure 4A; Appendix S1: Table S3, Appendix S3: Table S3). At all sites, *A. breviligulata* had greater proportional abundance than the hybrid, *A. arenaria*, and the native dune grass, *Leymus mollis*. The hybrid was similar in proportional abundance compared

with *A. arenaria* at all sites except Pacific City, where *A. arenaria* was more abundant. In addition, *A. arenaria* and *L. mollis* had higher proportional abundances at southern (Oregon) sites compared with northern (Washington) sites.

Finally, we detected numerous hybrid individuals within Critical Habitat Areas of the western snowy plover and streaked horned lark at Leadbetter Spit on Long Beach peninsula and Midway Beach and Graveyard Spit of Grayland Plains in Washington (Appendix S1: Figure S2). Hybrid patches were also found near, but not within, the Copalis Beach Critical Habitat Area of the western snowy plover in Washington, and the Clatsop Spit Western Snowy Plover Management Area in Oregon.

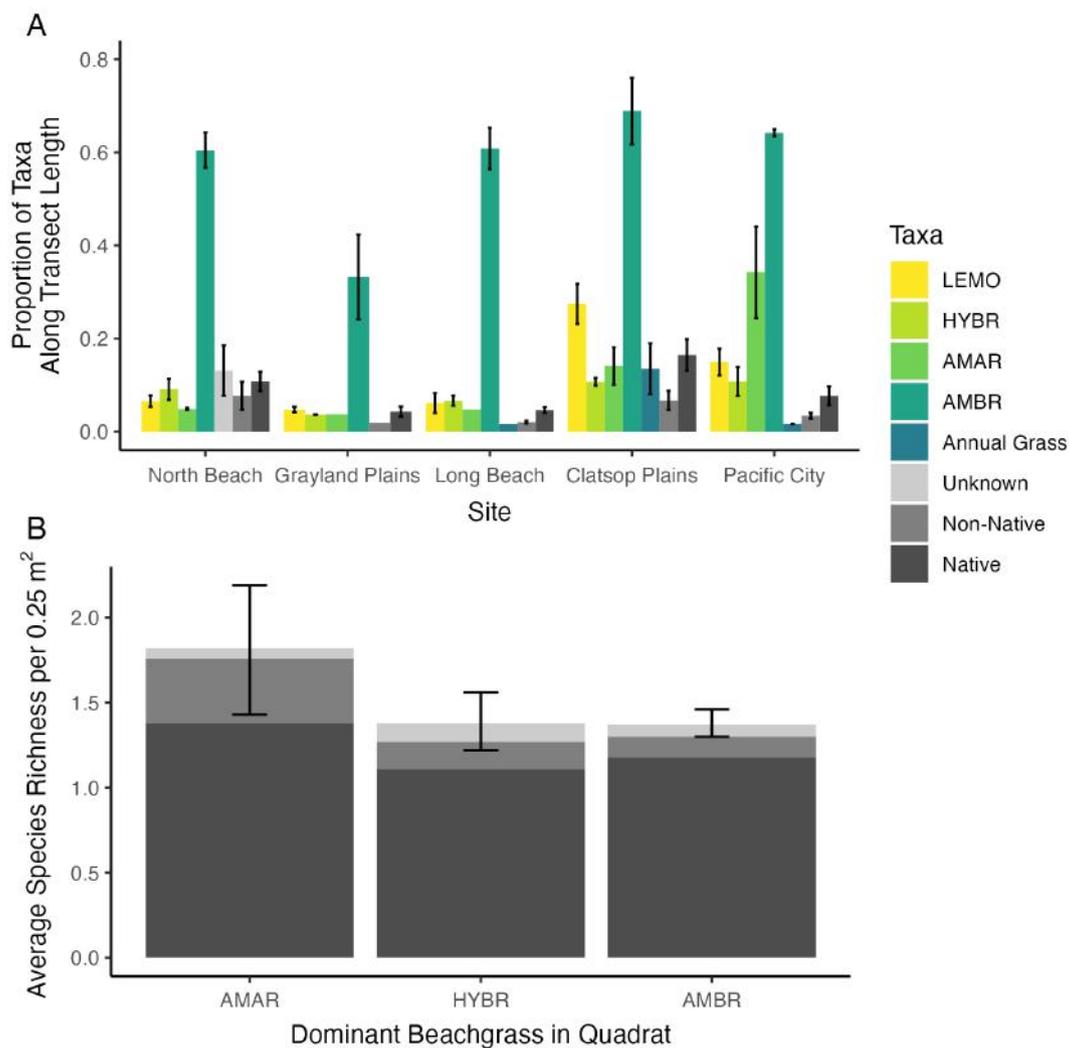


FIGURE 4 The mean (\pm SE) (A) proportion of all plant taxa occurrences along cross-shore transects, and (B) species richness of native, non-native (excluding *Ammophila* taxa), and unknown (unidentified annual grass spp. or other) plants among quadrats dominated by each *Ammophila* beachgrass taxa at five sites in Washington (North Beach, Grayland Plains, and Long Beach) and Oregon (Clatsop Plains, Pacific City) (Figure 2). Dune grass taxa abbreviations are LEMO, *Leymus mollis*; HYBR, *Ammophila* hybrid; AMAR, *A. arenaria*; AMBR, *A. breviligulata*. See Appendix S3: Table S3 for logistic regression results of proportional occurrence and Appendix S1: Tables S3 and S4 for a list of taxa.

Hybrid beachgrass growth and morphology compared with its parent species

Hybrid patches showed growth, measured as the LRR from 2021 to 2022, among sites and profile locations (Figure 5). One-sided t tests determined that patch growth was greater than zero at all sites except Grayland Plains and at all dune profile locations. However, we observed no differences in patch growth among sites ($F_{3,20} = 0.56$, $p = 0.65$) or profile locations ($F_{4,21} = 1.37$, $p = 0.28$).

The beachgrass hybrid had greater shoot densities than *A. breviligulata* and equal to or slightly lower shoot densities than *A. arenaria* at most sites, and there was an interaction between site and taxa (Figure 6A; Appendix S3: Tables S4 and S5), such that hybrid shoot densities were greater than *A. breviligulata* at the three northern sites (North Beach, Grayland Plains, and Long Beach) and similar to both parent species at Clatsop Plains. For all taxa and sites, shoot densities at the heel were lower than at the toe and crest locations of the foredune. The hybrid tended to be taller than at least one parent species at most profile locations and sites, but there were interactions among all three variables of taxa, sites, and profile locations. Additional lab-collected

functional morphology measurements show the hybrid to be similar to at least one of its parents in certain traits (e.g., leaf number per shoot, standardized below and aboveground biomass, leaf area, biomass per 0.25 m²) and intermediate in others (e.g., ligule length and blade width) (Appendix S3: Table S4).

Sand deposition and plant community structure with the hybrid beachgrass

Transects had greater sand deposition, measured as an increase in elevation, at the toe/face of the foredune than at the crest/heel of the foredune, but there was no difference between transects with the hybrid and those without the hybrid (average elevation change with hybrid = 0.13 m and without hybrid = 0.12 m) (Appendix S2: Figure S4, Appendix S3: Table S6). Moreover, sand elevation had greater variability in front of the hybrid patch than in the same location without the hybrid, especially at the crest/heel profile location.

We found no differences in species richness of non-*Ammophila* taxa among quadrats dominated by each of the three beachgrass taxa (Figure 4B; Appendix S1: Table S4; $H(2) = 1.18$, $p = 0.56$). The larger proportion of native species compared with non-native species observed from these quadrat surveys was also consistent with vegetation data from point-intercept data collected along the transects (Figure 4A). The most abundant native species was beach pea (*Lathyrus japonicus*), which was present in nearly 10% of quadrats and at over 50% of points on transects (Appendix S1: Tables S3 and S4).

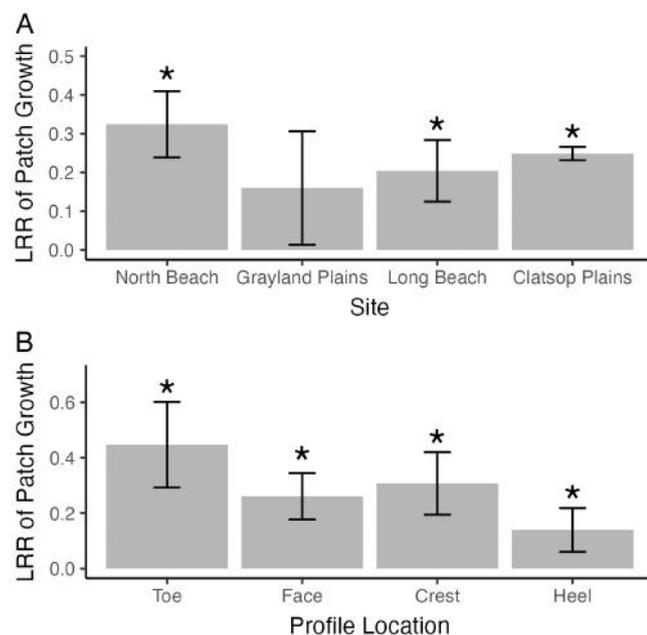


FIGURE 5 The growth of *Ammophila* hybrid patches, measured as the change in patch size (in square meters) from 2021 to 2022 using the log response ratio (LRR) for (A) site and (B) profile location. Data from Pacific City, Oregon, are excluded. Asterisks indicate a significant difference from zero using a one-sample, one-sided t test (true mean >0 , $p \leq 0.05$). One-factor ANOVAs showed no differences among sites or profile locations.

DISCUSSION

This study represents the first large-scale, systematic field survey of a new hybrid beachgrass *Ammophila arenaria* \times *A. breviligulata*. Most notably, we found that the hybrid is widespread and abundant across a 250-km range, especially at sites within southern Washington and northern Oregon (Figures 1–4; Hacker et al., 2012). Across our alongshore transects from North Beach, Washington, to Clatsop Plains, Oregon, we found nearly 300 hybrid individuals or an average of 8–14 hybrid individuals per kilometer of surveyed foredune, with hybrid patch sizes that ranged in average area from 26 to 126 m² (Figure 3B). We also found that hybrid individuals increased in area on average by 30% over the one-year observation period (Figure 5), indicating the potential for further rhizomatous spread of this new taxon, especially in open sandy areas at the leading edge of the dune.

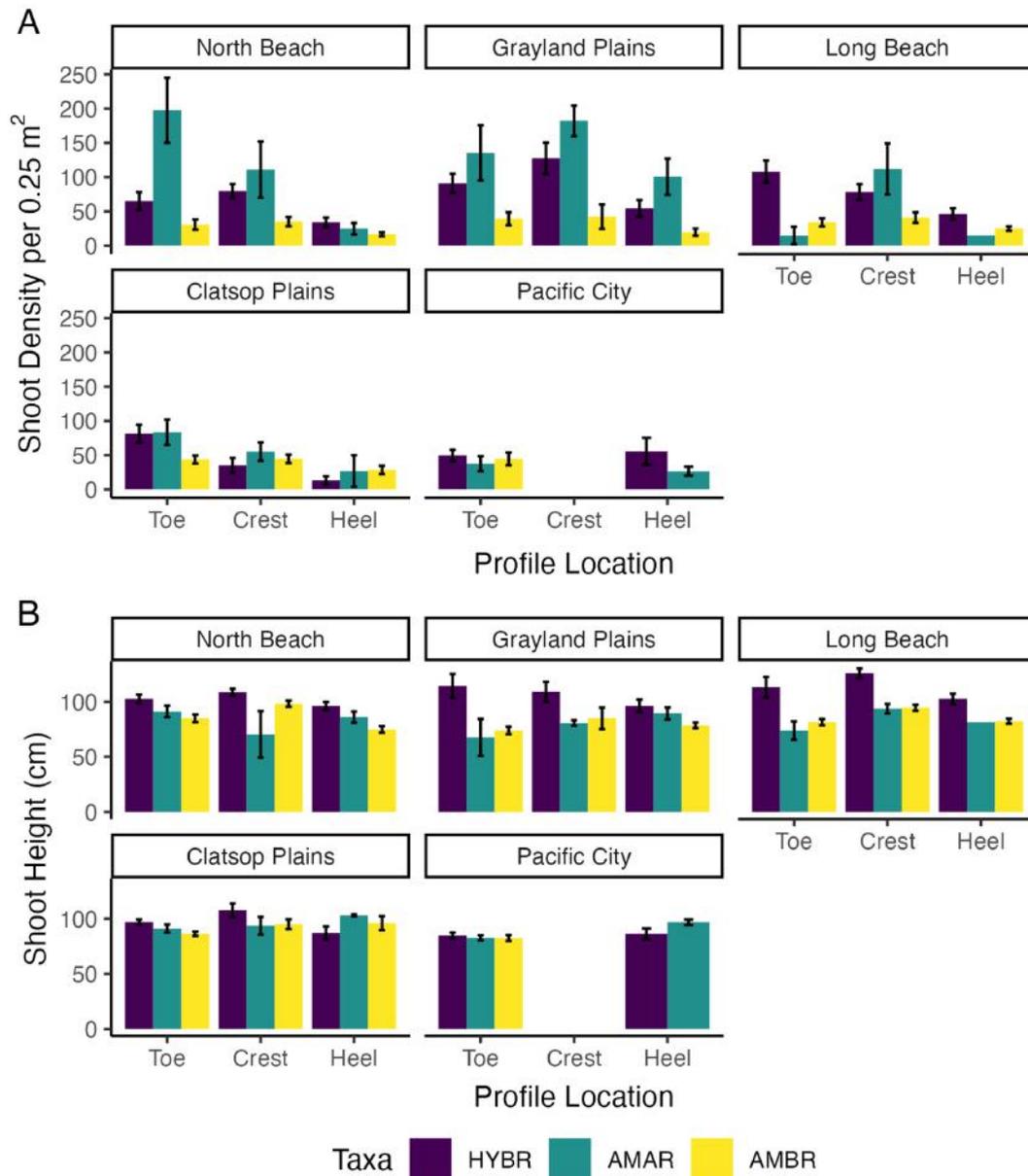


FIGURE 6 Mean (\pm SE) of (A) beachgrass shoot density and (B) beachgrass shoot height across profile locations and dune sites in Washington (North Beach, Grayland Plains, and Long Beach) and Oregon (Clatsop Plains, Pacific City) (Figure 2). There were no hybrid individuals at the crest location of Pacific City foredunes. Beachgrass taxa abbreviations are HYBR, *Ammophila* hybrid; AMAR, *A. arenaria*; AMBR, *A. breviligulata*. See Appendix S3: Table S5 for statistical results.

Although our results illustrate that the hybrid has functional traits, including shoot density and height, that could allow it to accrete more sand than its parent species (Figure 6), we did not find differences in sand deposition around the hybrid compared with adjacent areas with the parent species over the one-year period (Appendix S2: Figure S4). Similarly, we found that the hybrid beachgrass had similar associated plant species richness compared with both parent species (Figure 4), despite the concern that it could have more detrimental effects on native plant species.

Distribution and abundance of the hybrid beachgrass and its parent species

Most hybrid individuals occurred at sites within southern Washington and northern Oregon, especially in the sites North Beach, Grayland Plains, Long Beach, and Clatsop Plains (Figures 2 and 3A). The hybrid was scarcer along the southern extent of its range, including Pacific City, the southernmost site where we found just two patches, one of which is a backcross between the hybrid and *A. arenaria* (Mostow, 2022). There was a negative

relationship between hybrid number and their size, suggesting that sites such as Grayland Plains and North Beach, where there are many small individuals, are new and active areas of hybridization compared with southern sites such as Pacific City where there are many fewer and larger patches (Figure 3).

We did not find the hybrid beachgrass at any locations between Pacific City and Clatsop Plains, Oregon, despite thorough and repeated searches in several areas where both hybrid parent species co-occur (Figures 1 and 2; Appendix S1: Table S2). The two *Ammophila* beachgrass species also co-occur outside of the currently detected range of the hybrid in several locations, including the west coast of Vancouver Island, British Columbia, the Salish Sea and the northern Washington coast, the central to southern Oregon coast, and dunes in Eureka and San Francisco, California (Figure 1). Of these locations, we suspect that the hybrid may be present on Vancouver Island, where both parent species are in high abundance on the island's western coast.

At sites where the hybrid beachgrass was most abundant, *A. breviligulata* represented nearly 75% of plant taxa, compared with the roughly 10% represented by *A. arenaria* (Figure 4; Appendix S3: Table S3), which typically occurred as relict populations in the heel and back dune, or discrete clumps closer to the beach. Indeed, there was a positive relationship between the number of hybrid individuals and the number of *A. arenaria* individuals along our transects, with a peak number of hybrid patches at roughly 10 *A. arenaria* patches per 0.2 km (Figure 3C; Appendix S3: Table S2). However, the relationship was weak, suggesting that other factors are probably at play. The hybridization rate could depend on, for example, which species is serving as the maternal parent of the hybrid, the overlap in flowering time between the parent populations, the presence and breeding of hybrids in different generations (Mostow, 2022), and/or post-reproductive processes such as seed germination, seedling survival, or adult survival (Baye, 1990; Huiskes, 1977; Maun, 1984).

We also found more hybrid individuals at the toe and face of the foredune than at the crest and heel locations (Appendix S3: Figure S1). There could be two interrelated reasons for this pattern. First, the hybrid individuals at these locations are likely younger than those located farther back on the dune that we know correspond to later successional stages (David et al., 2015). Thus, there could be fewer hybrid individuals in back dune locations because they are older F_1 hybrid individuals, originating before the hybrid population which started reproducing with itself and creating hybrid swarm conditions

(Mostow, 2022). Future research should explore if greater hybridization rates and survival occur at the leading edge of the foredune, where the beachgrasses show greater biomass, growth, and flowering because of marine-derived nutrients from the beach (Constant, 2019) and/or open and potentially competitor-free space. Open, sparsely vegetated areas, such as we see on prograding beaches (e.g., Grayland Plains, Long Beach, and Clatsop Plains; Figure 2) or within habitat conservation areas designed to protect the breeding grounds of two endangered bird species (Appendix S1: Figure S2), will require additional surveys and targeted studies to understand if they are, or may become, hybrid beachgrass “hots spots” requiring management attention.

Hybrid beachgrass growth and morphology compared with its parent species

Besides being widespread and common within the main region of co-occurrence of the two *Ammophila* parents, our hybrid growth and morphology results indicate the likelihood for the hybrid to spread quickly through vegetative growth and potentially pose a competitive challenge to its parent species. Hybrid individuals grew on average by 10%–40% in area over a year, with patches at the foredune toe showing higher growth rates (Figure 3C). Although we do not have field data to compare the growth rate of the beachgrass hybrid with its parents, we did find similar results to those of a mesocosm experiment in which the hybrid and its parent species were planted in monoculture and polyculture to explore possible differences in growth, morphology, and species interactions under common garden conditions (Mostow et al., *in press*). In a monoculture setting, the hybrid beachgrass grew faster and displayed higher shoot densities than its parent counterparts after 18 months of growth. In the polyculture experiment, the faster growth and shoot production of the hybrid resulted in its competitive advantage and a further projected outcome of local extinction of *A. breviligulata* and possibly *A. arenaria* depending on the relative abundances of the taxa (Mostow et al., *in press*). Experimental results also showed that the hybrid exceeded both parents in average shoot density and height, similar to our field measurements despite variability among sites and profile locations (Appendix S3: Tables S4 and S5). These field observations and experimental results present consistent and compelling evidence that the hybrid beachgrass has growth and morphological traits that will allow it to spread quickly, increase in abundance, and successfully compete with both *Ammophila* parents.

Implications of the hybrid beachgrass for dune ecosystem services and functions

We found that at this point in the hybrid invasion, and albeit after only a relatively short study period, there is little evidence that the hybrid varies in its effects on sand deposition or plant species richness compared with its parent species. Over a year, there was no difference in sand deposition under hybrid-dominated locations versus replicate locations nearby (Appendix S2: Figure S4, Appendix S3: Table S6). Due to the difficulty of detecting the effect of beachgrass vegetation on dune morphology over short time scales with variable sand supply rates, longer studies that control for sand availability either statistically (e.g., Biel et al., 2019; Hacker et al., 2012) or through experiments (Laporte-Fauret et al., 2023; Zarnetske et al., 2012) will be necessary.

Although we observed that plant species richness was slightly lower within patches of the hybrid and *A. breviligulata* than of *A. arenaria*, the differences were not significant (Figure 4), indicating that the hybrid does not currently pose a greater threat than its parents to native plant community composition. This may also be explained by the fact that the hybrid is less abundant than its parents and thus has not yet reached the threshold abundance above which plant communities may be significantly affected (O'Loughlin et al., 2021). Hacker et al. (2012) also found that plant species richness was lower in *A. breviligulata* than in *A. arenaria*, with explanations that include competitive ability, latitudinal range, and foredune location of the two beachgrass species. This emerging hybrid beachgrass represents an important opportunity to better understand the spread of novel non-native species and the effects on important ecosystem functions and services of the communities in which they invade.

AUTHOR CONTRIBUTIONS

Risa Askerooth and Sally D. Hacker conceived and designed the experiment. Risa Askerooth collected and analyzed the data, with assistance from Rebecca S. Mostow, Sally D. Hacker, and Peter Ruggiero. Risa Askerooth wrote the manuscript with help from Sally D. Hacker, and all authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Askerooth et al., 2024) are available from Dryad: <https://doi.org/10.5061/dryad.x0k6djhr4>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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