

AN ABSTRACT OF THE DISSERTATION OF

Reuben Gabriel Biel for the degree of Doctor of Philosophy in Zoology presented on September 12, 2017.

Title: Coastal Dune Ecology, Geomorphology, and Ecosystem Services: How Invasive Beachgrasses, their Interactions, and Sediment Dynamics Shape U.S. Pacific Northwest Dunes

Abstract approved:

Sally D. Hacker

Biological invasions and climate change represent two preeminent threats to ecological communities and biodiversity, altering the distribution and abundance of species, disrupting existing species interactions and forming unprecedented ones, and creating novel ecological communities. Many of the most successful invasive species are also ecosystem engineers, species that physically modify the abiotic state of the ecosystem, and consequently have broad impacts on community structure, ecosystem processes, and ecosystem services. As ecosystems face dual hazards from biological invasions and climate change, it is imperative to understand what factors influence invasion success, how invasive species alter physical and biological processes, and how a changing climate alters the course of invasion.

In this dissertation, I investigate the interactions of two invasive, dune-forming beachgrasses within the U.S Pacific Northwest coastal dune ecosystem and their influence on dune geomorphology and ecosystem services. Two species of non-native beachgrasses, *Ammophila arenaria* (L.) Link and *A. breviligulata* (Fernald), were intentionally introduced to the Pacific Northwest in the early 20th century for the purpose of sand stabilization. Since their introductions, they have displaced numerous endemic plants and animals, and facilitated the formation of tall, stable, and well-vegetated shore-parallel dune ridges throughout the region. However, the two *Ammophila* species differ in

their distributions and their impacts on dunes: biogeographically, *A. arenaria* dominates coastal dunes in central Oregon and southward, whereas *A. breviligulata* dominates dunes in northwest Oregon and southwest Washington; geomorphologically, *A. arenaria*-dominated dunes are taller and narrower than *A. breviligulata*-dominated dunes. *Ammophila breviligulata*-dominated regions also experience higher sediment supply and rates of shoreline change, typically creating wider beaches and shorter dunes. Although *Ammophila* biogeography in part reflects historical planting patterns, invasion success might also relate to latitudinal variations in sand supply. Similarly, while some differences in dune shape may relate to species-specific differences in grass density, morphology, and growth form, spatially correlated sand supply and beach characteristics might also explain the differences.

Using a combination of observational surveys, experimental manipulations, and statistical and numerical modeling, I examine how species identity, species characteristics, and sediment supply influence dune geomorphology, invasion success, species interactions, and ecosystem services. In Chapter 2, I investigate the relative role of beachgrass density, species identity, beach characteristics, and sediment supply on dune geomorphology and rates of sand accretion using Gaussian Bayesian networks. I found that dune shape was primarily influenced by beach sediment supply and backshore slope, whereas beachgrass density was a smaller, albeit important determinant of foredune shape. Still, *A. arenaria*-dominated dunes were taller and narrower than those of *A. breviligulata*, even after accounting for sediment supply and beach characteristics. These differences in dune shape likely arose because of the functional difference in sand capture of the two *Ammophila* species as a result of differences in growth form.

In Chapter 3, I use reciprocal transplant experiments to examine how species invasiveness and community invasibility contribute to the survival and growth of the two *Ammophila* species across a sand supply gradient. I determined that *A. breviligulata* and *A. arenaria* exhibit higher survival and productivity than the native dune grass *Elymus mollis*. Further, *A. breviligulata* and *A. arenaria*-dominated foredune communities were less invasible than *E. mollis* communities, primarily because *E. mollis* communities facilitated the survival and productivity of non-native species. Thus, the invasion success

of the two *Ammophila* species results from both their high invasiveness and the high invasibility of the native *E. mollis* community.

In Chapter 4, I explore how rising temperatures and variations in sand burial rates associated with climate change might impact the growth, morphology, and species interactions of *A. arenaria* and *A. breviligulata* using a common garden experiment. I showed that *A. breviligulata* is competitively dominant to *A. arenaria* under a range of sand burial and temperature conditions by exhibiting higher productivity and exerting a negative density-dependent effect on *A. arenaria* tiller and biomass production. Although *A. breviligulata* was predicted to exclude *A. arenaria* across all experimental conditions, elevated temperatures and high rates of sand burial also increased the likelihood of coexistence between the two grass species. These results suggest that a warmer climate may limit the spread of *A. breviligulata* or promote coexistence between the two *Ammophila* species.

Finally, in Chapter 5, I assess how the removal of invasive beachgrass for the conservation of the threatened western snowy plover (*Charadrius nivosus nivosus*) creates context-dependent synergies and tradeoffs among coastal dune ecosystem services. I found that coastal protection, western snowy plover conservation, and endemic plant conservation varied among seven plover habitat restoration areas. Western snowy plover conservation services negatively covaried with coastal protection due to management actions. While dune shortening from beachgrass removal was the proximate cause of this tradeoff, the magnitude of the tradeoff was influenced by nearshore geomorphology in that dune shortening had a muted effect on coastal hazard exposure when it occurred on shallow-sloping, dissipative beaches. Thus, consideration of nearshore and beach geomorphology is important when managing for western snowy plover conservation because it may lessen tradeoffs among competing Pacific Northwest dune ecosystem services.

Overall, the findings from this dissertation research demonstrates the complex and interdependent connection between biological invasions and climate change on community structure, ecological processes, and ecosystem services of the U.S. Pacific Northwest coastal dunes. For management of coastal dunes, this research examines

multiple factors that may contribute to the present-day distribution and abundance of the two *Ammophila* species, and their potential to spread to new areas in the coming decades. Moreover, I demonstrated why the two *Ammophila* species produce distinct dune shapes and resultantly exhibit differing amounts of protection against flooding and erosion hazards. Finally, although I found that *Ammophila* removal for plover conservation created tradeoffs in ecosystem service supply, strategic management can minimize tradeoff severity and alleviate potential conflicts among stakeholders. For Pacific Northwest coastal management, these findings can help to inform coastal managers of the potential for changes in the distribution of the two *Ammophila* species, their impacts on dune ecosystems and the services that they provide, and some possible strategies possible strategies for establishing new habitat restoration areas for endangered species while managing resources for multiple stakeholders.

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Coastal dune ecology, geomorphology, and ecosystem services: How invasive beachgrasses, their interactions, and sediment dynamics shape U.S. Pacific Northwest dunes

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APPROVED:

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Chair of the Department of Integrative Biology

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Reuben Gabriel Biel, Author

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DEDICATION

Dedicated to my parents, Merrill Biel and Leslie Hahn, and my brother, Elie Biel.

Coastal Dune Ecology, Geomorphology, and Ecosystem Services: How Invasive
Beachgrasses, their Interactions, and Sediment Dynamics Shape U.S. Pacific Northwest
Dunes

1. Introduction

Drivers of global environmental change such as climate change and species invasions are dramatically disrupting ecosystems by causing changes to the distribution and abundance of species, to species interactions, and by creating novel ecological communities (e.g., Walther et al. 2002, Parmesan and Yohe 2003, Williams and Jackson 2007, Gilman et al. 2010, Chen et al. 2011). How invasive species will respond to climate change, though, is complex and difficult to predict (Dukes and Mooney 1999, Hellmann et al. 2008, Thuiller et al. 2008, Walther et al. 2009, Bradley et al. 2010), but may present both risks and opportunities for conservation, depending upon whether the changes increase (Stachowicz et al. 2002, Dukes et al. 2009) or decrease invasions (Bradley et al. 2009, Allen and Bradley 2016). As the rate of species invasions increases globally (MEA 2005), there is a growing need to understand how ecological and biophysical processes may alter invasion success under a changing climate, and to predict how species invasions and climate change may alter ecological communities and the ecosystem services that they provide.

Non-native species that physically modify their environment can be among the most successful invaders (Cuddington and Hastings 2004) and have some of the largest impacts on invaded ecosystems (Ehrenfeld 2010). Ecosystem engineers physically modify the abiotic state of an ecosystem, thereby altering resource availability and exposure to environmental conditions (Jones et al. 1997, Crain and Bertness 2006). As a result, these species and the changes they cause have the potential to not only harm native species that are maladapted to new abiotic conditions, but also increase the susceptibility of these systems to invasion by other non-native species (Simberloff and Von Holle 1999, Davis et al. 2000, Simberloff 2011).

Invasions by non-native ecosystem engineers are well documented in interface ecosystems at the land-sea margin (e.g., invasions by *Ammophila* spp., *Spartina* spp., and *Caulerpa taxifolia* in coastal dunes, salt marshes, or estuaries; Simberloff 2011). Because these systems face numerous abiotic stressors, including waves, wind, sedimentation, and salinity, many of these invaders modify exposure to environmental stressors, amplifying

exposure in some cases and moderating it in others (Bouma et al. 2009). Thus, it is important to determine which abiotic and biotic factors influence their distribution and abundance, to characterize how their abundance relates to ecosystem functions, and determine how they interact with both native and non-native species in their non-native range. Further, as climate change alters air temperatures, precipitation patterns, storminess patterns, and resource availability, the distribution and abundance of invaders and their impacts can shift.

To predict how biological invasions and climate change might alter ecological communities and ecosystem processes, it is important to examine how invasive ecosystem engineers influence, and are influenced by, numerous interrelated processes. Specifically, we need to consider the following questions: (1) What is the impact of invasive ecosystem engineers on their physical environment, and what processes and mechanisms cause these changes? (2) Will climate change alter the distribution and abundance of invasive species and thus their potential impact on ecosystem processes? (3) How might these invasions and their management alter the provisioning of ecosystem services for society?

Here I investigate the mechanisms by which two non-native invasive beachgrasses have bio-engineered United State Pacific Northwest coastal dunes. I further examine which factors have contributed to their invasion success, and whether sand burial and rising temperature from climate change might alter their distribution and abundance, and their interactions with other species. Finally, I assess how *Ammophila* management and removal has impacted the threatened western snowy plover (*Charadrius nivosus nivosus*), endemic plant species, and coastal vulnerability along Pacific Northwest dunes.

The United States Pacific Northwest dune ecosystem was historically sparsely vegetated, hummocky dune environment with numerous endemic grasses and forbs that grew on shifting sand and relatively mobile dunes (Cooper 1958, Wiedemann and Pickart 1996). However, the blowing sand from these shifting dunes endangered coastal infrastructure, leading coastal managers and communities to intentionally introduce two *Ammophila* beachgrass species (*Ammophila arenaria* from Europe and *Ammophila*

breviligulata from the Atlantic Coast and Great Lakes regions of North America) for dune stabilization in the early- to mid-20th century (Schwendiman 1977). The beachgrasses monopolized coastal dune habitats, forming tall, well-vegetated, and stable shore-parallel foredunes. Although the two beachgrass species are morphologically similar, they produce distinctly shaped foredunes: *Ammophila breviligulata*-dominant dunes are typically shorter and wider than their *A. arenaria*-dominant counterparts (Seabloom and Wiedemann 1994, Hacker et al. 2012, Zarnetske et al. 2015). These species-specific dune morphologies may arise from subtle differences in stem density and growth form between the two congeners that could alter patterns of sand accretion on foredunes (Hacker et al. 2012, Zarnetske et al. 2012). However, some differences in foredune morphology might also arise from spatially correlated gradients in sediment supply and beach characteristics that coincide with the respective ranges of the two congeners (Mull 2010, Hacker et al. 2012, Zarnetske et al. 2012, 2015). Specifically, *A. breviligulata* dominates in Washington and northern Oregon, where beaches are prograding (widening) as a result of the mobilization and onshore deposition of sand around the Columbia River (Kaminsky et al. 2010). Here, the majority of foredunes are shorter and wider. In contrast, *A. arenaria* dominates south of the northern Oregon coast, where shorelines are either stable or eroding as a result of lower sand supply to the beach. In these regions, foredunes tend to be taller and narrower. Given the covarying factors of vegetation differences and sand supply, it is important to understand the relative importance of both factors to foredune morphology and coastal protection.

After their initial introduction, the two *Ammophila* species had remarkable invasion success, spreading to all dune communities within the Pacific Northwest. We know from many studies of invasive species that their success depends upon a combination of propagule pressure, life history characteristics of the invading species, and the capacity for the invaded community to resist the invasion. Although the intentional planting of the beachgrasses aided in overcoming the geographic barriers imposed by coastal headlands and currents, the two *Ammophila* species have subsequently spread unassisted through the region, displacing numerous endemic plants (e.g., the American dune grass

Elymus mollis and the pink sand verbena *Abronia umbellata*) and animals (e.g., the western snowy plover *Charadrius nivosus nivosus*). Presently, *A. arenaria* has spread to dunes from Los Angeles, California (34°N) to the Queen Charlotte Islands, British Columbia (54°N) (Green 1965, Breckon and Barbour 1974, Wiedemann and Pickart 2008) and *A. breviligulata* from Pacific City, OR (45°N) to Vancouver Island, British Columbia (49°N). As *A. breviligulata* continues to expand its range both northward and southward (Hacker et al. 2012), understanding which factors contribute to its success and spread is essential for managing this ongoing invasion.

As mentioned previously, within the Pacific Northwest, the two *Ammophila* species also exhibit distinct patterns of distribution and abundance: *A. breviligulata* is dominant in northern Oregon and southwest Washington, whereas *A. arenaria* is dominant in central and southwest Oregon. These distributions have arisen because of historical planting patterns and, more recently, competitive interactions between the *Ammophila* congeners, where the competitively dominant *A. breviligulata* is displacing *A. arenaria* and further reducing native species richness as it expands its range (Hacker et al. 2012, Zarnetske et al. 2013, David et al. 2015, 2016). However, based on the thermal tolerances of the two species in their native ranges, *A. breviligulata* may be more sensitive to high temperature conditions than *A. arenaria* (Seneca and Cooper 1971, Huiskes 1979, Emery and Rudgers 2013). As *A. breviligulata* spreads both northward and southward to new locations, rising temperatures might influence the productivity and species interactions of both *Ammophila* species. Because the *Ammophila* congeners differ in their effect on dune geomorphology and native plant diversity, changes to the distribution, abundance, or dominance of either species could significantly influence dune ecosystem processes and services.

Finally, management of the two *Ammophila* species poses challenges because the invasion has led to the decline in numerous endemic dune plants and animals (Wiedemann and Pickart 1996), but also has resulted in valuable sand stabilization, erosion control, and coastal protection ecosystem services. For example, the Pacific Coast population of the western snowy plover nests in open-sand habitat along coastal dunes.

When the two *Ammophila* species started to dominate, they eliminated nearly all the plover nesting habitat, leading to a rapid decline in plover populations. Since the early 1990s when the plover was federally listed as threatened (USFWS 1993), numerous federal and state agencies began restoring plover nesting habitat, which included removal of beachgrasses (USFWS 2007, Zarnetske et al. 2010). Because beachgrass and foredune removal results in shorter foredunes, restoration of plover nesting habitat has the potential to increase coastal exposure to flooding and erosion hazards. Thus, invasive species management must contend with tradeoffs in ecosystem services that may create hurdles to dune habitat restoration.

In Chapter 2, I investigate how the invasive beachgrasses, beach geomorphology, and sand supply interact to shape foredunes along the Pacific Northwest coast. Using Gaussian Bayesian network analyses, I determine how vegetation characteristics, beach characteristics, and sediment supply directly and indirectly relate, and quantify their relative importance for explaining variation in foredune shape and rates of sand accretion across the foredune. Through this work, I show that while beach morphology and sediment supply are the primary determinants of foredune height, beachgrass density does explain a substantial amount of variation and is positively associated with steeper and taller foredunes. Additional analyses demonstrate that density alone does not explain species-specific differences in foredune morphology and sand accretion; rather, distinct growth forms and rates of lateral propagation explain why *A. breviligulata* foredunes are shorter and wider than their *A. arenaria* counterparts. Overall, this analysis indicates that sediment supply and beach morphology are the predominant controls of foredune morphology in the Pacific Northwest, but that beachgrass density and growth form also significantly alter patterns of foredune development.

In Chapter 3, I examine both the invasiveness of three dune grass species and the invasibility of foredune communities across a gradient of sand deposition along the US Pacific Northwest coast using field reciprocal invasion trials. The results of this experiment show that the two non-native beachgrasses, *Ammophila breviligulata* and *A. arenaria* colonists exhibit higher survival and growth than the native dune grass *Elymus*

mollis colonists, and that the *Ammophila* foredune communities are less invasible than *E. mollis* communities to invasion. However, differences in invasibility are not primarily due to negative interactions by the competitive dominant *A. breviligulata*; rather, *E. mollis* appears to have facilitated invasion by increasing the survival and growth of colonizing plants. This study illustrates the value of concurrently considering species invasiveness and community invasibility for understanding determinants of invasion success.

In Chapter 4, I explore how rising temperatures might alter the survival, growth, and biotic interactions of *A. arenaria* and *A. breviligulata* along the US Pacific Northwest coast. Using a split-split-plot common garden experiment, I subject *A. arenaria* and *A. breviligulata* plants to varying levels of heat, sand burial, and initial densities of *A. arenaria* and *A. breviligulata*. I then assess whether temperature and sand burial alter the growth response of each species and its interactions with its congener. This experiment shows *Ammophila breviligulata* to be less tolerant of elevated temperatures than *A. arenaria*, but the observed differences are generally small. High rates of sand burial also reduce biomass production and tiller production in *A. breviligulata*, with few reductions in *A. arenaria* productivity. Nevertheless, under all combinations of temperature and sand burial, *A. breviligulata* exerts a comparatively strong negative effect on *A. arenaria* tiller and biomass production, while *A. arenaria* exerts a weaker negative effect on *A. breviligulata* on those same measures. Based on this experiment, *A. breviligulata* would still be predicted to exclude *A. arenaria* under most circumstances, but elevated temperatures and high rates of sand burial would increase the likelihood of coexistence between the two grass species. These results further illustrate how climate change alters the biotic interactions of invasive species, their distribution and abundance, and consequently their impact on biological communities.

In Chapter 5, I assess tradeoffs in coastal foredune ecosystem services that arise from the beachgrass invasions, from invasive species and conservation management, and from spatial variation nearshore geomorphology. Using surveys of foredune community composition, foredune topography, and western snowy plover nest monitoring datasets,

in combination with XBeach, a process-based numerical model for assessing coastal hazard exposure, I measure variations in coastal protection, western snowy plover conservation, and endemic plant conservation ecosystem services at seven coastal dune habitat restoration areas and nearby non-restored areas. I demonstrate that western snowy plover conservation and coastal protection ecosystem services exhibit tradeoffs, but the magnitude of their tradeoff are context-dependent. While the ecosystem services are collectively influenced by the invasive beachgrasses and the foredunes they create, both nearshore geomorphology and changes in foredune shape because of restoration can amplify or diminish ecosystem service tradeoffs. I discuss how tradeoffs among ecosystem services can be reduced by incorporating context dependent analyses in coastal management planning.

Overall, my dissertation explores several components of environmental change and their effects on coastal dune ecosystems and the services that they provide. This work not only elucidates how beachgrasses invade, interact, and build foredunes, it provides further insights into how these species might respond to climate change and their contributions to dune ecosystem services. More broadly, this collection of studies illustrates the value of integrating techniques across disciplines for managing the various aspects of coastal ecosystems. Through use of observational surveys, manipulative experiments, and statistical and numerical models, scientists and managers can holistically approach biological invasions and their potential responses to a changing climate.

2. Coastal foredune ecomorphodynamics in the US Pacific Northwest: the influence of sand supply, beach type, and invasive beachgrasses

Reuben G. Biel, Sally D. Hacker, and Peter Ruggiero

Abstract

As sea-level rise and changing storminess threaten coastal communities and infrastructure, sandy beaches and dunes are increasingly relied upon to provide erosion control, flood protection, and many other ecosystem services. The capacity for foredunes to provide protection depends on their geometry, which is determined by interactions between sediment supply, beach characteristics, and vegetation. While relationships between sediment supply, beach type, and foredune morphology are well-described in the literature, until recently few studies have examined vegetation controls on foredunes. Here we examine how sediment supply, beach characteristics, and two species of beachgrass (*Ammophila arenaria* and *A. breviligulata*) alter foredune morphology and patterns of sand accretion on U.S. Pacific Northwest foredunes using Gaussian Bayesian network analyses. We show that both rates of shoreline change (i.e., beach sediment supply) and beach type primarily determine foredune morphology. Beachgrass density also significantly influences foredune geometry, but its effects differ among species: increasing density of *A. arenaria* was associated with taller, steeper sloping dunes, whereas increasing density of *A. breviligulata* was associated with shorter, more shallow sloping dunes. When examining sand accretion patterns over a two-year period on the foredune, sand accretion was most strongly influenced by species-specific patterns of vegetation growth and beach type. Based on these results, we argue that species-specific differences in grass growth form produced distinct patterns of sand deposition on foredunes. Specifically, *A. breviligulata* exhibited greater lateral growth, resulting in greater sand accretion at the seaward margin of the foredune. In contrast, *A. arenaria* exhibited little lateral growth, resulting in comparatively more sand accretion near the foredune crest. Consequently, growth form-generated sand accretion patterns resulted in tall, narrow *A. arenaria*-dominated foredunes and shorter, wider *A. breviligulata*-dominated foredunes. These results illustrate that vegetation density and patterns of growth appreciably influence foredune morphology and rates of sand accretion, and can thus alter coastal resilience to storms and sea-level rise.

2.1. Introduction

In recent decades, increasing coastal development, extreme oceanic storms, and sea level rise have caused unprecedented and growing property damage (Pielke et al. 2008, IPCC 2014). Thus, there is growing interest in reducing hazard exposure with coastal protection structures. Although we have significant experience using engineered structures (e.g., seawalls, revetments, groins) and know their capacity to provide protection, they can also present numerous geomorphological, ecological, and economic problems (van Slobbe et al. 2013, Sutton-Grier et al. 2015). Natural infrastructure of beaches and dunes may provide an alternative source of protection (Barbier et al. 2011, Spalding et al. 2014). However, to reliably use natural infrastructure for coastal protection, more information is needed about the level of protection provided by these features, their spatiotemporal variation in protection, and their recovery and long-term resilience following storms (Sutton-Grier et al. 2015).

Sandy beaches and dunes represent one of the most important ecosystems for regulating coastal hazard exposure, and also provide many ecosystem services (Everard et al. 2010, Barbier et al. 2011). As waves propagate towards shore, the shoreface, beach, and foredunes attenuate wave energy as waves shoal, break, runup the beach face, and possibly collide or overtop the foredune. These morphological features significantly alter the magnitude of wave attenuation, where shallow sloped (i.e., dissipative (Wright and Short 1984)) beaches provide greater incident wave energy dissipation than more steeply sloped beaches (Stockdon et al. 2006). Foredunes serve as a further impediment to inundation by providing a barrier to wave attack and by supplying sediment, via dune erosion, to beaches during storms (Kriebel and Dean 1985, Morton 2002). Because the severity of flooding and erosion during storm events depends upon the intensity and the duration of wave impact on beaches and foredunes (Larson et al. 2004), coastal hazard exposure is driven by a combination of storm wave characteristics, beach slope, foredune width, and foredune height (Sallenger 2000, Morton 2002, Plant and Stockdon 2012). While regional climate determines storm wave characteristics and is beyond local control, beach slope, foredune width, and foredune height vary spatiotemporally (Ruggiero et al.

2005, Mull and Ruggiero 2014). Modifying the geometry of these features may provide communities and coastal managers with management opportunities for mitigating coastal hazard exposure (Nordstrom et al. 2012, Williams et al. 2016).

To employ foredunes as a coastal defense tactic, we must understand how geomorphology and ecology interact to alter foredune development and post-storm recovery. Although dune vegetation is recognized to alter patterns of aeolian sand deposition on foredunes and influence foredune formation, shape, and stability (Hesp 1989, 2002, Hacker et al. 2012, Zarnetske et al. 2012, 2015, Durán and Moore 2013), most geomorphological research focuses on sediment supply, sediment characteristics, and wind as determinants of foredune geomorphology. Based on empirical observations and conceptual models, dissipative beaches with wide fetches provide greater sand supplies to foredunes than narrow, reflective beaches, given a similar wind climate. Beach dissipativity, in turn, results from interactions between sediment grain size distributions and the wave climate, whereby dissipative beaches typically exhibit fine grained sediments and persistently high wave energy (Wright and Short 1984). Consequently, this combination of small sediment grain sizes and wide fetches on dissipative beach types may promote the formation of large foredunes through heightened aeolian sand transport (Short and Hesp 1982, Saye et al. 2005, Houser et al. 2008, Houser and Mathew 2011).

Beach-dune sediment budgets and rates of shoreline change may also alter foredune morphology. We define beach and dune sediment budgets as the net sediment surplus or deficit on beaches and on dunes, respectively, per unit area and time. Progradation (seaward expansion of the shoreline) results from positive beach sediment budgets and often produces dune fields that consist of a series of short active and relict dunes. However, due to the rapid rate of dune ridge formation, prograding shorelines are associated with short foredunes, despite positive dune sediment budgets. In contrast, neutral or slightly retreating shorelines with neutral or slightly negative beach sediment budgets are associated with taller foredune (Psuty 1988, Moore et al. 2016, Ruggiero et

al. 2016). In general, beach morphology, wind regime, and sediment supply are considered the primary determinants of foredune shape.

The influence of vegetation on foredune morphology, though, remains relatively understudied. Vegetation density, height, and growth form are associated with different dune forms: low or patchy plant density often produces local variations in airflow and sediment deposition, leading to the formation of dunelets or hummocks. In contrast, dense, tall vegetation produces more uniform sediment deposition, leading to the formation of continuous, linear foredunes (Hesp 1989, 2002). Moreover, based on models and small-scale experiments, as plant height and density increases, foredune height increases and foredune width decreases (Hesp 1989, Van Dijk et al. 1999). While several studies have examined the role of vegetation in foredune evolution using mathematical models (e.g., Van Dijk et al. 1999, Durán and Moore 2013, Moore et al. 2016, Goldstein et al. 2017) and wind tunnel experiments (Zarnetske et al. 2012), field studies that link vegetation morphology and density to foredune morphology and evolution are rare (Hesp 1989, Hacker et al. 2012). Moreover, few have examined the relative importance of geomorphological and ecological drivers for controlling foredune morphology (e.g., Zarnetske et al. 2015).

To explore the relative roles of geomorphological drivers and vegetation species identity and morphology for influencing foredune geomorphology and evolution, we examined ecological and geomorphological spatiotemporal variability in U.S. Pacific Northwest coastal dunes. The Pacific Northwest exhibits a variety of beach types that range from highly dissipative to intermediate-reflective and consist of fine- to coarse-grained sand (Shih and Komar 1994, Ruggiero et al. 2005, Mull and Ruggiero 2014, Di Leonardo and Ruggiero 2015). In addition, the region exhibits a range of shoreline change rates (SCR) due to differences in spatial variation in beach sediment budgets, where some areas produce multidecadal progradation rates in excess of 3 m/yr, while others produce shoreline retreat of up to 0.5 m/yr. (Buijsman et al. 2003, Ruggiero et al. 2013). Consequently, the region exhibits substantial variations in numerous

geomorphological drivers of foredune morphology, including shoreface slope, beach slope, median grain size, and beach sediment budgets.

In addition, the Pacific Northwest dune system is dominated by two species of invasive beachgrasses, *Ammophila arenaria* (L.) Link, and *A. breviligulata* Fernald. Since their introduction in the early 20th century, the two species have spread and monopolized foredunes along the entire Pacific coast and formed dense monocultures on the foredune face and crest (Wiedemann and Pickart 1996, Hacker et al. 2012). However, *A. arenaria* and *A. breviligulata* are implicated in producing unique dune morphotypes due to differences in the morphology and growth form of each species, such that *A. arenaria*-dominated foredunes are often taller and narrower than their *A. breviligulata*-dominated counterparts (Hacker et al. 2012, Zarnetske et al. 2012, 2015). These differences are the result of morphological and growth form differences between the two species. *Ammophila arenaria* has thin but dense stems (known as tillers) that form tussocks and are efficient at sand capture. In contrast, *A. breviligulata* has more robust stems but they are more sparsely distributed and thus capture less sand per given area. Nevertheless, spatially-correlated geomorphological and ecological drivers of foredune morphology have confounded rigorous analyses of the relationship between beachgrass species identity and foredune morphology (Hacker et al. 2012).

Here we build on previous research by disentangling the relative effects of beach and dune geomorphology and beachgrasses using Bayesian network (BN) analyses. A BN is a probabilistic graphical model that describes how variables within a multivariate system relate to one another, using a directed acyclic graph (DAG). BNs have been used to represent wave dynamics, coastal vulnerability, and foredune response to storms (Gutierrez et al. 2011, Plant and Stockdon 2012, Plant et al. 2014), and to synthesize information from disparate data sources (Borsuk et al. 2004). For example, Plant and Stockdon (2012) used a BN to predict barrier island responses to hurricanes, by parameterizing Sallenger's (2000) Storm Impact Scaling model with existing datasets.

We used BN analyses to explore two aspects of foredune ecomorphodynamics: first, we determined the relative contributions of sediment supply, shoreface and beach

morphology, and vegetation species identity and density for influencing foredune morphology; second, we determined how these same variables influence rates of vertical sand accretion across the foredune face to look more closely at the role of the two beachgrass species in shaping foredune features. We hypothesized that (1) backshore slope, SCR (as a proxy for beach sediment budget), and beachgrass density would directly relate to foredune height and rates of vertical sand accretion. If patterns described by Short and Hesp (1982) hold, then shallow-sloping beaches should be positively associated with both foredune height and rates of vertical accretion. In contrast, SCR may disparately influence foredune morphology and sand accretion: while progradational shorelines may accelerate sand accretion because of positive beach and dune sediment budgets, it may also be associated with shorter foredunes from rapid development of multiple foredune ridges. Finally, based on wind tunnel experiments, field experiments, and numerical models (Hesp 1989, Van Dijk et al. 1999, Zarnetske et al. 2012), we further hypothesize (2) that increasing beachgrass stem density will be associated with taller and narrower foredunes, (3) that inclusion of species-specific stem density variables will improve the accuracy and precision of the BN for predicting foredune morphology, and (4) that *A. breviligulata* stem density will be more positively associated with foredune height than *A. arenaria* stem density due to species-specific differences in stem morphology.

To test these four hypotheses, we examined coastal foredune ecomorphodynamics through machine learning and parameterization of two sets of Gaussian Bayesian network (GBN) analyses. First, we explored how SCR, shoreface and beach morphology, sediment characteristics, and mean beachgrass stem density on the foredune face are associated with foredune morphological structure. Second, we explored how SCR, shoreface and beach morphology, sediment characteristics, and the distribution and abundance of beachgrasses along the foredune face relate to patterns of sand accretion on the foredune face over time.

2.2. Methods and analyses

2.2.1. Study sites, beach and foredune geomorphology, and vegetation surveys

To measure foredune geomorphology and vegetation abundance, we conducted dune surveys in the summers of 2012 and 2014 at 20 sites spanning 500 km along the Oregon and southwest Washington coastlines, USA (Figure 2.1, Appendix A, Table A1). Seventeen of the 20 sites were used in our previous dune research (Hacker et al. 2012). The sites are located within 11 distinct littoral or sublittoral cells, or areas along the coast containing the same sediment sources, transport pathways, and sinks (Inman and Frautschy 1965), and thus differ in sand supply and beach and dune geomorphology (e.g., Peterson et al. 1994).

Among the 20 sites, we established 233 shore-normal transects at 80 transect locations (3 transects per location, and 2-10 transect locations per site; see Appendix A, Table A1) and conducted topographic surveys to determine the elevation between the waterline and foredune heel (d_h) using network real time kinematic differential GPS (network RTK DGPS) (Figure 2.2). Using methods described in Chapter 5, we then measured latitude, longitude, and elevation at 20 cm intervals along each of the 233 transects at sub-decimeter accuracy (Ruggiero et al. 2005). Using the surveys, along with the methods of Mull and Ruggiero (2014), we measured the position of the shoreline (defined as Mean High Water (MHW), which is approximately 0.9-1.0 m above Local Mean Sea Level (LMSL) at these locations) and the position and elevation of several metrics of foredune morphology (foredune defined as the seaward-most shore-parallel sand ridge, whose landward extent is delimited by a 0.6 m or greater elevation drop relative to the maximum elevation of the foredune (Cooper 1958, Mull and Ruggiero 2014)). Foredune measurements included the foredune toe position (d_t = the seaward-extent of the foredune) and elevation, the 4m contour position, and the foredune crest position (d_c = the highest elevation location of the foredune) and elevation (Figure 2.2). From these metrics, we determined backshore slope (slope between MHW and 4m contour cross-shore locations), foredune face slope (d_{face} slope; slope between 4m contour and d_c locations), and foredune face width (d_{face} width; horizontal distance between the

4m contour and d_c locations) along each cross-shore transect. The 4m contour provided a consistent approximation of the foredune toe position, enabling direct comparison of backshore slope, d_{face} slope, and d_{face} width among transects. We also determined shoreface slope (defined as the slope between 10 and 15 m below LMSL) by extracting bathymetry along each transect from NOAA tsunami inundation DEM datasets (Carignan et al. 2009a, 2009b, 2009c, Love, M.R. et al. 2012), fitting an exponential beach profile (Bodge 1992), and calculating the slope between the 10 m and 15 m isobaths using the resulting fit. All morphometric data were converted to a LMSL vertical datum using VDatum v3.3 prior to analysis.

For each transect, we further characterized sediment supply, sediment characteristics, and vegetation density. We obtained multi-decadal end point shoreline change rates (SCR) from Ruggiero et al. (2013) for each transect location, where SCR represents an annualized rate of shoreline change between 1967-2002 in Oregon and 1986-2002 in southwest Washington. To characterize sediments, we collected sediment samples at the seaward most vegetation line in 2012 for each cross-shore transect and determined mean sediment grain size via sieving at half phi resolution. To characterize dune vegetation, we further conducted georeferenced vegetation surveys along each along each of the 233 transects in 2012, measuring the abundance of all plant species within 0.25 m² quadrats at 5 m intervals along the transect line as described in Hacker et al. (2012) and Chapter 5. From these surveys, we calculated mean beachgrass density (beachgrass tillers per m²) within quadrats for both *Ammophila* species along the foredune face (d_{face} ; between the 4m contour and d_c).

Finally, in 2014, we resurveyed topography and vegetation along 70 transects at 70 of the 80 locations that were surveyed in 2012 (1 transects per location, and 2-10 transect locations per site; see Appendix A, Table A1). From these data, we determined the changes in beachgrass density and elevation change for each georeferenced quadrat location between 2012 and 2014. Of the 320 quadrat locations on the foredune face that were surveyed in both 2012 and 2014, 273 locations (85%) exhibited positive elevation

change, indicating accretion of sand. All analyses were performed in ArcGIS v10.3.1, R v.3.2.2 (R Core Team 2015), and Matlab R2015b.

2.2.2. Bayesian network analysis

We used Gaussian Bayesian network (GBN) analyses to investigate the relationships between geomorphological drivers, ecological drivers, and foredune shape. Bayesian networks are probabilistic graphical models that describe direct relationships among a network of variables using directed acyclic graphs (DAG). GBNs are a subcategory of Bayesian networks that assumes that the joint probability distribution of all random variables follows a multivariate Gaussian distribution, and that the conditional probability density function for each variable (node) correspondingly follows a univariate Gaussian distribution, given its parent variables.

More generally, BNs are characterized by both structure learning and parameter learning components. In the structure learning component, all dependent, independent, and conditionally independent relationships are identified within the multivariate system and depicted using a DAG. In a DAG, variables (nodes) are represented by circles (Figure 2.3), while direct dependent relationships between parent and daughter random variables are denoted by arrows (edges). Upon identifying the BN structure, the model is parameterized by calculating the probabilistic relationship among all variables in the system. By using the dependence structure specified in the BN, we can then calculate the joint probability distribution of the entire BN and conditional probability distributions for each node within the BN.

2.2.2.1. GBN models of foredune morphology

To assess how shoreface and beach morphology and beachgrass density relate to foredune morphology, we created a GBN (named Foredune Morphology-GBN_{combined}) to relate nodes of shoreface and beach morphometrics (shoreface slope, SCR, and backshore slope), sediment characteristics (median sediment grain size), and vegetation (mean beachgrass density on d_{face}) to foredune morphometrics (d_t elevation, d_c elevation, d_{face} slope, and d_{face} width; Figure 2.3A). To meet distributional assumptions, we transformed

the variables in the GBN using log and box-cox transformations, as necessary (Appendix A, Table A2).

To identify direct relationships among these variables (i.e., structure learning), we used a combination of expert knowledge and machine learning to identify an optimal network structure. Previous knowledge was incorporated into the GBN by prohibiting direct relationships (edges) between variables that we considered unlikely, given our understanding of the system. In addition, blacklisting of edges ensured that specific target nodes for prediction (e.g., d_c , d_t metrics) were daughter nodes (Appendix A, Table A3). For example, we hypothesize that SCR is directly related to d_c elevation. This direct relationship could be represented within a GBN as ($SCR \rightarrow d_c$ elevation) or as (d_c elevation \rightarrow SCR). Given our understanding of the cause-effect relationship between SCR and d_c elevation and our intent to predict d_c elevation, we prohibited (d_c elevation \rightarrow SCR) as a possible direct relationship.

In combination with user knowledge (blacklisted edges), we employed a hill climb machine learning algorithm to identify the best supported DAG structure, given the observed dataset. We generated 100 random initial DAGs and implemented the search algorithm, which iteratively added, removed, or reversed edges (excluding blacklisted edges) within each DAG. With each iteration, we then used a Bayesian Gaussian equivalent uniform score (BGe) to assess whether these changes increased the probability of the GBN posterior distribution, given the observed dataset. Iterative modification of edges allowed for identification of 100 GBNs with local BGe score minima. To identify the globally optimal GBN, we performed model averaging to compute the average network structure (Scutari and Denis 2014). GBN modeling was performed using bnlearn (Scutari and Denis 2014) in R v3.22 (R Core Team 2015).

To further examine whether the two species of beachgrass were associated with distinct foredune morphologies, we created a second GBN (named Foredune Morphology-GBN_{species}) that separated mean beachgrass density into its component species, *A. arenaria* and *A. breviligulata*, and defined a parent indicator variable to categorize the dominant species along each transect (Figure 2.3B). Structure learning was

performed using the methods described above (for blacklisted edges, see Appendix A, Table A3). Upon identification of the optimal Foredune Morphology-GBN_{combined} and Foredune Morphology-GBN_{species} network structures, parametric relationships between nodes were estimated from each respective dataset.

2.2.2.2. *GBN models of sand accretion*

To explore how beach sediment supply, shoreface and beach morphology, and beachgrass density alter rates of sand accretion and erosion along d_{face} , we implemented two additional GBNs to relate changes in beachgrass density to elevation change along d_{face} quadrats over time. Using data from 320 quadrats located along the d_{face} of 70 transects that were sampled in both 2012 and 2014, we identified relationships between measures of beach sediment supply, beach morphology, vegetation density and growth patterns, and changes in elevation. The modeled variables were shoreline change rate, shoreface slope, beach slope, mean sediment grain size, quadrat elevation in 2012, quadrat log(beachgrass density) in 2012, log(beachgrass density) in directly adjacent quadrats (5m landward and seaward), and changes in both log(beachgrass density) and foredune elevation between 2012 and 2014 (Accretion-GBN_{combined}; Figure 2.4A, Appendix A, Table A4). To further examine possible impacts of beachgrass species identity, we separated all beachgrass variables into their respective species, and defined a parent indicator variable to categorize the dominant species within the transect (Accretion-GBN_{species}; Figure 2.4B). For both the Accretion-GBN_{combined} and Accretion-GBN_{species} networks, we prohibited edges based on user knowledge (Appendix A, Table A5), generated 100 random initial DAGs, and implemented a hill climb search algorithm to identify locally optimal network structures. As described previously, we then performed model averaging to identify the globally optimal network structure for the two sand accretion GBNs. Upon identification of the optimal GBN structures, parametric relationships between nodes were estimated from each respective dataset.

2.2.3. Bayesian network performance evaluation

BNs use a Bayesian approach for predicting outcomes and their associated uncertainty, based on Bayes Theorem:

$$\text{Posterior distribution} \propto \text{Likelihood} \times \text{Prior distribution} \quad (\text{Eqn. 2.1})$$

where the likelihood associated with each BN node is the relative likelihood of observing any condition in the sample space; the prior distribution represents one's knowledge or belief about the sample space; and the posterior is the probability density function for observing a condition in the sample space, after accounting for prior system knowledge. Based on this framework, BNs allow input of user knowledge through two avenues: first, through the specification of network structure as previously described; second, by combining known information about a system (via constraints on the priors) with empirical data (likelihood function) to predict both the expected outcome and uncertainty associated with a target node (posterior distribution). Using the Foredune Morphology-GBN_{combined} as an example, if we wish to predict d_c elevation given a known SCR, we can constrain the prior distribution to reflect our belief and then determine the posterior Gaussian distribution of d_c elevation based on data (Appendix A, Figure A1). This process of updating the posterior distribution based on prior knowledge is useful for prediction, for evaluation of model performance, and for evaluation of the relative importance of nodes within a model.

To assess the prediction skills of each GBN, we determined pseudo- R^2 , root-mean-square error (RMSE), and log-likelihood ratio (LLR) between observed and predicted values of target nodes, based on different combinations of updated (prior) knowledge. Pseudo- R^2 , RMSE, and LLR values were determined by comparing GBN predictions of target variables (e.g., d_c elevation, d_t elevation, d_{face} width, d_{face} slope) with observed data and are both measures of GBN prediction accuracy and precision. Pseudo- R^2 values were calculated as,

$$R^2 = 1 - \frac{\sum_{i=1}^N (y_i - \hat{y}_i)^2}{\sum_{i=1}^N (y_i - \bar{y})^2} \quad (\text{Eqn. 2.2})$$

where N is the number of observations in the model, y is the target variable, y_i is the i^{th} observation of y , \bar{y} is the mean of all y_i , and \hat{y}_i is the value predicted by the GBN for the i^{th} observation. Higher pseudo- R^2 values indicate better goodness-of-fit.

The log-likelihood ratio was calculated as the difference in the log likelihood of observations under an informed prior distribution relative to an uninformed (uniform) prior distribution,

$$LLR = \sum_{i=1}^N \loglik(obs_i \sim N(\mu_i^{post}, v_i^{post})) - \sum_{i=1}^N \loglik(obs_i \sim N(\mu_i^{prior}, v_i^{prior})) \quad (\text{Eqn. 2.3})$$

where the prior and posterior distributions for the target node were determined by inclusion or exclusion of updated knowledge, respectively (Eqn. 2.3; Gutierrez et al. 2011). A positive LLR value would indicate that observations were more likely under the posterior distribution than the prior distribution. Positive LRR values could arise from either a shift in the maximum likelihood value of the posterior distribution (i.e., increased model accuracy) or from a reduction in the posterior distributions standard deviation (i.e., increased model precision) (Appendix A, Figure A1).

For the foredune morphology GBNs, we calculated pseudo- R^2 , RMSE, and LRR skill metrics for predicting foredune morphometrics (d_i elevation, d_c elevation, d_{face} slope, and d_{face} width) based on different combinations of updated (prior) knowledge for non-foredune morphology nodes. For the sand accretion GBNs, we calculated skill metrics for predicting the change in elevation using combinations of updated knowledge for all other nodes. To do this, we predicted foredune morphology metrics and elevation change with no updated knowledge (null model), updated knowledge of one node, updated knowledge of all but one node, and full knowledge of all parent nodes (full model) using observed data. LLR metrics were calculated by comparing GBN predictions with updated knowledge of one node (posterior) to those of the null model (prior), and by comparing GBN predictions of the full model (posterior) to those of a model with updated knowledge of all but one node (prior). Thus, LLR metrics indicated the relative improvement in model accuracy and precision due to the inclusion of prior knowledge of a single node in an uninformed GBN, and the relative loss in model accuracy and

precision due to the loss of prior knowledge of a single node in a well-informed GBN, respectively. Thus, LLR metrics based on changes in prior knowledge provided a measure of the importance of each parent node for predicting foredune morphology metrics and change in elevation.

2.3. Results

2.3.1. Gaussian Bayesian networks for foredune morphology

2.3.1.1. Sample space and likelihood functions

The likelihood function for each node of the foredune morphology GBNs illustrate the diverse ecological and geomorphological conditions that our dune dataset encompassed (Appendix A, Figure A2). For example, shoreline change rate (SCR) varied from -1.6 to 9.2 m/yr. (median: 0.7 m/yr.), indicating that our dataset covered both rapidly accreting and modestly eroding portions of the coast. Similar variation exists in other variables: shoreface slope varied from 0.003 m/m to 0.018 m/m (median: 0.011 m/m); backshore slope varied from 0.01 m/m to 0.16 m/m (median: 0.04 m/m), representing both dissipative and reflective beach types (Wright and Short 1984); mean sediment diameter ranged from 0.11 mm to 0.31 mm (median: 0.18 mm); beachgrass densities between 0 and 516 tillers/m² (median: 74 tillers/m²); d_{face} slope varied between 0.05 m/m and 1.57 m/m (median: 0.40 m/m), d_{face} width between 3.2 m and 107.7 m (median: 15.7 m); d_t elevation ranged from 3.0 m to 10.9 m above LMSL; and d_c elevation ranges between 5.2 and 18.1 m above LMSL (median: 9.6 m).

2.3.1.2. Skill assessments for foredune morphology GBNs

Comparison of skills assessments (i.e., MSE, LLR, and pseudo-R²) for the two foredune morphology GBNs showed that *Ammophila arenaria* and *A. breviligulata* exert distinct effects on foredune morphology. The GBN that distinguished between *A. arenaria* and *A. breviligulata* (Foredune Morphology-GBN_{species}; Figure 2.3B) exhibited moderately higher prediction skill for the four foredune morphometrics than did the GBN that combined both beachgrass species (Foredune Morphology-GBN_{combined}; Figure 2.3A, Table 2.1). Consequently, GBN_{species} provided some improvement for predicting foredune

morphology, with greatest improvement in prediction of d_{face} width and d_{face} slope. Because the prediction skill of the Foredune Morphology-GBN_{species} exceeded that of Foredune Morphology-GBN_{combined}, we concluded that the two species of beachgrass produce distinct foredune morphologies.

When exploring the relative importance of variables for predicting foredune morphometrics, prior knowledge of backshore slope, SCR, and beachgrass density acted as the strongest predictors of d_c elevation at these sites. When provided with prior knowledge for all predictors, the Foredune Morphology-GBN_{species} exhibited an LLR value of 58.9 for the d_c elevation node relative to a model with no prior knowledge. Using prior knowledge of a single predictor (Table 2.2, Figure 2.5) and prior knowledge of all but one predictor (Table 2.3), we found that backshore slope, SCR, and beachgrass density increased the LLR of the d_c elevation node by 34.6-42.5, 0.6-16.3, 5.1-8.6, respectively. Foredune face slope (d_{face} slope) exhibited a LLR value of 37.1 when the Foredune Morphology-GBN_{species} was provided with full prior knowledge. Among the predictor variables, d_{face} slope was best predicted by prior knowledge of a combination of dominant beachgrass species and *Ammophila* species density (LLR: 21.3-29.4), as well as backshore slope (LLR: 8.1-22.4). In contrast, SCR and shoreface slope were less important predictors of d_{face} slope variation. Finally, the dominant beachgrass species and *Ammophila* species density increased the LLR of d_{face} width and d_t elevation by 13.0 and 6.3-14.8, respectively, but other predictors provided little additional improvement in prediction accuracy and precision.

2.3.1.3. Geomorphological determinants of foredune morphology

Backshore slope and SCR are strongly associated with variation in d_c elevation and d_{face} slope. SCR exhibited both direct and indirect interactions with multiple metrics of shoreface, beach, and foredune morphology (Figure 2.3A). Through direct and indirect interactions, SCR was positively associated with foredune face width, and negatively associated with backshore slope, d_t elevation and d_c elevation. Backshore slope was similarly directly positively related to both d_{face} slope and d_c elevation, and negatively associated with d_t elevation. Together, these results suggest that locations with high SCR

exhibit shallow-sloped (i.e., dissipative) shoreface and backshore zones and foredunes that are shallow-sloping and short. In contrast, locations with low SCR exhibit steeper-sloped shoreface and backshore zones, with steeper and taller foredunes.

2.3.1.4. Ecological determinants of foredune morphology

Beachgrass density similarly influenced each of the four foredune morphometrics included in the two GBNs. When *Ammophila* species were pooled into a single random variable (Foredune Morphology-GBN_{combined}; Figure 2.3A), beachgrass density was directly related to d_{face} slope and indirectly related to d_c elevation. This pattern suggests that as beachgrass density increases, foredunes become steeper and taller. When considered separately (Foredune Morphology-GBN_{species}; Figure 2.3B), *A. breviligulata* density exhibited a positive direct relationship with d_{face} width, a negative indirect relationship with d_{face} slope, and both positive and negative indirect relationships with d_c elevation. In contrast, *A. arenaria* density exhibited a positive direct relationship with d_{face} slope and both a negative direct and positive indirect relationship with d_c elevation. This pattern suggests that as *A. breviligulata* density increases, the foredune face becomes wider, more shallow sloping, and taller; for *A. arenaria*, as density increases, the foredune becomes steeper and taller.

2.3.2. Gaussian Bayesian networks for sand accretion

2.3.2.1. Sample space and likelihood functions

Similar to the foredune analysis above, the sand accretion GBNs (Accretion-GBN) encompassed varied ecological and geomorphological conditions (Appendix A, Figure A3). However, the sand accretion dataset differed from the foredune morphology in two key respects: first, the accretion dataset encompassed a subset of transects because not all transects were resampled in 2014; second, the morphology dataset focused solely on transect-scale variables (e.g., mean beachgrass density for the transect) while the accretion dataset focused on both transect-scale variables (e.g., SCR, shoreface slope, backshore slope, grain size) and quadrat-scale variables (e.g., landward, middle, seaward beachgrass density within quadrats). Thus, transect-scale variables in the accretion

dataset exhibited similar ranges and distributions to variables in the foredune morphology dataset, but many quadrat-scale measurements differed. Within the sand accretion dataset, SCR varied from -1.5 to 8.3 m/yr. (median: 0.9 m/yr.); shoreface slope varied from 0.005 to 0.018 (median: 0.008); backshore slope varied from 0.01 to 0.11 (median: 0.03); median sediment diameter ranged from 0.106 to 0.282 mm (median: 0.176); beachgrass densities ranged from 0 and 557 tillers/m² (median: 35 tillers/m²); change in beachgrass density ($\log(\text{density}_{2014} / \text{density}_{2012})$) ranged from 99.2% decrease to a 413% increase in d_{face} beachgrass density (median: 15.5% increase); and change in elevation (indicative of sand accretion) between 2012 and 2014 within quadrats ranges from -1.1 m and 1.7 m (median: 0.4 m). The distributions and likelihood functions of all sand accretion GBN variables can be found in Appendix A, Figure A3.

2.3.2.2. Skill assessments for sand accretion GBNs

Comparison of the skill metrics (i.e., MSE, LLR, and pseudo-R²) for the two sand accretion GBNs showed that *A. arenaria* and *A. breviligulata* differed in their influence on sand accretion. The GBN that distinguished between *A. arenaria* and *A. breviligulata* (Accretion-GBN_{species}; Figure 2.4B) exhibited lower RMSE, higher pseudo-R², and higher LLR for predicting elevation change along d_{face} between 2012 and 2014 than the GBN that combined both beachgrass species (Accretion-GBN_{combined}; Figure 2.4A, Table 2.4). Because inclusion of species-specific information improved model accuracy and precision, the two beachgrass species appeared to differ in their impacts on elevation change (i.e., sand accretion).

When exploring the relative importance of variables for predicting elevation change along d_{face} , prior knowledge of both vegetation and geomorphological variables provided strong predictors of this change (Figure 2.6). Full knowledge of all variables in the Accretion-GBN_{species} increased the LLR of elevation change by 38.3 relative to a model with no prior knowledge (Table 2.5). Among ecological variables, elevation change was best predicted by the dominant species (LLR: 0-4.9) at each location, seaward *A. breviligulata* density (LLR: 6.2-17.0), initial *A. breviligulata* density (LLR: 0-10.4), and the change in tiller density for both *A. breviligulata* (LLR: -0.3-3.4) and *A. arenaria*

(LLR: 4.8-6.0) (Table 2.5 - Table 2.6). Among geomorphological variables, elevation change was best explained by backshore slope (LLR: 11.7-14.3), initial elevation (LLR: 0-5.3), and SCR (LLR: 0.9-5.8). Prior knowledge of all vegetation-related variables increased the LLR for predicting elevation change along d_{face} by 15.9-22.4, whereas prior knowledge of all non-vegetation variables increased the LLR 14.8-23.5.

2.3.2.3. *Geomorphological determinants of d_{face} elevation change*

Based on the Accretion-GBN_{species}, both backshore slope and SCR exhibited direct, positive relationships with elevation change, while SCR also exhibited an indirect, negative relationship with elevation change. These relationships suggest that foredunes along steep sloping backshore environments accreted sand more rapidly per unit area than foredunes along shallow-sloping backshore environments, under similar SCR conditions (Appendix A, Figure A4). The impact of SCR on elevation change is characterized by two counteracting processes: higher SCR (i.e., prograding beaches) was directly associated with increased vertical sand accretion, yet was also associated with lower backshore slopes and by extension, reduced vertical sand accretion (Appendix A, Figure A5). Initial elevation exhibited negative, indirect relationship with elevation change, via *A. breviligulata* density variables. This pattern suggests that higher elevation regions on d_{face} accrete less sand than low elevation regions, due in part to patterns of beachgrass distribution and abundance on d_{face} .

2.3.2.4. *Ecological determinants of d_{face} elevation change*

Vegetation growth patterns. *Ammophila arenaria* and *A. breviligulata* exhibited differing growth patterns along d_{face} . In locations where *A. arenaria* was dominant, initial *A. arenaria* density in a d_{face} quadrat was positively associated with its 2012 elevation and with the abundance of beachgrasses growing in the adjacent landward quadrat. However, the log response ratio of *A. arenaria* tiller density between 2012 and 2014 appeared to be independent of the 2012 spatial distribution and abundance of beachgrasses along each transect. Instead, *A. arenaria* tiller density increased by an average of 44% between 2012 and 2014 when *A. arenaria* was dominant, when all other variables were held constant.

Ammophila breviligulata exhibited a markedly different growth pattern. Similar to *A. arenaria*, initial *A. breviligulata* density in a d_{face} quadrat was positively associated with its 2012 elevation and with the abundance of beachgrasses growing in the adjacent landward quadrat. Unlike *A. arenaria*, the log response ratio in *A. breviligulata* tillers between 2012 and 2014 was directly, positively related to initial landward and seaward *A. breviligulata* density, and negatively related to initial *A. breviligulata* density at that particular quadrat. When holding other variables constant, *A. breviligulata* density increased by an average of 276% when *A. breviligulata* was the dominant species and initial *A. breviligulata* density in neighboring quadrats was low, suggesting a higher intrinsic growth rate than *A. arenaria*. Neighboring landward and seaward *A. breviligulata* further boosted new tiller growth by 35% and 14%, respectively, for every doubling of neighboring beachgrass tiller density. However, *A. breviligulata* exhibited negative density-dependent growth, such that every doubling of initial beachgrass density reduced new growth by 41%.

Differential influence on accretion. *Ammophila arenaria* and *A. breviligulata* further differed in their effect on elevation change over time. The log response ratio of tiller density between 2012 and 2014 (indicative of tiller production) for both *A. arenaria* and *A. breviligulata* were directly, positively associated with elevation gain. Seaward *A. breviligulata* was directly, negatively associated with elevation change and indirectly, positively associated with elevation change (via its positive association with the growth of new beachgrass tillers). For *A. arenaria*, a doubling of tiller density between 2012 and 2014 produced a 0.04 m elevation gain during the same period. For *A. breviligulata*, doubling of density between 2012 and 2014 produced a 0.03 m elevation gain. However, elevation gain from new *A. breviligulata* tiller production was also limited by seaward *A. breviligulata*, which reduced elevation by 0.05 m for every unit increase in seaward beachgrass density. Consequently, while production of *A. breviligulata* tillers on d_{face} may facilitate deposition, their impact is counteracted by seaward beachgrasses, which inhibit deposition on landward portions of d_{face} .

2.4. Discussion

In this study, we developed two sets of Gaussian Bayesian network (GBN) models to (1) evaluate interactions among shoreface and backshore morphology, vegetation abundance, and foredune morphology (Figure 2.3) and sand accretion patterns (Figure 2.4); and (2) investigate whether species-specific differences in density and growth form between *A. arenaria* and *A. breviligulata* may explain spatial variation in foredune morphology (Figure 2.3A vs. Figure 2.3B) and sand deposition patterns along the foredune (Figure 2.4A vs. Figure 2.4B). For examining determinants of foredune morphology, we found that backshore slope, SCR, dominant *Ammophila* species, and beachgrass density were the best predictors for metrics of foredune morphology (Figure 2.5, Table 2.2, Table 2.3). Parameterization of the Foredune Morphology-GBN models further showed that locations with high shoreline change rates (SCR) exhibit shallow-sloped (i.e., dissipative) shoreface and backshore zones, and short, shallow-sloping foredunes. Beachgrass density, in turn, altered the height, width, and slope of foredunes, but its mode of impact varied between *A. arenaria* and *A. breviligulata*: with increasing *A. arenaria* density, foredunes became steeper and taller, but width remained unchanged; in contrast, with increasing *A. breviligulata* density, foredune height still increased, but foredunes become wider and more shallow-sloped.

An examination of sand deposition patterns at locations along the foredune face (d_{face} ; between d_t and d_c) over a two-year period showed that sand deposition was most strongly influenced by species-specific patterns of vegetation growth, backshore slope, and SCR (Figure 2.6, Table 2.5, Table 2.6). Based on the Accretion-GBNs, we found that locations with high SCR and shallow-sloping backshore zones experienced higher rates of elevation gain on the foredune face, indicative of sand accretion. We further found that sand accretion was concentrated at lower elevations and gradually decreased as elevation increased. Plant species identity and tiller density also altered patterns of deposition: although initial plant density did not alter deposition rates, quadrat locations in which *Ammophila* density increased over the two-year period had heightened accretion relative to locations where density did not change. In contrast, seaward-occurring *A. breviligulata*

inhibited sand accretion on landward portions of the foredune face. Finally, the Accretion-GBN_{species} model demonstrated that *A. arenaria* and *A. breviligulata* exhibit differing growth patterns, with substantial morphodynamic impacts as will be discussed below.

2.4.1. Geomorphological regulation of foredune morphodynamics

Empirical studies of foredune morphology have shown that foredune size is associated with beach type, such that dissipative beaches (i.e., wide, shallow sloping, fine sediment grain size) typically have larger foredunes than reflective beaches (Short and Hesp 1982, Hesp 1988, Durán and Moore 2013). Corresponding observations and conceptual models suggest that dissipative beaches may offer a higher sand supply to dunes due to elevated wave driven sediment supply to the beach and/or fetch length, thereby generating enhanced aeolian sediment fluxes from beaches to foredunes (Short and Hesp 1982, Saye et al. 2005, Houser et al. 2008, Houser and Mathew 2011). By extension, this heightened flux is hypothesized to facilitate formation of larger foredunes (Short and Hesp 1982). However, this direct relationship between beach morphology and foredune morphology is overly simplified, as there are numerous counter-examples of dissipative beaches with high sediment supplies and short foredunes (Ruggiero et al. 2005, Saye et al. 2005, Miot da Silva and Hesp 2010). Our findings further illustrate that the relationship between beach type, sediment supply, and foredune morphology is complex.

In the Accretion-GBN models, we show that high SCR locations (i.e., high beach sediment supply) are commonly associated with dissipative beach conditions with fine sand grain sizes (Figure 2.4B). Although high SCR was directly associated with high sand deposition on the dune face, dissipative beach conditions counteracted this effect (Appendix A, Figure A5). Instead, after accounting for SCR, locations with shallow backshore slopes exhibited lower sand deposition across the dune face (Appendix A, Figure A4). Thus, foredunes in locations with high SCR and steeper sloped backshore environments experienced higher rates of sand deposition along d_{face} . Although a steeper backshore was also associated with taller foredunes, beaches with high rates of shoreline

change had significantly shorter foredunes than low SCR beaches (Figure 2.3, Figure 2.4B). Consequently, the relationships between beach type, sand accretion, and foredune morphology in our study sites fits poorly with observations by Short and Hesp (1982); rather, foredune morphology may be better explained by beach-dune sediment budget models such as those by Psuty (1988) and Pye (1990).

Psuty (1988) proposed that foredune development depends upon the sediment supply to the beach and to the dune, while Pye (1990) included availability of wind energy and sand-trapping vegetation efficacy as additional modifiers of foredune development. Under both beach-dune sediment budget models, foredune development is maximized under near-neutral beach-dune budgets, where a net-neutral supply of sand to the beach provides a net-positive supply of sand to the foredune: over years, shoreline and foredune position remain stable, allowing sand to accumulate along the foredune crest, resulting in the development of large foredunes. In contrast, as shoreline progradation rates increase, foredune dimensions gradually decrease as they instead form a series of small foredune ridges (Psuty 2008). If SCR approximates beach sediment budgets, then the Foredune Morphology-GBN models are consistent with these beach-dune sediment budget models: foredune development, as measured by foredune height, was maximized at neutral to slightly negative SCR. Numerical modeling and long-term observations of the Columbia River Littoral Cell, which encompasses many of the progradational sites in this study, are similarly consistent with our findings, and with the Psuty and Pye models. In the Columbia River Littoral Cell, beach sediment budgets are mostly positive. Between 1997 and 2014, this positive sediment budget produced an average SCR of 1.1 to 3.7 m/yr. and resulted in the formation of one to two new foredune ridges (Ruggiero et al. 2016). While backshore slope and sand grain size may control the dune sediment flux, rates of shoreline change may equally influence foredune morphology by altering the rate of formation of new dune ridges (Moore et al. 2016).

2.4.2. Ecological regulation of foredune morphodynamics

The morphodynamics of U.S. Pacific Northwest foredunes are further influenced by vegetation dynamics, including plant density, plant morphology, and growth patterns.

Historically, Pacific Northwest coastal foredunes were dominated by endemic grasses (American dune grass; *Elymus mollis*) and forbs (e.g., *Abronia latifolia*, *Lathyrus littoralis*) that grew in sparse assemblages (Wiedemann 1984). This low vegetation cover, combined with a high sand supply and seasonal wind patterns allowed for the formation of dune hummocks, barchan dunes, transverse ridges, and oblique ridges (Cooper 1958). However, with the introductions of *A. arenaria* and *A. breviligulata* as sand stabilizers and their subsequent spread throughout the region, the historically open-sand dune system transitioned to a highly vegetated, stabilized system of shore-parallel, linear foredunes (Wiedemann and Pickart 1996). Differences in grass physiology, morphology, and growth form between the native *E. mollis* and invasive *Ammophila* species have driven this geomorphological transformation. Although *E. mollis* is a larger grass than the *Ammophila* species, it grows at lower densities and produces tillers at a slower rate than the *Ammophila* species, and is thus less capable of inducing sediment deposition and immobilizing sand (Pavlik 1983a, Hacker et al. 2012, Zarnetske et al. 2012). Because the density of *E. mollis* drastically differs from that of the *Ammophila* species, the *Ammophila* invasion altered ecomorphodynamic feedbacks, resulting in foredune morphological change.

While *E. mollis* and *Ammophila* species clearly exhibit distinct ecomorphodynamic effects, *A. arenaria* and *A. breviligulata* are more similar in plant morphology, density, and growth form. Despite their similar appearance, it has been hypothesized that the two *Ammophila* species produce distinct foredune morphotypes due to subtle differences in plant traits. Previous research has shown that *A. breviligulata*-dominated foredunes in the U.S. Pacific Northwest are shorter, wider, and more shallow-sloping than *A. arenaria*-dominated foredunes (Seabloom and Wiedemann 1994, Hacker et al. 2012). Yet, these differences in foredune morphology could be explained by either ecomorphodynamic differences between the two *Ammophila* species, or by spatially correlated sediment supply patterns (e.g., SCR, backshore slope, grain size). Thus, three questions arise from these uncertain relationships. (1) Do *Ammophila* density patterns explain regional variation in foredune morphology, after accounting for sediment supply and sediment

characteristics? (2) Do the two *Ammophila* species exhibit species-specific differences in foredune morphology, after accounting for sediment supply and sediment characteristics? And (3) If so, which species-specific characteristics most influence foredune morphology and sand accretion rates: morphology, density, or growth form?

2.4.2.1. Influence of *Ammophila* on foredune morphodynamics

Based on the Foredune Morphology-GBN analyses, foredune morphology appeared to be influenced by both ecological and sediment supply patterns (Figure 2.3). While backshore slope and SCR best predicted foredune morphology, beachgrass density also explained a sizable amount of variation (Figure 2.5, Table 2.2, Table 2.3), and was positively associated with steeper and taller foredunes. Correspondingly, rates of sand accretion along the d_{face} over a two-year period were primarily explained by beachgrass abundance and backshore slope (Figure 2.4, Table 2.5). Consequently, beachgrass density explained some variation in foredune morphology and rates of sand accretion that was not explained by sediment supply patterns alone.

These results are consistent with our understanding of boundary layer dynamics along vegetated foredunes. When the vegetation canopy decreases near-surface airflow, suspended and saltating sand grains are deposited near the leading edge of the plant canopy. The reduced bed-shear stress within the canopy further prevents re-entrainment of deposited sediments, allowing for gradual accretion of sediment along vegetated portions of the foredune. Correspondingly, as plant density increases, airflow velocity beneath the canopy further decreases, leading to more localized deposition at the windward canopy margin (Hesp 1989, Van Dijk et al. 1999). In effect, as vegetation density increases, dune height increases due to greater sand entrapment at the seaward canopy margin (Hesp 1989).

2.4.2.2. Species-specific differences in foredune morphology

Foredune morphology and sand accretion along the dune face also appeared to differ among the *Ammophila* species, even when accounting for sediment supply and sediment characteristics. For the Foredune Morphology-GBN models, inclusion of distinct nodes for the two *Ammophila* species increased log-likelihood ratios (LLRs; i.e., improved

accuracy and/or precision of model predictions) for each foredune morphometric, with the greatest improvement observed in dune face width (Table 2.1). Separating the *Ammophila* species into separate nodes similarly improved GBN performance for predicting elevation change along the dune face over time. Therefore, our results were consistent with previous research showing distinctive morphologies between *A. arenaria*- and *A. breviligulata*-dominated foredunes.

Hacker et al. (2012) hypothesized that subtle differences in the morphology and growth form of *A. arenaria* and *A. breviligulata* may facilitate the formation of species-specific foredune morphologies in the U.S. Pacific Northwest. For example, *A. breviligulata* tillers are 30% wider and 15% taller than *A. arenaria* tillers, and have been shown to induce greater sediment deposition per tiller than *A. arenaria* in a wind tunnel (Zarnetske et al. 2012). Yet, *A. arenaria* grows at a higher density than *A. breviligulata*, potentially facilitating faster vertical dune growth due to higher aggregate sand capture (volume of deposited sand per unit area). Consequently, it is possible that differences in morphology and density may explain why *A. arenaria*-dominated foredunes are taller and narrower than their *A. breviligulata*-dominated counterparts.

However, neither the species-specific differences in sand capture efficiency, nor the relationship between natural beachgrass density and foredune height were well supported by our analysis. Based on the Accretion-GBN_{species} model (Figure 2.4B) and its underlying field observations, *A. arenaria* appeared to accrete marginally more sand per doubling of new tillers than *A. breviligulata*. Similarly, while we found that increased beachgrass density was associated with taller foredunes, *A. arenaria* was always predicted to produce higher foredune crest elevations than *A. breviligulata* at comparable densities (in tillers/m²), when other parent nodes are held constant (Appendix A, Figure A6). This pattern is at odds with wind tunnel experiments by Zarnetske et al. (2012) that showed *A. breviligulata* to be the superior sand binder. Even more perplexing, the Foredune Morphology-GBN_{species} (Figure 2.3B) suggests that increasing *A. breviligulata* density is associated with taller and wider foredunes. This pattern directly contradicts our *a priori* hypothesis that increasing density would be associated with taller and narrower

foredunes because of more localized sediment deposition along the foredune face (Hesp 1989, Van Dijk et al. 1999). Consequently, neither species-specific density nor morphology supports the differences in foredune morphology we document here.

Alternatively, *A. arenaria* may produce taller, narrower foredunes than *A. breviligulata* due to differences in growth form (Hacker et al. 2012). *Ammophila breviligulata* engages in greater lateral growth than *A. arenaria*, such that *A. breviligulata* can propagate laterally at rates in excess of 3 m/yr., whereas *A. arenaria* propagates at rates less than 1 m/yr. (Maun 1985, Baye 1990, Keijsers et al. 2015). Hacker et al. (2012) propose that the laterally-expansive growth form of *A. breviligulata* may facilitate the formation of wider and therefore shorter foredunes than *A. arenaria*.

Our GBN analyses suggest that these differences in growth form may be primarily responsible for species-specific differences in foredune morphology (Figure 2.7). In the Accretion-GBN_{species} model, we observed that production of new tillers in *A. breviligulata* was positively associated with its density in adjacent landward and seaward quadrats, while no such relationship existed for *A. arenaria* (Figure 2.4B). This pattern suggests that *A. breviligulata* laterally propagated into neighboring areas over the two-year observation period, while no such spreading was detected for *A. arenaria*. Further, *A. breviligulata* tiller production within a quadrat was reduced when its initial density was high (i.e., it produced greater per-capita tiller production when initial tiller density was low), while *A. arenaria* did not exhibit a similar negative density-dependent relationship. This negative-density dependent relationship in tiller production indicates that *A. breviligulata* primarily increased in density between 2012 and 2014 when its 2012 density was low, whereas *A. arenaria* growth was unaffected by 2012 density. Because most unoccupied habitat occurred near the foredune toe, new *A. breviligulata* tillers primarily grew seaward and subsequently accreted sand. Finally, when *A. breviligulata* was present in adjacent seaward quadrats, those seaward growing plants reduced deposition along landward quadrat locations. For *A. arenaria*, no such spatial relationship between tiller density and deposition was observed.

When combined with reduced sand accretion in landward quadrats, *A. breviligulata*-dominated foredunes appear to grow laterally, with limited vertical sand accretion at the foredune crest. Although new tiller production effectively increased mean *A. breviligulata* density on the foredune face, its primary impact was to increase foredune face width rather than foredune crest elevation. In contrast, the less laterally-expansive growth form of *A. arenaria*, where tiller production was concentrated at the face and crest of the foredune, appeared to allow for greater sand deposition on the foredune face and crest. This suggests that *A. arenaria*-dominated foredunes may accrete sand over long periods of time because lateral expansion of the foredune is limited by the low rate of lateral propagation for *A. arenaria*. Thus, *A. arenaria* foredunes grow in height over time from sand accretion across all of the foredune face, while *A. breviligulata* foredunes grow in width over time from sand accretion near the foredune toe.

More generally, rates of lateral vegetation growth are likely to alter patterns of foredune development. Although an imperfect comparison, relationships between rates of shoreline progradation and foredune development may offer insight into potential effects of lateral propagation rates. As progradation rates increase, foredune ridges form at logarithmically increasing frequency: at a stable SCR (when $SCR = 0$), a single dune ridge may form, while regions with SCRs of 2-4 m/yr. can form additional seaward ridges within 5-6 years as incipient foredunes develop in front of mature foredunes (Moore et al. 2016). This higher frequency of incipient foredune development reduces the total time in which mature dunes can develop before being supplanted by the formation of a new dune ridge, and consequently prevents the formation of large foredunes (Moore et al. 2016).

Lateral propagation rates for vegetation similarly alter the frequency of incipient foredune development and thus foredune size. On stable or eroding shorelines, overwash and erosion are likely to prevent vegetation colonization of the seaward foredune margin and maintain the existing vegetation line and mature foredune. However, on prograding shorelines, as plant lateral propagation rates increase, vegetation will be able to colonize seaward habitat at a more rapid rate and facilitate incipient dune development seaward of

the mature foredune. We surmise that propagation could alter two controls of dune development: (1) rate of lateral growth of the mature foredune ridge, and (2) rate of seaward foredune ridge development. As lateral propagation rates increase, plants will vegetatively propagate along the face and near the toe of the mature, active foredune via stolons and rhizomes. As progradation creates new available habitat, rapid vegetative expansion further seaward may then promote sand accretion at the leading edge of the vegetation canopy, leading to a widening of the active dune ridge. Because most sand deposition occurs within the first few meters of dense vegetation due to rapid wind deceleration (Hesp 1989), and given that vegetation is propagating to regions of lower elevation, increased lateral vegetative growth rates would promote the formation of shorter and wider foredunes.

Lateral propagation rate might also affect the rate of foredune ridge formation on prograding beaches. Vegetation lateral growth rates alter the hummockiness of foredunes and the time required for foredune hummocks to anneal to form a continuous foredune ridge. Typically, plants with low lateral propagation rates form hummocky dunes with long annealing times (e.g., *U. paniculata*, *A. arenaria*), while those with higher lateral propagation rates form linear foredunes with short annealing times (e.g., *A. breviligulata*). Numerical modeling suggests that slow propagating species are capable of forming linear foredunes, but their annealing time is long and they are especially vulnerable to overwash and erosion at early stages of incipient foredune development, prior to annealing (Duran Vinent and Moore 2015, Goldstein et al. 2017). These overwash events erode incipient foredunes and hummocks, effectively resetting the backshore to a flatter, unvegetated state. In contrast, fast propagating species would rapidly form continuous foredune ridges that are resistant to overwash, and would thus tolerate higher frequency high water events.

This disparity in the rate of foredune ridge formation could affect the size of foredunes on prograding beaches. For species with rapid lateral propagation, as the beach progrades, seed and rhizomes will establish hummocks on new backshore habitat that quickly anneal into new foredune ridges (Goldstein et al. 2017). Because of the rapidity

of development of a seaward ridge, leeward foredunes will experience a shortened timeframe under which they actively accrete sediment, resulting in volumetrically smaller dune ridges. In contrast, slower propagating species will more slowly anneal into foredune ridges, and may be further inhibited by high water events. Consequently, slow lateral propagation may slow development of seaward dune ridges, allowing leeward foredunes to accrete sand for longer time periods and thus grow larger.

While it may be plausible that lateral growth rates may affect either rates of lateral growth of the foredune ridge, or rates of foredune ridge development on stable and prograding shorelines, neither of these relationships has ever been examined using either numerical models or field studies. Although variants of the Coastal Dune Model incorporate vegetation lateral growth rate as a parameter (Duran Vinent and Moore 2015, Goldstein et al. 2017), none have examined the sensitivity of foredune morphometrics to lateral propagation rates on non-stable shorelines (i.e., Goldstein et al. (2017) examined the sensitivity of hummockiness to alongshore lateral propagation rate on a stable shoreline). Resultantly, foredune research would benefit from future work that examines how vegetation life history characteristics may alter foredune development.

2.4.3. Coastal foredunes as green infrastructure

Many scientists, governments, and non-governmental organizations view beaches, dunes, marshes, mangroves, and coral reefs as viable risk-reduction infrastructure for mitigating flooding and erosion hazards, and for enhancing resilience to coastal storms and sea-level rise (Costanza et al. 2008, Arkema et al. 2013, Bloomberg 2013, Spalding et al. 2014, Ruckelshaus et al. 2016). They not only attenuate wave energy from storms and reduce or prevent coastal flooding and erosion, they are also self-sustaining, can self-recover following storm events, may have both lower up-front costs and long-term maintenance costs, and may keep pace with sea-level rise (Sutton-Grier et al. 2015). Moreover, coastal green infrastructure provides many co-benefits that are typically absent from hard (gray) infrastructure by providing tourism and recreational opportunities, food and resource provisioning, carbon sequestration, wildlife habitat, and other goods and services (Everard et al. 2010, Barbier et al. 2011, Sutton-Grier and Moore 2016).

However, use of green infrastructure for coastal protection comes with risk: topography and vegetation composition and abundance in coastal ecosystems can be spatiotemporally variable, creating uncertainty in the level of coastal protection provided (Koch et al. 2009). Consequently, for green infrastructure to offer a viable alternative to gray infrastructure, we must understand the causes of this variability, so that we can accurately predict the level of coastal protection offered by natural systems.

Within coastal dune systems, both sediment supply and vegetation contribute to variation in foredune development, morphology, and resultantly, coastal protection. Dense vegetation growth encourages the development of taller foredunes that may provide superior risk-reduction against overwash and erosion (Sallenger 2000, Stockdon et al. 2006, Plant and Stockdon 2012), but the overall foredune shape may also depend upon the ability of plants to engage in lateral growth. Yet, beach type (e.g., backshore slope, mean grain size) and sediment budgets (e.g., SCR) explained equal or greater amounts of foredune morphological variation. For governments, municipalities, and property owners that are considering use of coastal foredunes as protective infrastructure, these results show that decision-making must consider both sediment supply and vegetation conditions for predicting the degree of protection that may be provided by dunes and the rate at which foredunes will develop and/or recover following storm events.

Vegetated coastal dunes, however, are not a panacea for coastal hazard risk-reduction, as excessive vegetation and stabilization of beaches and dunes also carries risk. Ecologically, over-vegetated dunes may eliminate critical habitat for species that depend upon open-sand habitat or frequent disturbance from sand burial. On the U.S. west coast, *A. arenaria* and *A. breviligulata* eliminated nesting habitat for the federally-threatened western snowy plover (*Charadrius nivosus nivosus*) (USFWS 1993) and have outcompeted numerous endemic plants (e.g., *Abronia umbellata*, *Tanacetum bipinnatum*) (Wiedemann and Pickart 1996). On the U.S. east coast, dune stabilization similarly impedes nesting by the federally-threatened piping plover (*Charadrius melodus*), which depend upon overwash processes for the creation of nesting and forage habitat (Schupp et

al. 2013). Depending upon stakeholder interests and management objectives, coastal managers may seek less vegetation cover in order to destabilize foredunes and encourage overwash.

Overstabilization of dunes may also threaten the long-term sustainability of coastal landforms facing relative sea-level rise. Coastlines and barriers respond to changes in sea-level over annual to millennial timescales, and typically retreat landward when sea-level rises. Sea-level rise increases the probability of overwash during storm events, thereby facilitating wave-driven landward sediment transport. Although this “rolling over” of sediments from the seaward to the landward side of the coastal dune/barrier causes shoreline retreat, it enables redevelopment of the foredune/barrier at a landward and upland position that is more resilient to ocean forcing (Bruun 1962, Leatherman 1979). However, when foredunes are overstabilized, they prevent overwash (potential near-term benefit: reduced flooding and erosion), precluding the equilibration of coastline and barrier positions with present-day sea-level and storm conditions. Over long time periods, then, prevention of overwash and barrier rollover reduces coastal and barrier resilience, leading to narrowing, breaching, and ultimately, the possible drowning of barrier islands (Magliocca et al. 2011, Rogers et al. 2015). Consequently, while management efforts to stabilize and build tall foredunes may increase coastal resistance to near-term hazards from storms and sea-level rise, they may also reduce the long-term resilience of coastal systems for adapting to environmental change.

To further our understanding of ecomorphodynamics processes and their influence on foredune development and coastal resilience to storms and sea-level rise, future work needs to further characterize ecomorphodynamic feedbacks. While this, and related studies, examined grasses (e.g., *Ammophila* species, *E. mollis*) as dune builders (Zarnetske et al. 2012, 2015), beach and dune plants exhibit a wide range of morphologies and life history strategies. Dune-forming plants also including prostrate forbs (e.g., *Glehnia littoralis*, *Lathyrus* species, *Cakile* species), both annual and perennial plants, and plants that primarily propagate via seed and via rhizomes and stolons. These different morphologies, methods of propagation, life history strategies, and

physiological tolerances may alter sand capture efficiency, seasonality and temporal variability in accretion, and rates of ecological and geomorphological recovery following storms. Finally, while our research on ecomorphodynamic feedbacks in the U.S. Pacific Northwest demonstrated impacts of beachgrasses on prograding and stable shorelines, many regions worldwide exhibit eroding shores and are expected to suffer more severe erosion with accelerating sea-level rise. Future work that examines ecomorphodynamic processes on retreating shorelines would help to fill this knowledge gap.

Foredunes provide a promising coastal structure for delivering flood and erosion protection and a complement of other goods and services (Barbier et al. 2011). Our findings show that vegetation is a significant influencer of foredune shape, and that species-specific plant characteristics can alter foredune dimensions, even among closely related and morphologically-similar species. Because the ability for foredunes to withstand storms is contingent upon its shape prior to the storm, vegetation characteristics can modify coastal resilience. As coastal management plans increasingly recommend the use of foredunes for storm protection (Bloomberg 2013, Christie 2013), it is imperative to consider the capacity for vegetation to build and maintain foredunes to meet the needs of coastal communities and to consider the social and ecological costs and benefits associated with each potential management option.

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Table 2.1. Comparison of Bayesian network skill metrics for two foredune morphology Gaussian Bayesian networks (GBN) that either combined beachgrass species (Foredune Morphology-GBN_{combined}; Figure 2.3A) or treated them separately (Foredune Morphology-GBN_{species}; Figure 2.3B). The three skill metrics (root mean square error (RMSE); pseudo-R²; log likelihood ratio (LLR)) allowed for comparison of prediction accuracy and precision among hypothesized GBN structures.

Predicted Foredune Morphometric	Model	RMSE	pseudo-R ²	LLR
		(Lower is better)	(Higher is better)	(Higher is better)
d_t Elevation	GBN _{combined}	0.254	0.0767	9.6
	GBN _{species}	0.254	0.0786	10.1
d_{face} Width	GBN _{combined}	0.705	0.0768	9.3
	GBN _{species}	0.694	0.106	13.0
d_{face} Slope	GBN _{combined}	0.608	0.261	35.3
	GBN _{species}	0.601	0.273	37.1
d_c Elevation	GBN _{combined}	0.009	0.389	57.4
	GBN _{species}	0.009	0.397	58.9

Table 2.2. Relative importance of variables for predicting foredune morphometrics (d_t elevation, d_{face} width, d_{face} slope, and d_c elevation) in the Foredune Morphology-GBN_{species} network (Figure 2.3B), based on addition of prior knowledge of a single variable. The full model included prior knowledge of all non-foredune morphometric nodes; the null model included no prior knowledge; and all other models included prior knowledge of a single variable. Influential variables were associated with larger reductions in root mean square error (RMSE), increases in Pseudo-R², and increases in LLR relative to the *null* model. Due to covariation among predictor variables, skill metrics based on the addition of a single variable provided an upper bound-estimate of variable importance.

Predicted Foredune Morphometric	Prior Knowledge	RMSE	Pseudo-R ²	LLR
d_t elevation	Full	0.254	0.079	10.1
	+ Beachgrass Density	0.258	0.049	6.3
	+ Dominant Species	0.258	0.047	6.1
	+ Backshore Slope	0.265	-0.003	-0.3
	+ Mean Sediment Diameter	0.266	-0.014	-1.3
	+ Shoreface Slope	0.269	-0.036	-3.7
	+ SCR	0.272	-0.058	-5.9
	Null	0.265	0	0
d_{face} width	Full	0.694	0.106	13.0
	+ Dominant Species	0.69	0.114	14.0
	+ Beachgrass Density	0.694	0.106	13.0
	+ Dominant Species	0.694	0.106	13.0
	+ SCR	0.733	0	0
	+ Shoreface Slope	0.733	0	0
	+ Mean Sediment Diameter	0.733	0	0
	+ Backshore Slope	0.733	0	0
Null	0.733	0	0	
d_{face} slope	Full	0.601	0.273	37.1
	+ Dominant Species	0.617	0.235	30.7
	+ Beachgrass Density	0.621	0.224	29.4
	+ Dominant Species	0.621	0.224	29.4
	+ Backshore Slope	0.639	0.178	22.4
	+ SCR	0.674	0.087	10.5
	+ Shoreface Slope	0.689	0.045	5.4
	+ Mean Sediment Diameter	0.707	-0.005	-0.6
Null	0.705	0	0	
d_c elevation	Full	0.0099	0.394	58.9
	+ Backshore Slope	0.0106	0.305	42.5
	+ SCR	0.0119	0.129	16.3
	+ Beachgrass Density	0.0123	0.070	8.6
	+ Dominant Species	0.0123	0.070	8.6
	+ Dominant Species	0.0126	0.028	3.4
	+ Shoreface Slope	0.0126	0.026	3.1
	+ Mean Sediment Diameter	0.0127	0.014	1.7
Null	0.0128	0	0	

Table 2.3. Relative importance of variables for predicting foredune morphometrics (d_t elevation, d_{face} width, d_{face} slope, and d_c elevation) in the Foredune Morphology-GBN_{species} network (Figure 2.3B), based on subtraction of prior knowledge of a single variable. The full model included prior knowledge of all non-foredune morphometric nodes; the null model included no prior knowledge; and all other models included prior knowledge of all but one variable. Influential variables were associated with larger increases in root mean square error (RMSE), increases in Δ Pseudo- R^2 (Pseudo- R^2_{full} - Pseudo- R^2_{model}), and increases in Δ LLR (LRR_{full} - LRR_{model}) relative to the full model. Due to covariation among predictor variables, skill metrics based on the subtraction of a single variable provided a lower bound-estimate of variable importance.

Table 2.3

Predicted Foredune Morphometric	Prior Knowledge	RMSE	Pseudo-R ²	LLR	Δ Pseudo-R ²	Δ LRR
d_t Elevation	Full	0.254	0.079	10.1	0	0
	- Shoreface Slope	0.254	0.079	10.1	<0.001	0
	- Mean Sediment Diameter	0.253	0.083	10.6	-0.005	-0.5
	- Backshore Slope	0.255	0.072	9.28	0.007	0.8
	- Beachgrass Density	0.255	0.071	9.16	0.008	0.9
	- SCR	0.259	0.039	5.29	0.039	4.8
	- Beachgrass Density - Dominant Species	0.271	-0.047	-4.72	0.126	14.8
	Null	0.265	0	0	0.079	10.1
d_{face} Width	Full	0.694	0.106	13	0	0
	- Beachgrass Density	0.690	0.114	14	-0.008	-1.0
	- SCR	0.694	0.106	13	0	0
	- Shoreface Slope	0.694	0.106	13	0	0
	- Mean Sediment Diameter	0.694	0.106	13	0	0
	- Backshore Slope	0.694	0.106	13	0	0
	- Beachgrass Density - Dominant Species	0.733	0	0	0.106	13.0
	Null	0.733	0	0	0.106	13.0
d_{face} Slope	Full	0.601	0.273	37.1	0	0
	- Beachgrass Density	0.598	0.281	38.3	-0.008	-1.2
	- Shoreface Slope	0.598	0.280	38.1	-0.007	-1.0
	- Mean Sediment Diameter	0.597	0.283	38.7	-0.010	-1.6
	- SCR	0.601	0.273	37.1	0	0
	- Backshore Slope	0.622	0.221	29	0.052	8.1
	- Beachgrass Density - Dominant Species	0.659	0.127	15.8	0.146	21.3
	Null	0.705	0	0	0.273	37.1
d_c Elevation	Full	0.0099	0.397	58.9	0	0
	- SCR	0.0099	0.394	58.3	0.003	0.6
	- Beachgrass Density	0.0101	0.372	54.2	0.025	4.7
	- Beachgrass Density - Dominant Species	0.0101	0.370	53.8	0.027	5.1
	- Mean Sediment Diameter	0.0102	0.361	52.2	0.036	6.7
	- Shoreface Slope	0.0102	0.357	51.6	0.040	7.3
	- Backshore Slope	0.0115	0.187	24.3	0.210	34.6
	Null	0.0128	0	0	0.397	58.9

Table 2.4. Comparison of Bayesian network skill metrics for sand accretion between Gaussian Bayesian networks (GBN) that either combined beachgrass species (Accretion-GBN_{combined}; Figure 2.4A) or treated them separately (Accretion-GBN_{species}; Figure 2.4B). The three skill metrics (root mean square error (RMSE); pseudo-R²; log likelihood ratio (LLR)) allowed for comparison of prediction accuracy and precision among hypothesized GBN structures.

Predicted Metric	Model	RMSE	Pseudo-R ²	LLR
		(Lower is better)	(Higher is better)	(Higher is better)
Δ Elevation	GBN _{combined}	0.405	0.188	33.3
	GBN _{species}	0.398	0.213	38.3

Table 2.5. Relative importance of variables for predicting elevation change in the Accretion-GBN_{species} network (Figure 2.4B), based on addition of prior knowledge of a single variable. The full model included prior knowledge of all nodes except Δ Elevation; the null model included no prior knowledge; and all other models included prior knowledge of a single variable. Influential variables were associated with larger reductions in root mean square error (RMSE), increases in Pseudo-R², and increases in LLR relative to the null model. Due to covariation among predictor variables, skill metrics based on the addition of a single variable provided an upper bound-estimate of variable importance.

Prior Knowledge	RMSE	Pseudo-R ²	LLR
Full	0.398	0.213	38.3
+ Seaward AMBR Density	0.426	0.101	17.0
+ Backshore Slope	0.433	0.071	11.7
+ Initial AMBR Density	0.435	0.063	10.4
+ Landward AMBR Density	0.438	0.047	7.7
+ log(AMAR Density _{Final} / AMAR Density _{Init.})	0.441	0.037	6.0
+ Initial Elevation	0.442	0.033	5.3
+ Dominant Spp	0.442	0.031	4.9
+ Shoreface Slope	0.446	0.013	2.1
+ Mean Sediment Diameter	0.446	0.012	1.9
+ SCR	0.448	0.006	0.9
+ Seaward AMAR Density	0.449	0.000	0.0
+ Initial AMAR Density	0.449	0.000	-0.1
+ Landward AMAR Density	0.449	-0.001	-0.1
+ log(AMBR Density _{Final} / AMBR Density _{Init.})	0.450	-0.002	-0.3
Null	0.449	0	0

Table 2.6. Relative importance of variables for predicting elevation change in the Accretion-GBN_{species} network (Figure 2.4B), based on subtraction of prior knowledge of a single variable. The full model included prior knowledge of all nodes except Δ Elevation; the null model included no prior knowledge; and all other models included prior knowledge of all but one variable. Influential variables were associated with larger increases in root mean square error (RMSE), increases in Δ Pseudo- R^2 (Pseudo- R^2_{full} - Pseudo- R^2_{model}), and increases in Δ LRR (LRR_{full} - LRR_{model}) relative to the full model. Due to covariation among predictor variables, skill metrics based on the subtraction of a single variable provided a lower bound-estimate of variable importance.

Prior Knowledge	RMSE	Pseudo- R^2	LRR	Δ Pseudo- R^2	Δ LRR
Full	0.398	0.213	38.3	0	0
- Shoreface Slope	0.398	0.213	38.3	0	0
- Initial Elevation	0.398	0.213	38.3	0	0
- Landward AMAR Density	0.398	0.213	38.3	0	0
- Initial AMAR Density	0.398	0.213	38.3	0	0
- Seaward AMAR Density	0.398	0.213	38.3	0	0
- Dominant Spp	0.398	0.213	38.3	0	0
- Mean Sediment Diameter	0.398	0.213	38.3	0	0
- Landward AMBR Density	0.398	0.213	38.3	0	0
- Initial AMBR Density	0.398	0.213	38.3	0	0
- $\log(\text{AMBR Density}_{Final} / \text{AMBR Density}_{Init.})$	0.403	0.196	34.9	0.017	3.4
- $\log(\text{AMAR Density}_{Final} / \text{AMAR Density}_{Init.})$	0.404	0.189	33.5	0.024	4.8
- SCR	0.406	0.184	32.5	0.029	5.8
- Seaward AMBR Density	0.406	0.182	32.1	0.031	6.2
- Backshore Slope	0.417	0.139	24.0	0.074	14.3
Null	0.449	0	0	0.213	38.3

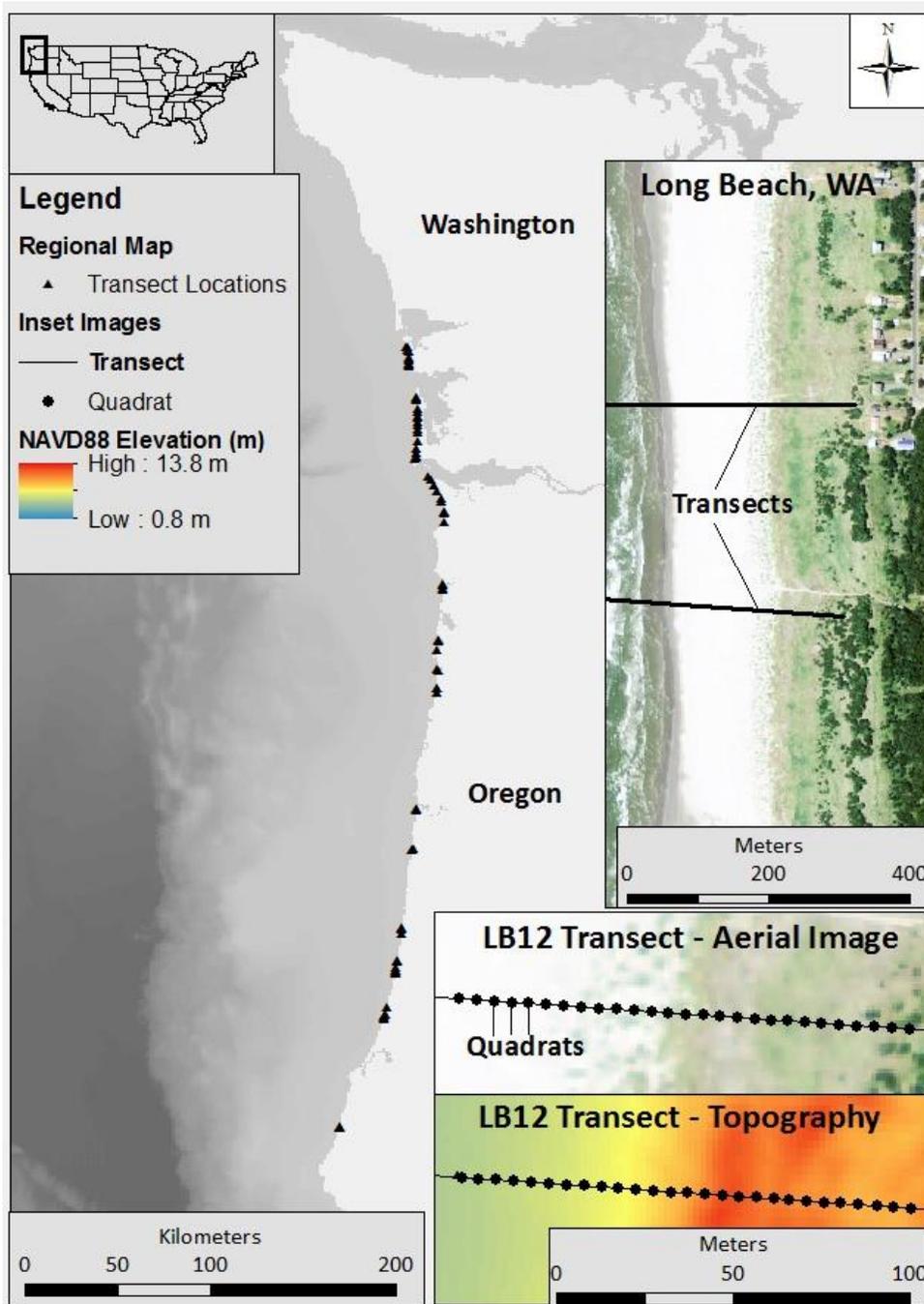


Figure 2.1. Topographic and vegetation transect locations in Oregon and southern Washington, USA (Appendix A, Table A1). Inset images illustrate cross-shore transects perpendicular to the foredune, with quadrats placed at 5 m intervals along the transect between the seaward vegetation line and the foredune heel.

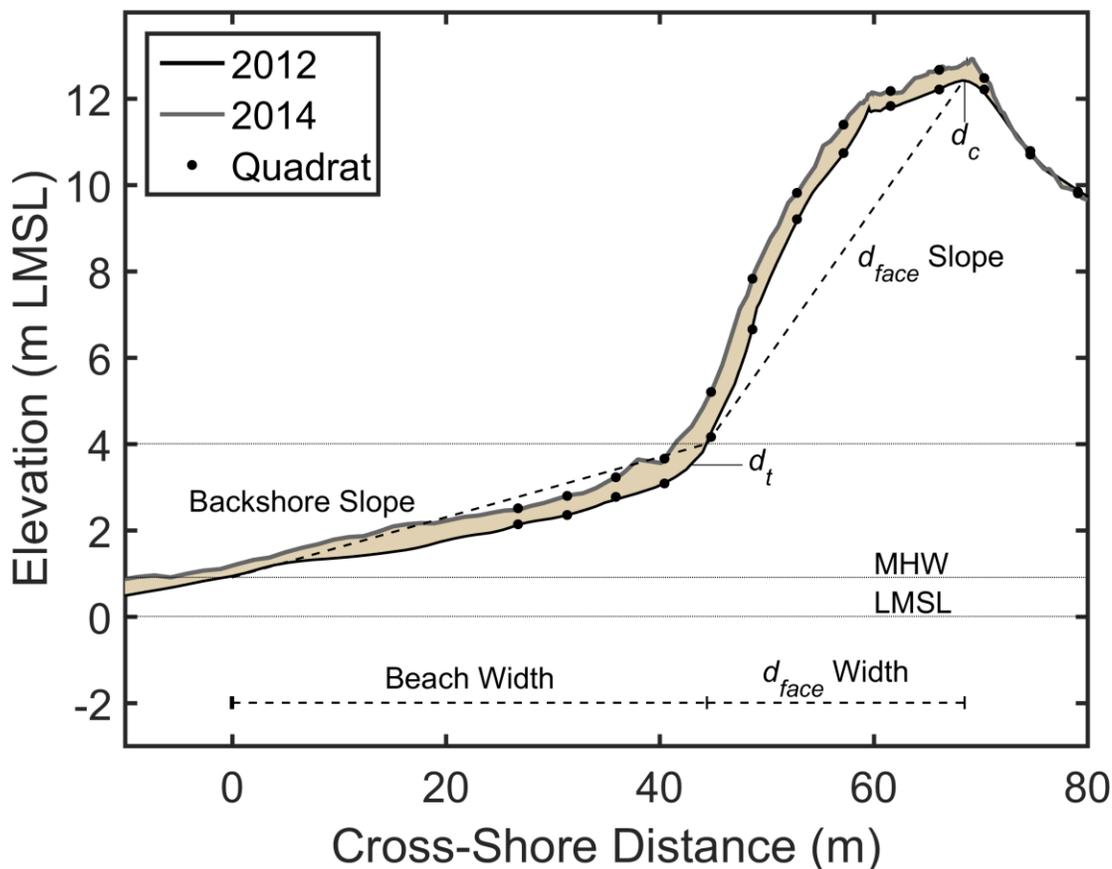


Figure 2.2. An example of smoothed cross-shore topographic profiles and foredune morphometrics for 2012 and 2014 at Fort Stevens, OR (FS02). Tan polygon indicates sand accretion over two years. Black points indicate quadrat placement in 2012 (lower foredune profile; black) and 2014 (upper foredune profile; gray). The foredune crest (d_c) is the elevation maximum on the seaward-most foredune. The foredune toe (d_t) is the topographic inflection point between the backshore and the foredune. Backshore slope is the slope between the shoreline (at mean high water (MHW) and the 4-meter contour. The foredune face slope (d_{face} slope) is the slope between the 4-meter contour and d_c . Fore-dune face width (d_{face} width) is the horizontal distance between 4-meter contour and d_c .

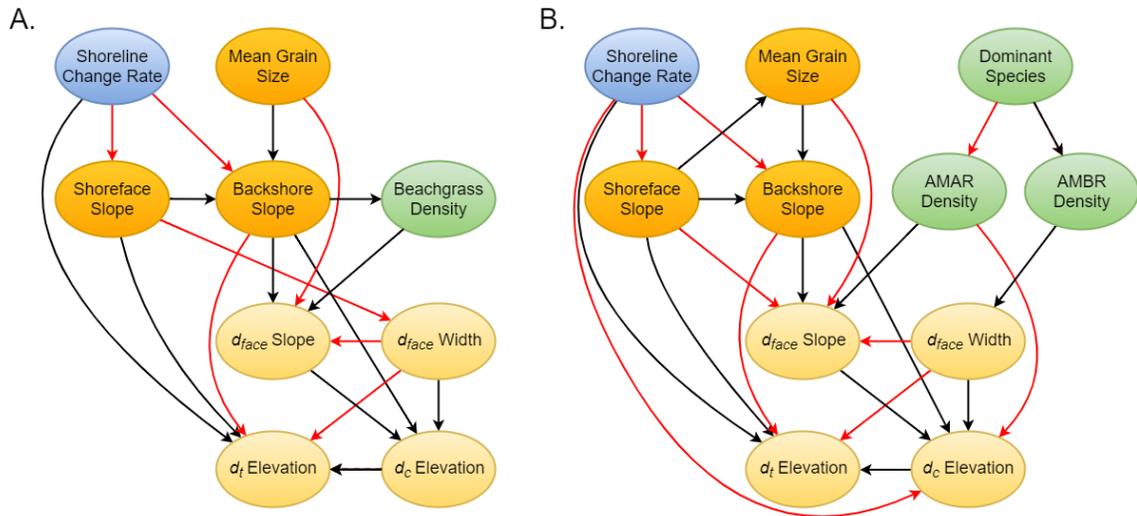


Figure 2.3. Gaussian Bayesian network (GBN) graphical models illustrating direct and indirect relationships among the two *Ammophila* species, and shoreface, beach, and foredune morphometrics. Black lines indicate positive direct relationships and red lines indicate negative direct relationships. (A) GBN in which *A. arenaria* and *A. breviligulata* densities are pooled into a unified beachgrass density variable (Foredune Morphology-GBN_{combined}). (B) GBN in which *A. arenaria* and *A. breviligulata* densities are treated as separate nodes (Foredune Morphology-GBN_{species}). Variable definitions presented in Appendix A, Table A2.

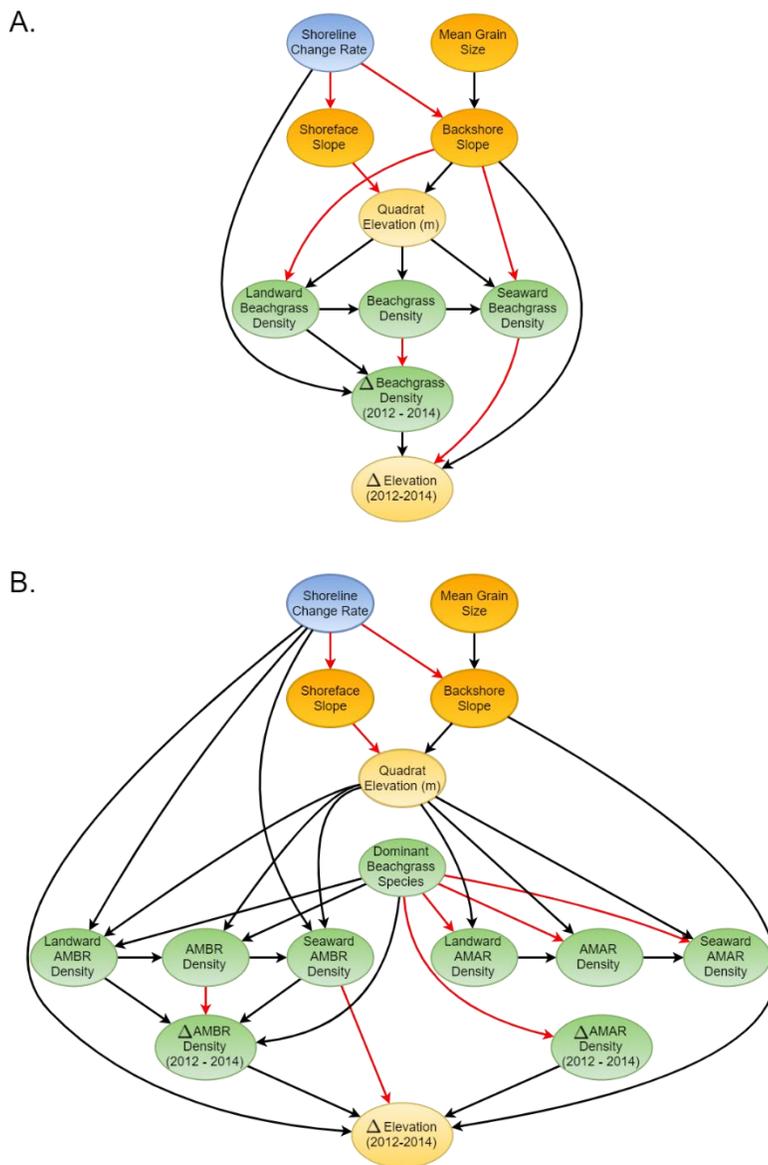


Figure 2.4. Gaussian Bayesian network (GBN) graphical models illustrating direct and indirect relationships among *Ammophila* density, shoreface and beach morphometrics, and sand accretion rates at quadrats along the foredune face between 2012 and 2014. Beachgrass density is that from 2012. Landward and seaward beachgrass density indicates beachgrass density in quadrats directly landward and seaward of the sampled quadrat in 2012. Δ beachgrass density (2012-2014) is the log response ratio of beachgrass density in the sampled quadrat between 2012 and 2014. Black lines indicate positive direct relationships and red lines indicate negative direct relationships. (A) GBN in which *Ammophila arenaria* and *A. breviligulata* densities are pooled into unified beachgrass density variables (Accretion-GBN_{combined}). (B) GBN in which *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) densities are treated as separate nodes (Accretion-GBN_{species}). Variable definitions presented in Appendix A, Table A4.

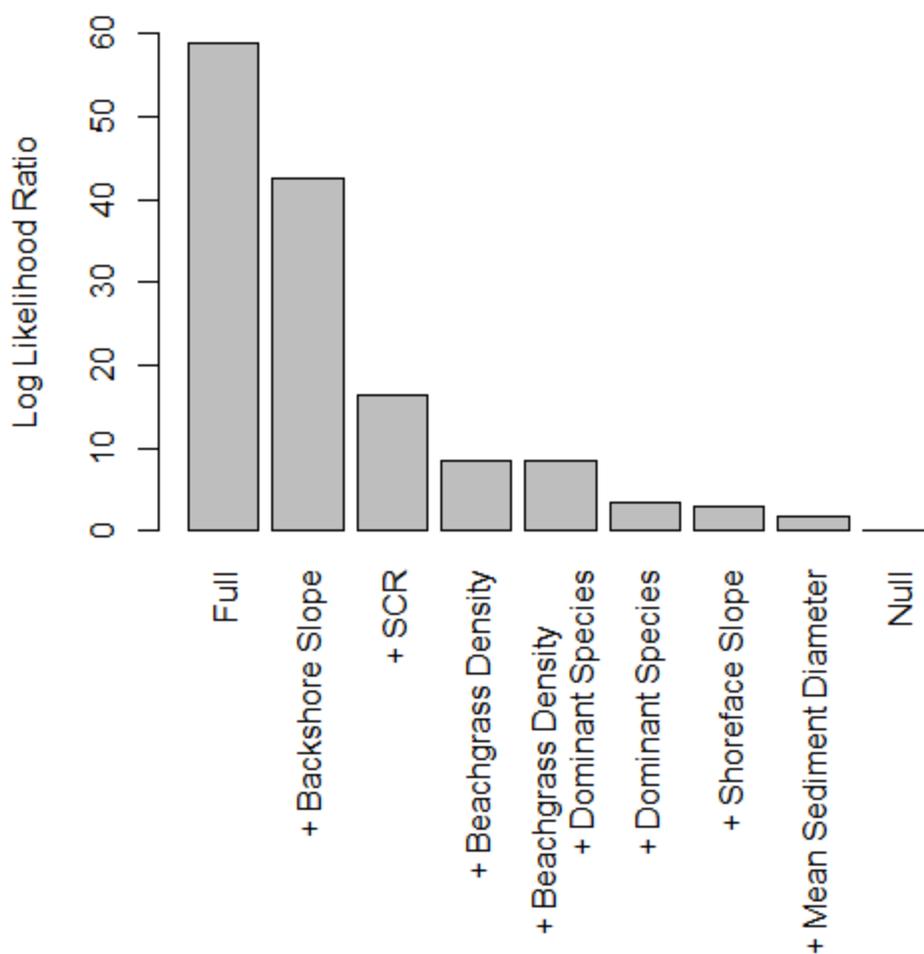


Figure 2.5. Using the *Ammophila* species-specific graphical model of foredune morphology (Foredune Morphology-GBN_{species}; Figure 2.3B), comparison of log likelihood ratios (LLR) of predicted foredune crest (d_c) elevations with prior knowledge of one node as compared to the non-informative null model. Full model indicates knowledge of all node values except foredune morphometrics (d_t elevation, d_{face} width, d_{face} slope, and d_c elevation). Null model indicates no prior knowledge of node values. More positive values indicate which nodes provide a greater increase in prediction accuracy and precision when included as prior knowledge.

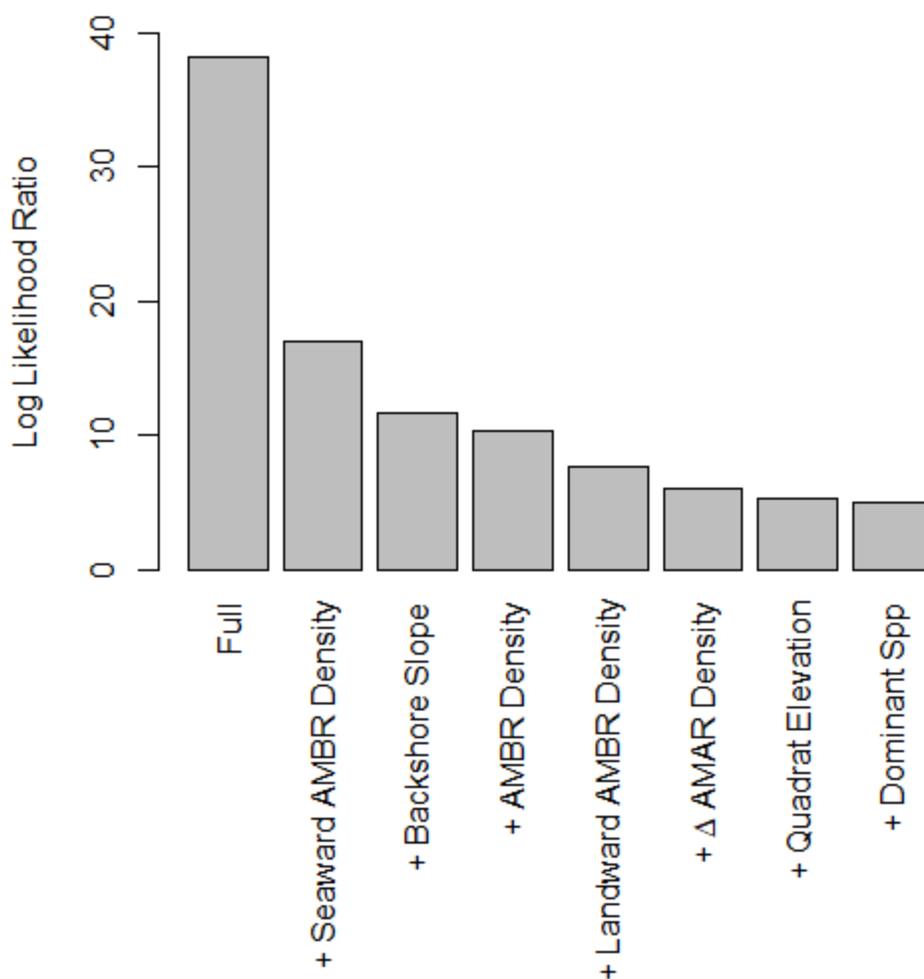


Figure 2.6. Using the *Ammophila* species-specific graphical model of sand accretion (Accretion-GBN_{species}; Figure 2.4B), comparison of log likelihood ratios (LLR) of predicted changes in elevation (sand accretion) at quadrats with prior knowledge of one node as compared to the non-informative null model. Full model indicates knowledge of all node values except Δ Elevation. Null model indicates no prior knowledge of node values. More positive LLR values indicate which nodes provide the greater increases in prediction accuracy and precision when included as prior knowledge.

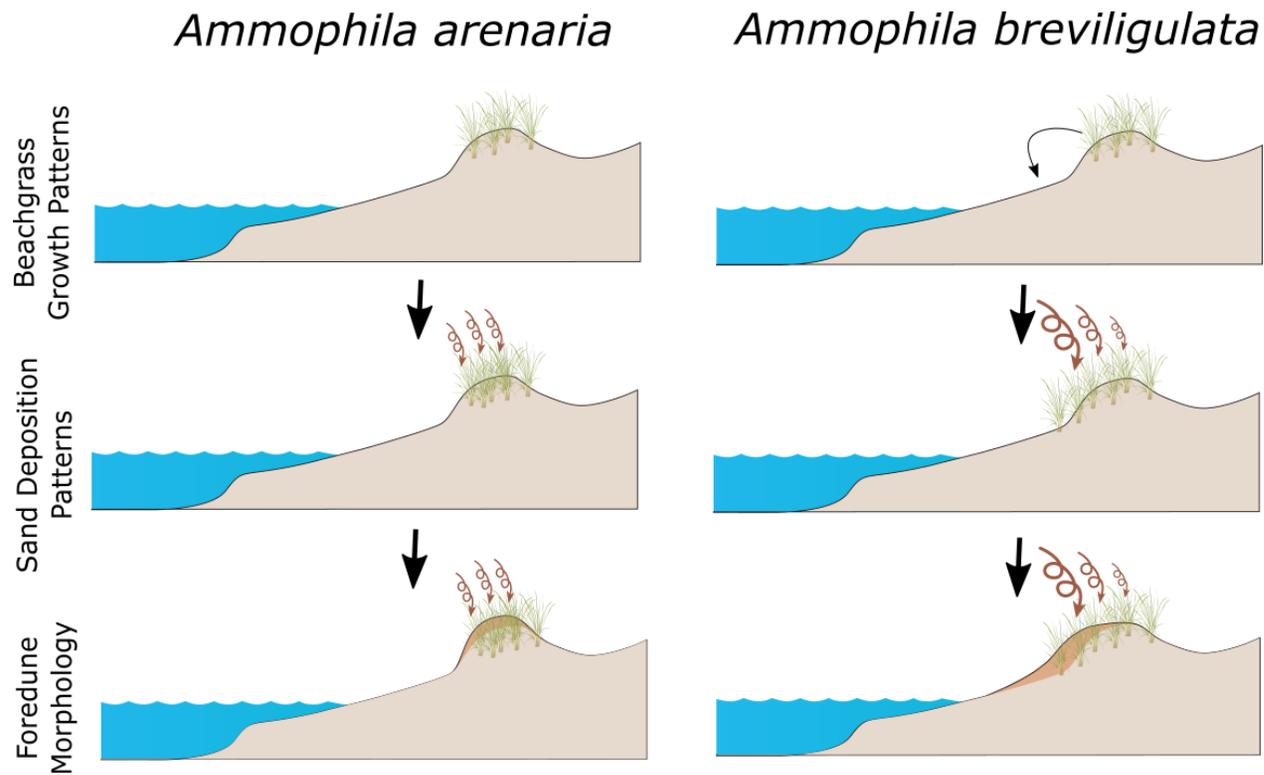


Figure 2.7. Illustration of proposed mechanism to explain differences in sand accretion and foredune morphology patterns between *A. arenaria* and *A. breviligulata*. Growth patterns: *Ammophila breviligulata* exhibits greater lateral growth than *A. arenaria*, resulting in greater seaward expansion of *A. breviligulata* (black arrow; Figure 2.4B). Sand deposition patterns: *Ammophila breviligulata* exhibit higher sand deposition on the leading edge of the vegetated dune, where new growth is occurring, while sand deposition on landward regions is inhibited by existing grasses. *Ammophila arenaria* exhibits more diffuse sand deposition where new growth is occurring. Foredune morphology: Due to both growth and sand deposition patterns, *A. breviligulata*-dominated dunes exhibit greater seaward expansion of the foredune, whereas *A. arenaria* exhibits greater vertical dune growth. Correspondingly, *A. breviligulata* abundance is associated with shallow-sloped, wide foredunes, while *A. arenaria* growth patterns are associated steeper sloped, taller foredunes (Figure 2.3B).

3. The invasion dynamics in a coastal foredune grass community depends on species and community level characteristics

Reuben G. Biel, Shawn Gerrity, Sally D. Hacker, Eric Seabloom, Aaron David, and Peter Ruggiero

Abstract

Researchers have long sought to understand what factors influence successful invasions by non-native plants. Most often, invasive species have been examined to classify traits that may indicate species invasiveness (e.g., growth rate, dispersal strategies), or invaded communities have been examined to identify community characteristics that influence habitat invasibility (e.g., resource availability, disturbance, stress, species diversity). In this study, we examined both the invasiveness of three dune grass species and the invasibility of foredune communities across a gradient of sand deposition along the U.S. Pacific Northwest coast. Our results show that the two non-native beachgrasses, *Ammophila breviligulata* and *A. arenaria* are more productive than the native *Elymus mollis*. Both *Ammophila* species generally exhibited higher survival, biomass, leaf area, and tiller abundance than *E. mollis* across a gradient of sand burial intensity. Moreover, of the three community types, *A. breviligulata* and *A. arenaria*-dominated foredune communities were less invasible than *E. mollis* communities. *Elymus mollis*-dominated communities, for example, fostered higher colonist survival and biomass than the *Ammophila*-dominated communities and the density of *E. mollis* tillers within the community was positively related to colonist survival and biomass. These differences in invasiveness and invasibility have significant implications for management of invasive species, conservation, and ecosystem services in the U.S. Pacific Northwest. They further illustrate the value of concurrently considering species invasiveness and community invasibility for understanding determinants of invasion success.

3.1. Introduction

The introduction of non-native invasive species is one of the pre-eminent drivers of biodiversity and ecosystem change over the past century (MEA 2005). Through intentional and unintentional translocations, the frequency and magnitude of non-native invasive species introductions has increased in recent decades (Pyšek and Richardson 2010). The invasion success of non-native species is influenced by dispersal, environmental, and biotic filters, affecting both the invasiveness of non-native species and the invasibility of established communities (Keddy 1992, Lawton and Kinne 2000, Theoharides and Dukes 2007, Gallien et al. 2015). Here we define invasiveness as the capacity for a species to increase its abundance and biomass upon colonization and define invasibility as the propensity for a community to allow invasion (Lonsdale 1999, Richardson and Pyšek 2006, Hui et al. 2016).

Researchers have long sought to identify patterns, processes, and characteristics that indicate invasiveness in plants (Baker 1965, Rejmánek 1999, 2000, Pyšek and Richardson 2008, Van Kleunen et al. 2010). Based on hundreds of case studies, invasive species often exhibit high rates of local and long-distance dispersal, high fecundity, and vegetative reproduction, which reduce barriers to dispersal. Large geographic ranges also confer advantages due to higher likelihoods of dispersal and greater tolerance for a broad range of environmental conditions (Rejmánek 2000, Richardson and Pyšek 2006). Moreover, invasive species often exhibit traits that are more extreme than functionally similar native species, allowing them to occupy vacant or extreme niches (Crawley et al. 1996) and thereby avoid biotic barriers to invasion. Nevertheless, few traits are universally predictive of invasiveness because the mechanisms of invasion vary based on the local environment, the native species pool, and the phase of invasion (Alpert et al. 2000, Dietz and Edwards 2006, Theoharides and Dukes 2007, Pyšek and Richardson 2008).

Invasion success also depends upon the invasibility of the invaded community: among other factors, climate, resource availability, and levels of disturbance and stress (Alpert et al. 2000, Richardson and Pyšek 2006) have been shown to influence

invasibility of communities (Hobbs and Huenneke 1992, Davis et al. 2000, Seabloom et al. 2003). Biotic interactions can further alter invasibility, although their influence may also vary with species diversity (Palmer and Maurer 1997, Levine and D'Antonio 1999), disturbance (Belote et al. 2008, Clark and Johnston 2011), stress (Alpert et al. 2000, Dethier and Hacker 2005, Bulleri et al. 2008, Zarnetske et al. 2013), and resource availability (Seabloom et al. 2003, Blumenthal 2006).

Because of these inherent differences in species invasiveness and community invasibility, the consequence of non-native species introductions varies not only among species but also with the communities they invade. For example, it is thought that communities with high resource availability, frequent disturbance, and high propagule pressure tend to experience more invasions (Lonsdale 1999, Davis et al. 2000), while harsh and abiotically stressful communities experience fewer invasions (Alpert et al. 2000, Zefferman et al. 2015). What attributes of harsh environments, then, prevents the colonization, establishment, and spread of invasive plants? Propagule limitation may explain some of these patterns because of the lower intensity of use and visitation rates of these communities by humans (Alpert et al. 2000, Zefferman et al. 2015). Stressful communities may also experience fewer invasions because of strong abiotic filters. Invaders may be intolerant of or poorly adapted to environmental extremes, toxins, or the exploitation of scarce resources (Hobbs and Mooney 1991, Dukes and Mooney 1999, Alpert et al. 2000, Going et al. 2009).

On the other hand, the role of biotic interactions in deterring invasions in stressful habitats is less certain. Ecological theory suggests that, the relative importance of positive and negative species interactions vary across gradients of environmental stress and disturbance, with positive interactions predicted to be more common in harsh environments (Bertness and Callaway 1994, Hacker and Gaines 1997, Brooker and Callaghan 1998, Bruno et al. 2003). The rationale is that as stress or disturbance increases, the potential ameliorating effects of one species on another will outweigh the potential negative effects on one another. However, even though positive interactions are now recognized as important determinants of community structure (e.g., see He et al.

2013), their influence on biological invasions across environmental gradients remains underappreciated (Bulleri et al. 2008, Traveset and Richardson 2014, Gallien and Carboni 2017) and are often ignored. Facilitation can alter the course of species invasions, where a primary invader facilitates secondary invasions (i.e., invasional meltdown (Simberloff and Von Holle 1999, Richardson et al. 2000, Simberloff 2006)), where the invader facilitates native species (Rodriguez 2006), and where a native species facilitates an invader (Dethier and Hacker 2005, Zarnetske et al. 2013, Traveset and Richardson 2014).

Thus, invasion success is determined both by the characteristics of the invading species (invasiveness; e.g., survival, growth rates, clonality) and properties of the community (invasibility; e.g., abiotic conditions, biotic interactions). However, studies rarely examine invasiveness and invasibility in tandem, or explore whether species interactions and abiotic conditions alter both species invasiveness and community invasibility. For example, does the competitiveness of an invading species confer invasiveness? Similarly, does the competitiveness of species within an established community confer invasion resistance? Finally, how do environmental gradients alter species invasiveness and community invasibility?

To approach these questions, we investigated both the species invasiveness and community invasibility of beach grasses on foredunes along the U.S. Pacific Northwest coast using field reciprocal invasion trials. Foredunes are defined as the seaward-most sand ridge, running parallel to the shoreline. The Pacific Northwest foredune system is currently undergoing two non-native grass species invasions as a result of many decades of intentional planting. Historically, the ecosystem was dominated by endemic hummock-building grass *Elymus mollis* and forbs (e.g., *Abronia latifolia*, *Ambrosia chamissonis*, *Tanacetum camphoratum*) (Wiedemann 1984). With development of coastal towns, industries, and military bases in the early 20th century, sand burial and dune blowouts presented a significant hazard to infrastructure (Schwendiman 1977). However, the low natural density of *E. mollis* prevented it from acting as an effective sand stabilizer in foredune habitats (Zarnetske et al. 2012). Consequently, coastal managers searched for other sand stabilization methods, settling on two species of *Ammophila*.

Ammophila arenaria and *A. breviligulata* were cultivated and extensively planted on coastal dunes throughout the Pacific coast to immobilize wind-blown sand. Native to Europe and North Africa, *A. arenaria* was first introduced to Oregon in 1910, was planted through the 1960s (Green 1965), and subsequently colonized all dunes in the Pacific Northwest. It is currently the dominant foredune grass in central and southern Oregon (Hacker et al. 2012). In contrast, *A. breviligulata*, native to the U.S. mid-Atlantic and Laurentian Great Lakes, was planted in southern Washington, USA in the 1930s. Since its introduction, the range of *A. breviligulata* expanded predominantly northward into British Columbia, Canada, but also slightly southward into northern Oregon, displacing *A. arenaria* as the dominant beachgrass (Seabloom and Wiedemann 1994, Page 2001, Hacker et al. 2012, David et al. 2015).

Current distributions and field surveys show that the two *Ammophila* congeners mostly occur as monocultures, with *A. breviligulata* dominating northern dunes and *A. arenaria* dominating southern dunes (Hacker et al. 2012). At most sites, the native *E. mollis* sparsely co-occurs with the dominant grass species present, sometimes in small monoculture patches at the toe of the dune or in meadows in the back of the dune. Based on a compendium of field surveys between 1988 and 2014, mesocosm experiments, and removal experiments, *A. breviligulata* outcompetes *A. arenaria* (Seabloom and Wiedemann 1994, Hacker et al. 2012, Zarnetske et al. 2012, 2013, 2015, David et al. 2015), potentially to the point of competitive exclusion (Chapter 4). Further, based on the invasion history and work by Zarnetske et al. (2013), *E. mollis* appears to be an inferior competitor in foredune habitats, although it may have conditionally positive interactions with the *Ammophila* species under high sand burial conditions. However, each of these studies examined species interactions in either a late stage of invasion (surveys) or within artificial polyculture assemblages that are rarely observed in nature (mesocosms). To understand the processes important to the invasion, we conducted a field based transplant experiment to examine the invasiveness of the three beach grass species and the invasibility of each grass community at sites in southwest Washington and northwest Oregon.

Specifically, we asked: Does the invasiveness of each species differ, and if so, why? What characteristics of the species are important to their invasiveness? Invasiveness is often associated with traits that foster fast growth and competitive performance during the colonization and establishment phases (Theoharides and Dukes 2007). Based on species-specific differences in productivity and growth form, we hypothesized that the *Ammophila* congeners would be more invasive than *E. mollis* due to greater rates of clonal growth, greater biomass production, higher resource use efficiency, and competitive dominance (Pavlik 1983b, 1985, Hacker et al. 2012, Zarnetske et al. 2013). However, species invasiveness might also vary across gradients in sand burial because the *Ammophila* species exhibit distinct tiller production responses to burial (Baye 1990, Zarnetske et al. 2012, Chapter 4).

To investigate how environmental and biotic filters alter invasibility, we asked: Do the foredune grass community types differ in their invasibility to the three species of dune grasses, and if so, why? How does community structure and sand deposition alter invasibility? If strong competitive interactions reduce habitat invasibility, we hypothesized that the *A. breviligulata* community type would be least invasible and the *E. mollis* community type would be most invasible to each of the three grass species. Correspondingly, if competitive interactions alter invasibility, we would observe a negative density-dependent effect of community tiller density on colonist survival and biomass, but per-tiller interaction strength could vary among species. The effects of sand burial on dune community invasibility was less certain; it could act as a stress or disturbance that increases abiotic resistance, or as a nutrient source from the beach that could facilitate the invasion. Finally, because positive interactions could alter community assembly under harsh conditions, some community types might provide positive density-dependent effects to invaders under high sand deposition regimes (Zarnetske et al. 2013).

Finally, we asked, is there an interaction between the invasiveness of the three grass species and invasibility of the three grass communities in which they invade? If so, is this modified by sand deposition rates? In particular, are species with high invasiveness also resistant to re-invasion by competing species, and do these invasiveness-invasibility

relationships vary across gradients in stress and disturbance? If competitive hierarchies and negative species interactions determine both species invasiveness and community invasibility, then we hypothesize that the species characteristics that make an invader invasive might also prevent re-invasion (i.e., confer invasion resistance).

To address these questions and hypotheses, we performed a transplant experiment in which we introduced beach grass colonists from each of the three species into monocultures of each of the three beach grass community types. We then assessed invader success and community invasibility based on the survival, biomass, and morphology of the colonists.

3.2. Methods

3.2.1. Study sites

We performed a transplant study at 10 sites (Washington: Grayland, Heather, Long Beach; Oregon: Iredale, Clatsop Plains, Seaside, Cape Lookout, Sand Lake, Pacific City) within seven littoral or sub-littoral cells (i.e., a self-contained unit of coastline in which sediment circulates, with sediment sources, sinks, and budgets that are independent of neighboring units) in southwest Washington and northwest Oregon USA that varied in their dominant beach grass community and sand supply (Figure 3.1; Appendix B, Table B1). The sites span 181 km of shoreline and vary in short-term annual rates of shoreline change from -1.47 m/yr. (erosion) to +31.8 m/yr. (progradation) (Ruggiero et al. 2013). Rates of shoreline change reflect beach sediment budget conditions and influence rates of sand deposition on beaches and dunes (Psuty 2004, Ruggiero et al. in press).

3.2.2. Transplant experimental setup

Between April and June of 2010 at each of the 10 sites, we established three plots in which each of the three grass species was dominant to serve as the community to be invaded (28 plots total; *A. arenaria* absent from two sites). Typically, *Ammophila arenaria*- and *A. breviligulata*-dominant plots were located on the foredune face or crest, while *Elymus mollis*-dominant plots were located near the foredune toe or face. To

examine the performance of invading plants within each plot, we subdivided each 90 cm x 180 cm plot into a 4 x 7 grid with 28 total grid coordinates spaced 30 cm apart. We then weighed, tagged, and randomly planted 9 replicate plants of each species (27 plants total) at 27 of the 28 grid coordinates within each plot. The plants were collected at the sites in which they were transplanted and had roughly 1-2 tillers per individual plant. They were held in buckets of water for up to a week before transplantation to reduce the shock from collection and to initiate rhizome and root growth.

To measure sand deposition rates within the plots, a large metal washer was set 5 cm below the surface of the sand at each of the four corners of the plot and held in place with a long metal nail driven through the washer and into the sand. We measured sand deposition by locating the washer with a metal detector, gently digging to find the top of the washer, and measuring the distance between the washer and the sand surface. After each measurement, washers and nails were reset 5cm below the sand surface.

We visited the plots quarterly between April 2010 and October 2012 to record the survival and tiller number for each transplant and to measure the vertical sand deposition at the four corners of the grid. During the establishment phase of the experiment (April to December 2010), some plants died and were replaced with similar sized plants of the same species. In addition, several plots suffered high plant mortality due to excessive erosion, sand burial, or overwash by waves. Consequently, between July and December 2010, we established eight additional plots nearby to replace eight of nine failed plots.

Upon completion of the experiment in October 2012, we destructively sampled each plot by excavating up to 2 m below the sediment surface to recover the aboveground and belowground portion of the transplanted plants. We also collected all background community plants within the plot to characterize each community. All plants were dried in bulk at 38°C for 24 hours. For each transplanted plant, we measured aboveground and belowground biomass, number of tillers, and leaf length, leaf width, and leaf count, from which we calculated the total leaf area for plant ($0.5 \cdot \text{length} \cdot \text{width} \cdot \text{leaf count}$). For the background community, we measured tiller number per species and total biomass per species within each plot.

3.2.3. Statistical analyses

To examine the relative invasiveness of colonizing grasses and the relative invasibility of established grass community types, we utilized an information theoretic approach to model comparisons using sample size corrected Akaike Information Criterion (AIC_c) methods. Based on AIC_c scores, we identify the relative support for competing statistical models and describe model parameter estimates from the best supported model.

To assess the relative invasiveness of the three grass species, we used generalized linear mixed models to estimate survival, biomass, leaf area, and tiller abundance among colonizing species, *within* each community type (i.e., one model per response variable (4) per community type (3) = 12 invasiveness models). For survival metrics, we performed mixed effects logistic regression (logit link function) to model the odds of colonist survival (count of live colonists per species per plot / count of dead colonists per species per plot) based on colonist species identity and annual sand deposition rate. For biomass metrics, we used a linear mixed model to estimate the relationship between log(total dry biomass) and initial wet biomass, colonist species identity, and annual sand deposition rate. For leaf area, we modeled how log(total leaf area) relates to colonist species identity and annual sand deposition rate using linear mixed models. Finally, for tiller abundance, we performed mixed effects Poisson regression (log link function) to model tiller abundance based on colonist species identity and annual sand deposition rate. To account for the nested structure of our sampling design (27 plants per plot), all invasiveness regression models included a random intercept term (1|plots) to account for plot-level variation in survival, biomass, leaf area, and tiller abundance.

To assess the relative invasibility of the three community types, we compared the relative survival and biomass of each transplant species *among* the three community types (i.e., one model per response variable (2) per transplant species (3) = 6 invasibility models). To assess survival, we performed mixed effects logistic regression (logit link function) to model the odds of colonist survival (count of live colonists per species per plot / count of dead colonists per species per plot) against community type and annual

sand deposition rate. To account for the nested structure of our sampling design (9 plants of a single species per plot; 3 plots per site), we included a nested random intercept term (1|site/plot) to account for variation in survival among plots and sites. To determine whether each community exerted a density-dependent control on the colonizing plants, we additionally modeled survival odds against the tiller density of each established species and sand deposition rate. For biomass, we performed linear mixed models to compare $\log(\text{total biomass})$ of each colonizing species against initial wet biomass, community type, and annual sand deposition rate, with a nested random intercept to account for site-level and plot-level variation. To determine whether biomass related to the tiller density of the communities, we similarly modeled the $\log(\text{total biomass})$ of each colonizing species against initial wet biomass, sand deposition rate, and the tiller density of each established species. All modeling was performed using the lme4 package (Bates et al. 2015) in R v3.4.0 (R Core Team 2017).

3.3. Results

3.3.1. Characteristics of foredune community types

Annual sand deposition rates (cm/yr.) varied among the sites and plots (Appendix B, Table B1) with the most deposition in a plot at Pacific City (PC-4; 60.1 cm/yr.) and the least deposition in a plot at Cape Lookout (CL-3; 4.1 cm/yr.). Across foredune community types, deposition in *A. breviligulata* communities ranged from 6.4 cm/yr. to 43.8 cm/yr. (mean: 21.7 cm/yr.); deposition in *A. arenaria* communities ranged from 12.0 cm/yr. to 51.9 cm/yr. (mean: 31.7 cm/yr.); and deposition in *E. mollis* communities varied from 4.1 cm/yr. to 60.1 cm/yr. (mean: 29.5 cm/yr.). Mean rates of sand deposition did not differ among community types (ANOVA, $F_{2,24} = 1.2$, $p=0.33$). The range of tiller densities varied by species and among community types (Appendix B, Table B2): *Ammophila arenaria* communities had an average *A. arenaria* tiller density of 367 tillers/m² (range: 267 to 469 *A. arenaria* tillers/m²); *Ammophila breviligulata* had an average *A. breviligulata* tiller density of 173.6 tillers/m² (range: 116 to 354 tillers/m²); and *Elymus mollis* communities had an average *E. mollis* tiller density of 41.4 tillers/m²

(range: 13 to 120 tillers/m²), but also contained some *A. breviligulata* tillers (i.e., ELMO communities were rarely monocultures; see Appendix B, Table B2).

3.3.2. Comparison of invasiveness of the dune grass species across community type and sand deposition

For most response variables, we found that *A. breviligulata* was the most invasive, exhibiting survival odds, biomass, and leaf area that were comparable to or higher than *A. arenaria* and consistently higher than *E. mollis* across all community types and sand deposition rates (Table 3.1). Within the *A. breviligulata* community type, *A. breviligulata* colonists exhibited greater odds of survival (odds ratio (OR): 3.42 [95% confidence interval: 1.82-6.59] and 3.39 [95% CI: 1.83-6.40], respectively) and higher biomass (by 46% [CI: 8%-98% higher] and 81% [CI: 36%-140% higher], respectively) than *A. arenaria* or *E. mollis* colonists, after accounting for initial biomass (Figure 3.2A, B). Moreover, *A. breviligulata* colonist total leaf area was 108% higher (CI: 6%-149% higher) and 166% higher (CI: 84%-290% higher) than *A. arenaria* and *E. mollis* colonist leaf area, respectively (Figure 3.2C, D). Nevertheless, colonist tiller abundance did not vary between the *Ammophila* species (*E. mollis* tiller abundance was not included in the analysis).

Within the *A. arenaria* community type, *A. breviligulata* survival odds were similar to those of *A. arenaria*, but were 165% higher than *E. mollis* survival (OR: 2.65; CI: 1.11-6.55) (Figure 3.3A), given similar rates of sand burial. However, total biomass was similar among all colonizing plant species (Figure 3.3B). Moreover, *A. breviligulata* colonist total leaf area was 64% higher (CI: 6%-149% higher) than *A. arenaria* colonist leaf area, but similar to *E. mollis* leaf area (Figure 3.3C, D). However, colonist tiller abundance did not vary between the *Ammophila* species.

Finally, within the endemic *E. mollis* community type, the odds of survival for *A. breviligulata* colonizers was similar to those of *A. arenaria* colonizers, but were 4.68 times higher than the survival odds for *E. mollis* colonizers (OR: 5.68; CI: 1.13-10.08; Figure 3.4A). Correspondingly, *A. breviligulata* and *A. arenaria* total biomass was comparably higher than colonizing *E. mollis* biomass per plant, but the degree of

difference varied with initial biomass (Figure 3.4B). *Ammophila breviligulata* colonist total leaf area was also 388% higher (CI: 204%-670% higher) than *E. mollis* colonist leaf area, but similar to *A. arenaria* leaf area (Figure 3.4C, D). Finally, *A. arenaria* tiller abundance was 101% higher (CI: 74%-133% higher) than *A. breviligulata* tiller abundance.

Rates of annual sand deposition also influenced invasiveness (depending on the response variable and community type), but it did not differ among the three colonizing species (Table 3.1). Within *A. breviligulata* communities, although every additional 10 cm of sand deposition reduced the odds of survival for all species by 37% (CI: 19%-52% decrease), it increased their total biomass by 29% (CI: 7%-55% increase) and had no effect on total leaf area (Figure 3.2A, B). Within the *A. arenaria* communities, higher annual rates of sand deposition also decreased the odds of survival for all species by 24% (CI: 44% decrease-3% increase) per 10 cm of annual sand deposition, did not affect their biomass, suggestively increased leaf area by 31% (CI: 3% decrease-77% increase), and increased tiller production by 28% (CI: 6%-50% increase) for all colonizing species (Figure 3.3A, B). Finally, within *E. mollis* communities, sand deposition had no observable impact on survival, total leaf area, and tiller abundance (Figure 3.4).

3.3.3. Comparison of invasibility of the foredune community types with tiller density and sand deposition

Of the three foredune community types, *A. breviligulata* and *A. arenaria* communities were the least invasible, contributing to lower colonist survival and biomass as compared to *E. mollis* communities across all sand deposition rates. (Table 3.2, Figure 3.5-Figure 3.6). In contrast, *E. mollis* communities either had a neutral or positive effect on these same metrics of colonist performance, especially as *E. mollis* tiller density and sand deposition increased (Table 3.2-Table 3.3, Figure 3.5-Figure 3.6). Colonist leaf area and tiller abundance for each grass species were also compared across community types and showed similar invasibility patterns (Table 3.2-Table 3.3). Results for leaf area and tiller abundance results are shown in Appendix B, Figures B2-B3.

Differences in colonist performance across community types demonstrates this invasibility hierarchy. For *A. breviligulata* colonists, survival was unaffected by foredune community type, but was mainly controlled by sand deposition (Table 3.2). Nevertheless, *A. breviligulata* colonist biomass was significantly lower in both *A. breviligulata* and *A. arenaria* communities than in *E. mollis* communities, by 52% (95% CI: 17%-72% lower) and 51% (CI: 4%-75% lower) respectively, after accounting for initial plant mass. Nevertheless, *A. breviligulata* colonist survival and biomass were not related to the density of established *A. breviligulata* or *A. arenaria* tillers within plots (hereafter, background tiller density) (Figure 3.5A, Figure 3.6A).

Ammophila arenaria colonist shows similarly poor performance in *A. breviligulata* and *A. arenaria* communities. The odds of survival for *A. arenaria* colonists was 60% lower (odds ratio (OR): 0.40; CI: 0.16-0.97) and 68% lower (OR: 0.32; CI: 0.15-0.72) in *A. breviligulata* communities than *A. arenaria* and *E. mollis* communities, respectively. Likewise, *A. arenaria* colonist biomass in *A. breviligulata* and *A. arenaria* communities was 67% lower (CI: 42%-81% lower) and 71% lower (95% CI: 44%-85% lower) than in *E. mollis* communities, respectively, and did not differ between *A. arenaria* and *A. breviligulata* community types, given similar rates of sand burial. When compared against background tiller density, *A. arenaria* colonist survival decreased by 28% (OR: 0.72; CI: 0.51-0.93) per 50 *A. breviligulata* tillers/m² but were unrelated to *A. arenaria* background tiller densities (Figure 3.5B). Correspondingly, *A. arenaria* colonist biomass decreased by 20% (CI: 35% decrease-0.4% increase) for every 50 additional *A. breviligulata* tillers/m² and decreased by 13% (CI: 4%-21% decrease) per 50 *A. arenaria* tillers/m² (Figure 3.6B), indicating density-dependent resistance to invasion.

Ammophila breviligulata communities were also inhospitable to *E. mollis* colonists, though *A. arenaria* communities were more invasible. The odds of *E. mollis* colonist survival neither varied among community types, nor varied with community tiller density (Table 3.2). However, *E. mollis* biomass was 66% higher (CI: 0.3% lower-190% higher) in *A. arenaria* communities than *A. breviligulata* communities (biomass did not differ between *E. mollis* communities and either of the *Ammophila* communities), given similar

rates of sand burial constant. When compared against background tiller density, *E. mollis* colonist biomass increased by 9% (CI: 4%-15% increase) per 50 *A. arenaria* background tillers/m² and *A. breviligulata* background tiller densities were unrelated to *E. mollis* colonist biomass (Figure 3.6C). Overall, then, *A. breviligulata* and *A. arenaria* communities often fostered lower survival and biomass for colonists than *E. mollis* communities. Based on density-dependent interactions between species-specific background tiller densities and colonists, *A. breviligulata* and *A. arenaria* communities had most neutral or negative effects on colonist survival and biomass (Figure 3.5-Figure 3.6).

In contrast, *E. mollis* communities fostered higher survival and growth in colonists. *Ammophila breviligulata* colonists exhibited 104% higher (12%-307% higher) and 107% higher (27%-239% higher) biomass in *E. mollis* communities than in *A. arenaria*- and *A. breviligulata* communities, respectively, after accounting for the initial mass of *A. breviligulata* colonists (Table 3.2). This increase in *A. breviligulata* colonist biomass was positively associated with *E. mollis* tiller density and with sand deposition rates (Table 3.3, Figure 3.6A). *Ammophila arenaria* colonist performance was also highest in *E. mollis* communities. The odds of survival for *A. arenaria* colonists was 278% higher (OR: 3.78; CI: 2.35-6.06) and 308% higher (OR: 4.08; CI: 2.34-7.10) in *E. mollis* communities than in *A. breviligulata* and *A. arenaria* community types. Correspondingly, the biomass of *A. arenaria* colonists in *E. mollis* communities were 278% higher (CI: 154%-500% higher) and 308% higher (CI: 145%-606% higher) than in *A. breviligulata* and *A. arenaria* communities, respectively. When compared against background tiller density, *A. arenaria* colonist survival odds increased by 97% (OR: 1.97; CI: 1.03-4.52) and colonist biomass increased by 90% (CI: 15%-206% increase) for every additional 50 *E. mollis* tillers/m² (Figure 3.5B, Figure 3.6B). Finally, the odds of *E. mollis* colonist survival neither varied among community types, nor varied with community tiller density. Nevertheless, biomass increased by 60% (CI: 19%-117% increase) per 50 tillers/m² of *E. mollis* in the community (Figure 3.5C). Based on the positive density-dependent interactions between *E. mollis* background tiller densities and colonists, *E.*

mollis communities had predominantly positive effects on colonist survival and biomass (Figure 3.5-Figure 3.6).

3.4. Discussion

In the U.S. Pacific Northwest foredune system, we found that the two non-native beachgrasses, *Ammophila arenaria* and *A. breviligulata* exhibited superior survival and growth as compared to the native *Elymus mollis* (Table 3.4). Both *Ammophila* species generally exhibited higher survival odds, biomass, leaf area, and tiller abundance than *E. mollis* when compared within community types and across a gradient of sand burial intensity (Figure 3.2-Figure 3.4). We further found that *A. breviligulata* survival and biomass conditionally exceeded those of *A. arenaria*, depending upon the dominant community type.

Correspondingly, we found that *Ammophila* communities were the least invulnerable community type, whereas *E. mollis* communities were most invulnerable. *Elymus mollis* communities often foster higher survival and biomass than the *Ammophila* communities for all colonizing species (Table 3.4). Further, background *E. mollis* tiller densities were often positively associated with colonist performance metrics, suggesting that *E. mollis* facilitated colonist survival and growth (Figure 3.5-Figure 3.6). In contrast, the *Ammophila* dominated communities exhibited similar, low levels of invulnerability to all three colonizing species, although they sometime differed by performance metric and colonist species identity. Further, the effect of background *Ammophila* tiller densities was often neutral, although *A. breviligulata* background tiller density was negatively associated the survival and biomass of *A. arenaria* colonists (Figure 3.5-Figure 3.6). Thus, it appears that the invasiveness of the three foredune grass species and invulnerability of the three foredune communities matches the competitive hierarchy of foredune plants (Seabloom and Wiedemann 1994, Hacker et al. 2012, Zarnetske et al. 2013, David et al. 2015, Chapter 4).

Finally, we found that sand burial exerted a moderate effect on invader performance, but its effect on survival (negative) differed from its effect on productivity (positive). Although the species differed in their response to sand burial, the natural gradient in sand

burial did not alter the rank order of species invasiveness or habitat invasibility.

Ammophila breviligulata was consistently superior to *A. arenaria* and *E. mollis* across all rates of sand deposition. Rather, the limited response to sand burial indicates that it was a minor stressor to the study species, even though it limits many species from occupying foredunes (Maun 2008). Thus, the observed rates of sand burial had little bearing on the outcome of invasion for the three dune grasses.

3.4.1. Invasiveness of foredune grass species

The hierarchy of invasiveness of the three foredune grass species is consistent with observational field surveys, trends, and manipulative mesocosm experiments. Since the introductions of *A. arenaria* and *A. breviligulata* to the Pacific Northwest in the 1910s and 1930s, respectively, they have displaced *E. mollis* as a dominant foredune grass, resulting in no extant *E. mollis*-dominated foredune communities and limited patches of *E. mollis* on the foredune itself (Wiedemann 1984, Wiedemann and Pickart 1996, Hacker et al. 2012). In addition, although *A. arenaria* was planted first and more extensively than *A. breviligulata*, *A. breviligulata* has almost completely displaced *A. arenaria* from foredunes in Washington, and is expanding its range northward and southward (Seabloom and Wiedemann 1994, Page 2001, Hacker et al. 2012, David et al. 2015). Based on manipulative mesocosm experiments, both *Ammophila* spp. are dominant to *E. mollis*, frequently resulting in exclusion of *E. mollis* (Zarnetske et al. 2013). In addition, *A. breviligulata* is dominant to *A. arenaria*, but studies differ as to whether exclusion occurs (Zarnetske et al. 2013, Chapter 4).

What traits might explain this invasiveness hierarchy? Sand deposition affected the survival and growth of the three dune grass species similarly: it reduced survival equally for all colonizing species, but also increased biomass across all species in most foredune community types (Figure 3.2-Figure 3.4). Thus, species-specific responses to sand deposition alone cannot explain this differential outcome. Rapid growth rates and clonal propagation are two common traits of successful invasive plants (Rejmánek 2000, Pyšek and Richardson 2008). In the foredune system, we found that *A. breviligulata* often exhibited higher survival, biomass, and total leaf area than *A. arenaria* and *E. mollis*, but

the magnitude of difference varied based on the community type (Figure 3.2B, Figure 3.3B, Figure 3.4B). Correspondingly, *A. arenaria* and *A. breviligulata* often produced more tillers than *E. mollis*. Thus, the foredune species that most rapidly increased in biomass, leaf area, and exhibited higher clonal growth were also the most pervasive foredune plant species. However, their relative success as colonists varied across community types, suggesting that habitat invasibility significantly influenced individual species' invasion success.

Although not explored in our study, invasion success for both *Ammophila* species may also be partly attributable to higher resource use efficiency. Each of the three dune grasses exhibits mutualistic associations with nitrogen fixing bacteria (Dalton et al. 2004). Even so, research shows that *A. arenaria* exhibits higher photosynthesis, lower concentrations of nitrogen in leaf blades, higher nitrogen use efficiency, and higher water use efficiency than *E. mollis*, resulting in higher overall biomass production (Pavlik 1983b, 1985). Correspondingly, preliminary data suggests that *A. breviligulata* water use efficiency is comparable to or exceeds *A. arenaria* water use efficiency, as measured by $\delta^{13}\text{C}$, while both species show lower $\delta^{13}\text{C}$ values than *E. mollis*, indicating that the *Ammophila* species are more physiologically adept at dealing with xeric conditions on foredunes (Constant and Hacker unpublished data). Thus, the success of the *Ammophila* invaders may in part be attributed to their superior growth rates, propagation, and resource use efficiency relative to the native grass.

On a broader scale, higher resource use efficiency and competitive dominance by non-native invasive species are not unusual phenomena (Funk and Vitousek 2007, Pyšek and Richardson 2008, Gioria and Osborne 2014). While there are many instances in which high resource availability disproportionately benefit invasive plants, other instances exist in which low resource availability benefits invasive non-natives at the expense of the native community (Daehler 2003, Seabloom et al. 2003, Funk and Vitousek 2007).

3.4.2. Invasibility of foredune grass communities

While the invasiveness of non-native species in part determines invasion success, community invasibility exerts an additional control on biological invasions. Both positive and negative biotic interactions, for example, may modify community invasibility. The most frequently studied negative interaction that alters community invasibility is resource competition (Theoharides and Dukes 2007), which can result from strong species interactions between a single species or guild and the invader (Smith et al. 2004, Fargione and Tilman 2005), or from multiple weaker interactions that aggregately reduce availability of a limiting resource (Fargione et al. 2003, Fargione and Tilman 2005). On northern Pacific Northwest foredunes, as described previously, *A. breviligulata* was competitively dominant to *A. arenaria* and *E. mollis*, resulting in displacement of both species. Based on our transplant experiment, *A. breviligulata*-dominated communities were also the least invasible (Table 3.4): for *A. arenaria* colonists, established *A. breviligulata* communities fostered lower survival than *A. arenaria* communities, and lower survival and biomass than *E. mollis* communities. The low invasibility of *A. breviligulata* communities likely arises in part due to negative interactions, as demonstrated by the negative density-dependent effects of *A. breviligulata* background tiller density *A. arenaria* colonist survival and growth. However, most per-tiller interactions with *A. breviligulata* communities were neutral (Figure 3.5-Figure 3.6), so negative interactions alone cannot fully explain differences in invasibility among community types. Moreover, because sand burial did not vary among community types, sand burial also could not explain this invasibility disparity.

Other biotic interactions may also influence invasion success, including interference competition (e.g., production of toxins; (Callaway and Ridenour 2004)) and facilitation (Richardson et al. 2000, Traveset and Richardson 2014). Facilitation is notable because it is commonly overlooked, but has significant potential to shape habitat invasibility. Facilitation can occur between two multiple non-native species (Simberloff and Von Holle 1999, Simberloff 2006), but also when a native species facilitates invasion by a non-native species, and vice-versa (Richardson et al. 2000, Cavieres et al. 2005,

Rodriguez 2006, Badano et al. 2007, Traveset and Richardson 2014). These latter cases can be intractable for management, where treatment of the invasive may pose risks to native species or to ecosystem services (Rodriguez 2006, Traveset and Richardson 2014, Lampert et al. 2014). In the Pacific Northwest foredune system, while competitive interactions may explain some variation in invasibility, facilitation by *E. mollis* may also influence invasion success. As established *E. mollis* density increased, biomass, tiller production, and leaf area for all colonizing species also increased (Figure 3.5-Figure 3.6; Appendix B, Figure B2 - Appendix B, Figure B3), suggesting that either (1) *E. mollis* is facilitating the invasion by the *Ammophila* species, or (2) patches where *E. mollis* are prolific are also highly suitable to the *Ammophila* invaders. Moreover, as annual rates of sand burial increased, the magnitude of the positive effects for both *Ammophila* species supra-additively increased with increasing *E. mollis* density (Appendix B, Figure B2 - Appendix B, Figure B3). This positive density-dependence between the native *E. mollis* and the other invaders is consistent with manipulative experimental work by Zarnetske et al. (2013). Mechanistically, *E. mollis* may provide structural support and shelter from sand scour (Zarnetske et al. 2013), or may facilitate *Ammophila* establishment by increase local elevation via aeolian sand deposition.

3.4.3. Influence of sand burial on invasiveness and invasibility

Environmental stress can alter invasion success by limiting availability of resources, altering costs of basal maintenance or productivity, or otherwise altering the relative growth rates of native and non-native plants (Alpert et al. 2000, Zefferman et al. 2015). Should stress sufficiently reduce survival or growth, it may transform an invasive species into a non-invasive non-native or prevent a non-native from establishing in the first place. In the Pacific Northwest foredune system, the effect of sand deposition differed by colonizing species across the stages of invasion (colonization versus establishment stages). In the colonization stage, for example, sand deposition had no impact on survival of *A. arenaria* or *E. mollis*, suggesting that sand burial neither increases nor decreases habitat invasibility to colonists of either species. In contrast, *A. breviligulata* survival decreased with sand deposition across all community types, indicating that habitat

invasibility to *A. breviligulata* is reduced with higher sand deposition. At the establishment phase of invasion, however, sand deposition increased biomass for all species (Appendix B, Figure B1, Figure 3.5). Thus, while sand burial did not alter or reduce invasion success during colonization, it increased invasion success during the establishment phase of invasion.

Within the invasibility literature, harsh environments are hypothesized to be less invulnerable due to environmental and biotic filtering (Alpert et al. 2000, Zefferman et al. 2015). However, our observed pattern of neutral to increasing invasibility with sand deposition is counter to this harshness-invasibility hypothesis (Alpert et al. 2000, Zefferman et al. 2015). Multiple processes relating to both species characteristics (i.e., invasiveness) and community properties (i.e., invasibility) might explain this disparity. At the species-level, while sand burial is the principal environmental filter that controls dune community composition (Maun 2008), it does not appear to limit the distribution and abundance of any of the grass species at levels of sand burial observed in this study. For example, both *Ammophila* species can survive more than one meter of sand burial per year, although they show reduced growth at those extremes (Huiskes 1979, Eldred and Maun 1982, Maun and Lapierre 1984, Zarnetske et al. 2012, Chapter 4). Additionally, sand burial might increase the invasiveness of the three grasses due to sand burial-associated adaptations. For example, in the *Ammophila* species, sand burial stimulates the development of young roots, which may be more efficient at absorbing nutrients than old roots (Marshall 1965) and have higher rates of bacterial nitrogen-fixation (Wahab and Wareing 1980). Similarly, moderate rates of sand burial have been shown to stimulate production of biomass and tiller production in the *Ammophila* species (Huiskes 1979, Eldred and Maun 1982, Disraeli 1984, Maun and Lapierre 1984). Thus, species-specific traits may enable the three grasses to exploit sand burial to increase productivity.

Sand burial might also operate at the community level, thereby increasing invasibility. For the *Ammophila* species, sand burial might permit a release from predation or competition. If colonizing foredune grasses are nitrogen or water limited (Pavlik 1983b, 1985), disturbance from sand burial might reduce resource utilization by

the community. For example, burial of beneath 60 cm/yr. of sand can cause greater than 50% mortality to *A. breviligulata* communities (Maun and Lapierre 1984), thereby lessening resource competition and freeing resources for colonizing plants. Sand burial might also broadly increase resource availability within the community via direct delivery of nutrients attached to sand grains or burial and subsequent decomposition of wrack (Constant and Hacker, unpublished data). Although sand burial is a stressor to many dune species, its propensity to increase invasion success for the three foredune grasses indicates that environmental filtering in harsh environments is species-specific. Thus, harsh environments do not confer abiotic resistance to invasion per se, but rather resistance may depend upon the interaction between habitat characteristics (invasibility) and the characteristics of invading species (invasiveness).

3.4.4. Conclusions and implications

We found that the relative invasiveness of Pacific Northwest dune grasses and the relative invasibility of the three dune grass communities were consistent with their competitive hierarchy: for invasiveness, *A. breviligulata* > *A. arenaria* > *E. mollis*; for invasibility, *A. breviligulata* communities < *A. arenaria* communities < *E. mollis* communities. Although negative species interactions partly influenced the invasibility of the *Ammophila* communities, positive interactions by *E. mollis* were the largest determinant of community invasibility; *E. mollis* communities were not solely invulnerable due to the competitive inferiority of *E. mollis*, but because *E. mollis* directly facilitated invasion. We further demonstrated that sand deposition can have contrasting impact on invasiveness and invasibility at different stages of invasion. While stress from sand burial may impede colonist survival, it can accelerate growth of established communities. Consequently, in regions with high rates of sand burial, the *Ammophila* species may have difficulty become established, but once established, they will thrive.

Prediction, prevention, and management of invasive species requires an understanding of the interactions among native and non-native species across environmental gradients. Our results have significant ecological and geomorphological ramifications for coastal management. From a coastal resilience perspective, *A.*

breviligulata builds shorter foredunes than *A. arenaria* (Seabloom and Wiedemann 1994, Zarnetske et al. 2012, 2015) because of its lower density of growth (Zarnetske et al. 2012) and lateral growth form (Chapter 2). Consequently, further invasion by *A. breviligulata* may increase storm-related coastal flooding along the Pacific coast due to shortened foredunes (Seabloom et al. 2013). Because these species co-occur in no other location on Earth, predicting *Ammophila* interactions and their ecological and geomorphological consequences would be unknowable without either direct experimentation (e.g., Zarnetske et al. 2013, Chapter 4) or post-invasion observation (Seabloom and Wiedemann 1994, Hacker et al. 2012).

In addition, our results show that the success of non-native invasive species depends upon complementarity between the characteristics of the invading species and the invaded habitat (Table 3.4). While few studies examine invasiveness and invasibility in tandem (Silvertown et al. 1994, Milbau et al. 2003), this Pacific Northwest foredune case study illustrates the value of reciprocal invasion trials for understanding both aspects of a community undergoing invasion for multiple stages of invasion. Investigation of invasiveness revealed the differing capacities for *A. breviligulata* and *A. arenaria* to successfully colonize and establish within different habitats, a relationship that was not apparent based on invasibility comparisons alone. Correspondingly, investigation of invasibility revealed that *E. mollis* may facilitate invasion by the *Ammophila* species, a relationship that could not be ascertained from examinations of species invasiveness. Simultaneous comparisons of species invasiveness and community invasibility reveal that invasion success is context-dependent, and is contingent upon both the identity of the invading species and the characteristics of the community.

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Table 3.1. Parameter estimates and 95% confident intervals for the best supported model (based on AIC_c and BIC model comparison) of log odds of survival, log(total biomass), and log(total leaf area) for *A. arenaria* (AMAR), *A. breviligulata* (AMBR), and *Elymus mollis* (ELMO) colonists among community types and with sand burial.

Community Type Response Variable	Fixed Predictor	Estimates	95% confidence interval	
			Lower	Upper
AMBR				
Log(Survival Odds)	Intercept	2.098	1.299	2.954
	AMAR Colonists	-1.230	-1.886	-0.597
	ELMO Colonists	-1.220	-1.856	-0.605
	Sand Burial	-0.047	-0.073	-0.021
Log(Biomass)	Intercept	2.099	1.592	2.623
	Initial Mass	0.178	0.062	0.306
	AMAR Colonists	-0.382	-0.627	-0.132
	ELMO Colonists	-0.591	-0.810	-0.315
Log(Leaf Area)	Intercept	4.939	3.746	6.141
	AMAR Colonists	-0.496	-0.911	-0.057
	ELMO Colonists	0.049	-0.420	0.531
	Sand Burial	0.027	-0.003	0.057
Log(Tiller Abundance)	Intercept	0.760	0.518	0.976
AMAR				
Log(Survival Odds)	Intercept	1.500	0.238	2.842
	AMAR Colonists	0.102	-0.787	0.996
	ELMO Colonists	-0.872	-1.770	-0.005
	Sand Burial	-0.027	-0.058	0.003
Log(Biomass)	Intercept	2.242	1.186	3.157
	Initial Mass	0.519	0.133	0.873
	Sand Burial	0.011	-0.013	0.038
	Initial Mass:Sand Burial	-0.009	-0.018	0.000
Log(Leaf Area)	Intercept	5.890	5.413	6.363
	AMAR Colonists	-0.735	-1.106	-0.366
	ELMO Colonists	-0.981	-1.360	-0.607
Log(Tiller Abundance)	Intercept	-0.252	-0.934	0.444
	Sand Burial	0.025	0.006	0.041
ELMO				
Log(Survival Odds)	Intercept	0.296	-0.383	0.985
	AMAR Colonists	0.649	-0.097	1.421
	ELMO Colonists	-0.895	-1.602	-0.212
Log(Biomass)	Intercept	3.505	2.952	4.048
	AMAR Colonists	-0.256	-0.583	0.076
	ELMO Colonists	-1.230	-1.550	-0.901
	Initial Mass:AMBR Colonists	0.040	-0.204	0.290
	Initial Mass:AMAR Colonists	-0.476	-0.807	-0.144
	Initial Mass:ELMO Community	0.260	-0.059	0.579
Log(Leaf Area)	Intercept	6.944	6.219	7.651
	AMAR Colonists	-0.050	-0.457	0.361
	ELMO Colonists	-1.585	-2.041	-1.113
Log(Tiller Abundance)	Intercept	1.539	0.953	2.088
	AMAR Colonists	0.698	0.554	0.844

Table 3.2. Parameter estimates and 95% confident intervals for the best supported model (based on AIC_c and BIC model comparison) of log odds of survival, log(total biomass), log(total leaf area), and log(tiller abundance per plant) for colonists of each grass species among the three community types and with sand burial.

Response Variable	Fixed Predictor	Estimates	95% confidence interval	
			Lower	Upper
AMBR				
Log(Survival Odds)	Intercept	1.654	0.955	2.413
	Sand Burial	-0.035	-0.055	-0.015
Log(Biomass)	Intercept	2.142	1.671	2.612
	Initial Mass	0.002	-0.008	0.013
	AMAR Community	0.254	-0.359	0.854
	ELMO Community	1.395	0.870	1.947
Log(Leaf Area)	Intercept	6.042	5.438	6.636
	AMAR Community	0.180	-0.403	0.818
	ELMO Community	0.863	0.339	1.372
Log(Tiller Abundance)	Intercept	0.726	0.321	1.134
	AMAR Community	-0.053	-0.606	0.505
	ELMO Community	0.621	0.196	1.062
AMAR				
Log(Survival Odds)	Intercept	-0.215	-0.887	0.417
	AMAR Community	0.926	0.058	1.870
	ELMO Community	1.128	0.346	1.958
Log(Biomass)	Intercept	1.590	1.174	2.003
	AMAR Community	-0.077	-0.596	0.487
	ELMO Community	1.329	0.875	1.816
	Sand Burial	0.028	0.013	0.042
Log(Leaf Area)	Intercept	4.267	3.754	4.791
	AMAR Community	-0.255	-0.870	0.365
	ELMO Community	1.614	1.096	2.138
	Sand Burial	0.043	0.025	0.061
Log(Tiller Abundance)	Intercept	-0.065	-0.437	0.331
	AMAR Community	-0.521	-0.946	-0.034
	ELMO Community	1.448	1.076	1.864
	Sand Burial	0.030	0.017	0.044
ELMO				
Log(Survival Odds)	Intercept	-0.282	-0.598	0.021
Log(Biomass)	Intercept	1.281	0.723	1.792
	Initial Mass	0.013	0.004	0.024
	AMAR Community	0.507	-0.003	1.066
	ELMO Community	0.340	-0.117	0.765
	Sand Burial	0.015	0.000	0.031
Log(Leaf Area)	Intercept	5.137	4.464	5.842
	AMAR Community	0.972	0.184	1.825
	ELMO Community	0.391	-0.324	1.127

Table 3.3. Parameter estimates and 95% confident intervals for the best supported model (based on AIC_c and BIC model comparison) of log odds of survival, log(total biomass), log(total leaf area), and log(tiller abundance per plant) for colonists of each grass species with species-specific community tiller density and with sand burial.

Colonizing Species Response Variable	Fixed Predictor	Estimates	95% confidence interval	
			Lower	Upper
AMBR				
Log(Survival Odds)	Intercept	1.872	1.144	2.733
	ELMO Tiller Density	-0.009	-0.020	0.002
	Sand Burial	-0.037	-0.058	-0.018
Log(Biomass)	Intercept	2.062	1.416	2.713
	Initial Mass	0.007	-0.001	0.016
	ELMO Tiller Density	0.015	0.006	0.023
	Sand Burial	0.017	0.002	0.032
Log(Leaf Area)	Intercept	5.525	4.778	6.278
	ELMO Tiller Density	0.018	0.008	0.028
	Sand Burial	0.018	-0.002	0.036
Log(Tiller Abundance)	Intercept	0.590	-0.025	1.176
	ELMO Tiller Density	0.005	-0.008	0.017
	Sand Burial	0.001	-0.017	0.020
	ELMO Tiller Density:Sand Burial	0.000	0.000	0.001
AMAR				
Log(Survival Odds)	Intercept	0.806	0.013	1.668
	AMBR Tiller Density	-0.007	-0.013	-0.001
	ELMO Tiller Density	0.014	-0.001	0.030
Log(Biomass)	Intercept	2.092	1.300	2.938
	Initial Mass	0.000	-0.010	0.012
	AMAR Tiller Density	-0.003	-0.005	-0.001
	AMBR Tiller Density	-0.004	-0.009	0.000
	ELMO Tiller Density	0.013	0.003	0.022
	Sand Burial	0.043	0.024	0.064
Log(Leaf Area)	Intercept	4.297	3.638	4.987
	ELMO Tiller Density	0.012	0.001	0.024
	Sand Burial	0.038	0.015	0.059
	ELMO Tiller Density:Sand Burial	0.001	0.001	0.002

Table 3.3. (Continued)

Colonizing Species		95% confidence interval		
Response Variable	Fixed Predictor	Estimates	Lower	Upper
Log(Tiller Abundance)	Intercept	0.238	-0.378	0.875
	AMAR Tiller Density	-0.002	-0.004	0.000
	AMBR Tiller Density	-0.001	-0.005	0.002
	ELMO Tiller Density	0.005	-0.004	0.013
	Sand Burial	0.029	0.011	0.048
	ELMO Tiller Density:Sand Burial	0.001	0.001	0.002
ELMO				
Log(Survival Odds)	Intercept	-0.282	-0.598	0.021
Log(Biomass)	Intercept	1.156	0.694	1.615
	Initial Mass	0.014	0.003	0.023
	AMAR Tiller Density	0.002	0.001	0.003
	ELMO Tiller Density	0.009	0.004	0.015
	Sand Burial	0.017	0.006	0.029
Log(Leaf Area)	Intercept	4.962	4.388	5.538
	AMAR Tiller Density	0.003	0.001	0.005
	ELMO Tiller Density	0.013	0.001	0.026

Table 3.4. A rank table of the invasiveness of *Ammophila breviligulata*, *A. arenaria*, and *E. mollis*, and the invasibility of the three foredune community types in the U.S. Pacific Northwest. For each pair, the first symbol indicates a ranking of species invasiveness (0 = low, ++ = high), and the second symbol indicates a ranking of community invasibility (0 = low resistance to invasion, ++ = high resistance to invasion).

		Invasibility (Ranked High to Low)		
		ELMO	AMAR	AMBR
Invasiveness (Ranked Low to High)	ELMO	0/0	0/+	0/++
	AMAR	+/0	+/+	0/+
	AMBR	+/0	+/+	++/+

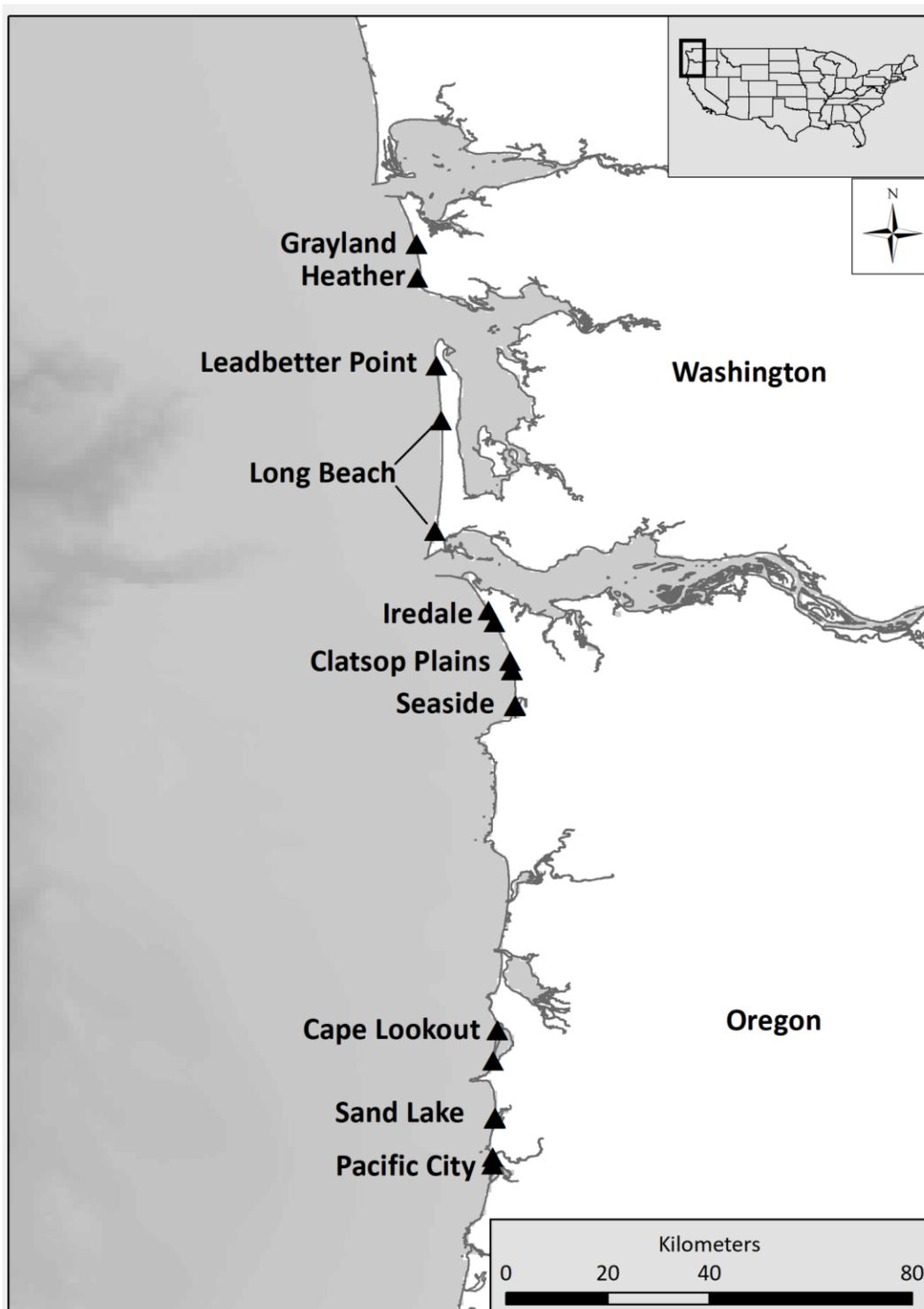


Figure 3.1. Location of 10 sites in northwest Oregon and southwest Washington, USA, used in the transplant experiment (see Appendix B, Table B1 for detailed site information).

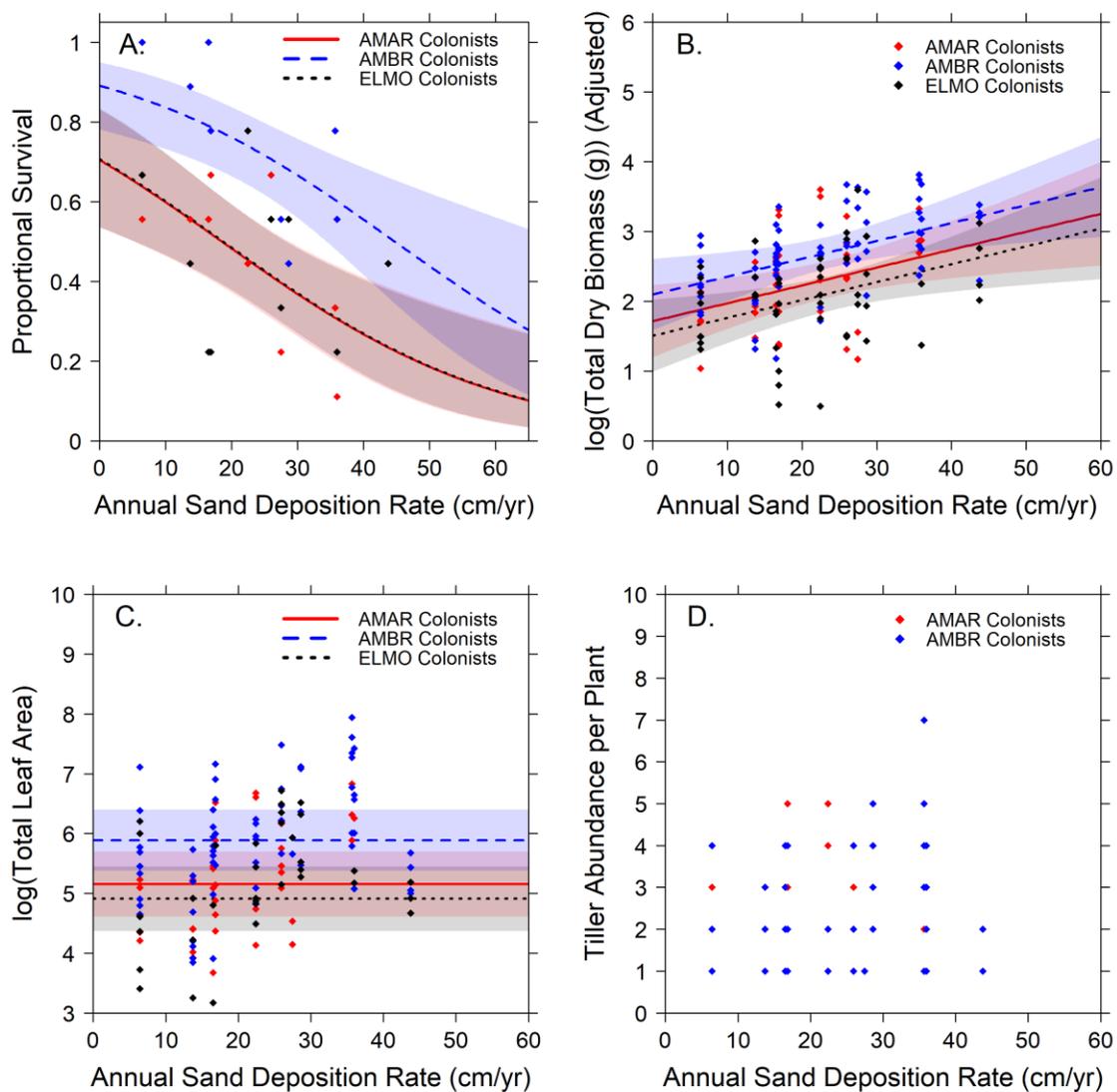


Figure 3.2. Within *Ammophila breviligulata*-dominated communities, (A) Proportional survival, (B) log(total dry biomass), (C) log(total leaf area), and (D) tiller abundance of *A. arenaria* (AMAR; red), *A. breviligulata* (AMBR; blue), and *E. mollis* (ELMO; black) colonists across a range of sand deposition regimes. Points represent plot-level measurements of proportion survival by species. Lines and error bands represent fitted response curves with associated 95% confidence intervals for each colonizing species.

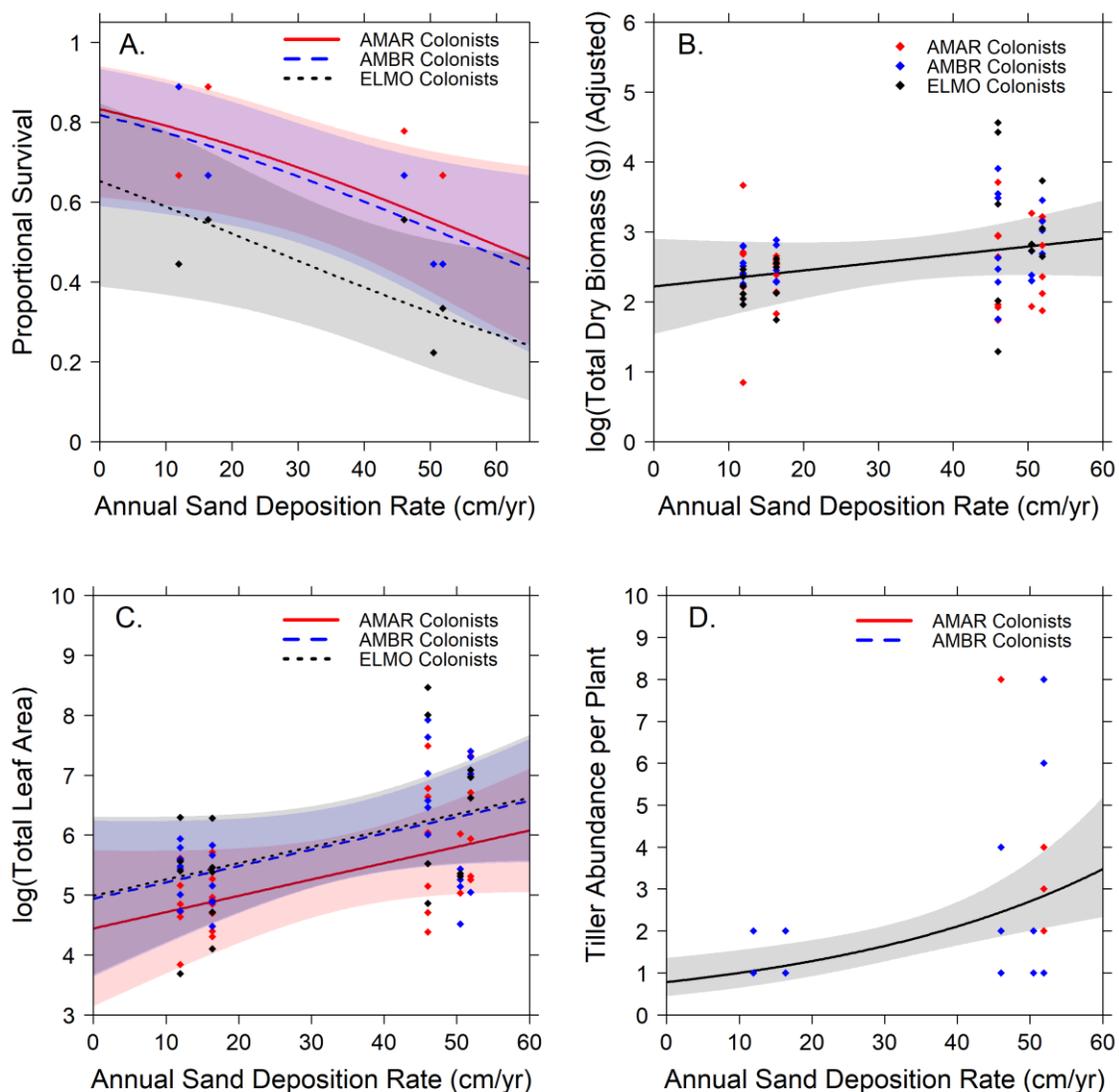


Figure 3.3. Within *Ammophila arenaria*-dominated communities, (A) Proportional survival, (B) log(total dry biomass), (C) log(total leaf area), and (D) tiller abundance of *A. arenaria* (AMAR; red), *A. breviligulata* (AMBR; blue), and *E. mollis* (ELMO; black) colonists across a range of sand deposition regimes. Points represent plot-level measurements of proportion survival by species. Lines and error bands represent fitted response curves with associated 95% confidence intervals for each invading species.

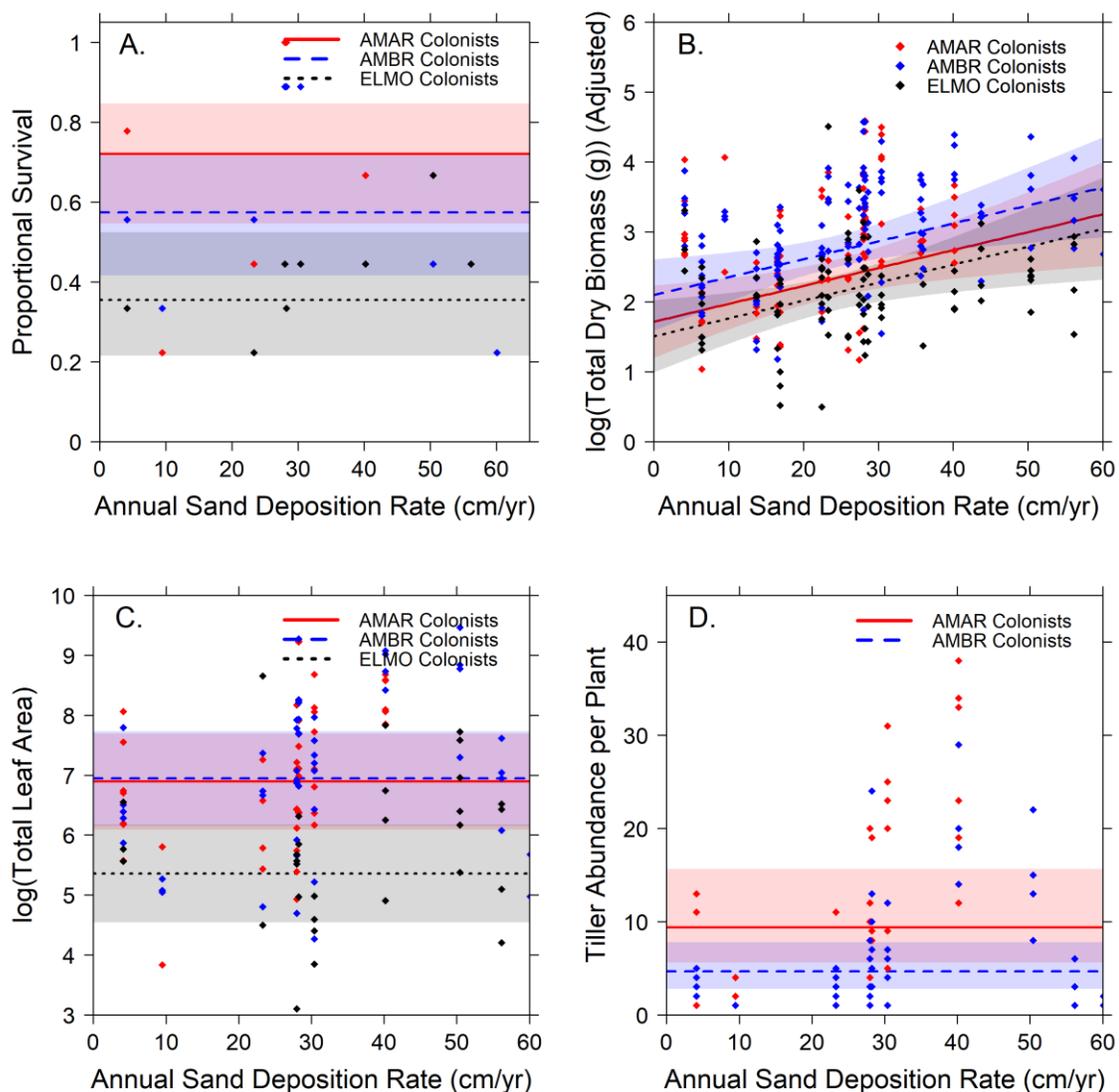


Figure 3.4. Within *Elymus mollis*-dominated communities, (A) Proportional survival, (B) log(total dry biomass), (C) log(total leaf area), and (D) tiller abundance of *Ammophila arenaria* (AMAR; red), *A. breviligulata* (AMBR; blue), and *E. mollis* (ELMO; black) colonists across a range of sand deposition regimes. Points represent plot-level measurements of proportion survival by species. Lines and error bands represent fitted response curves with associated 95% confidence intervals for each colonizing species.

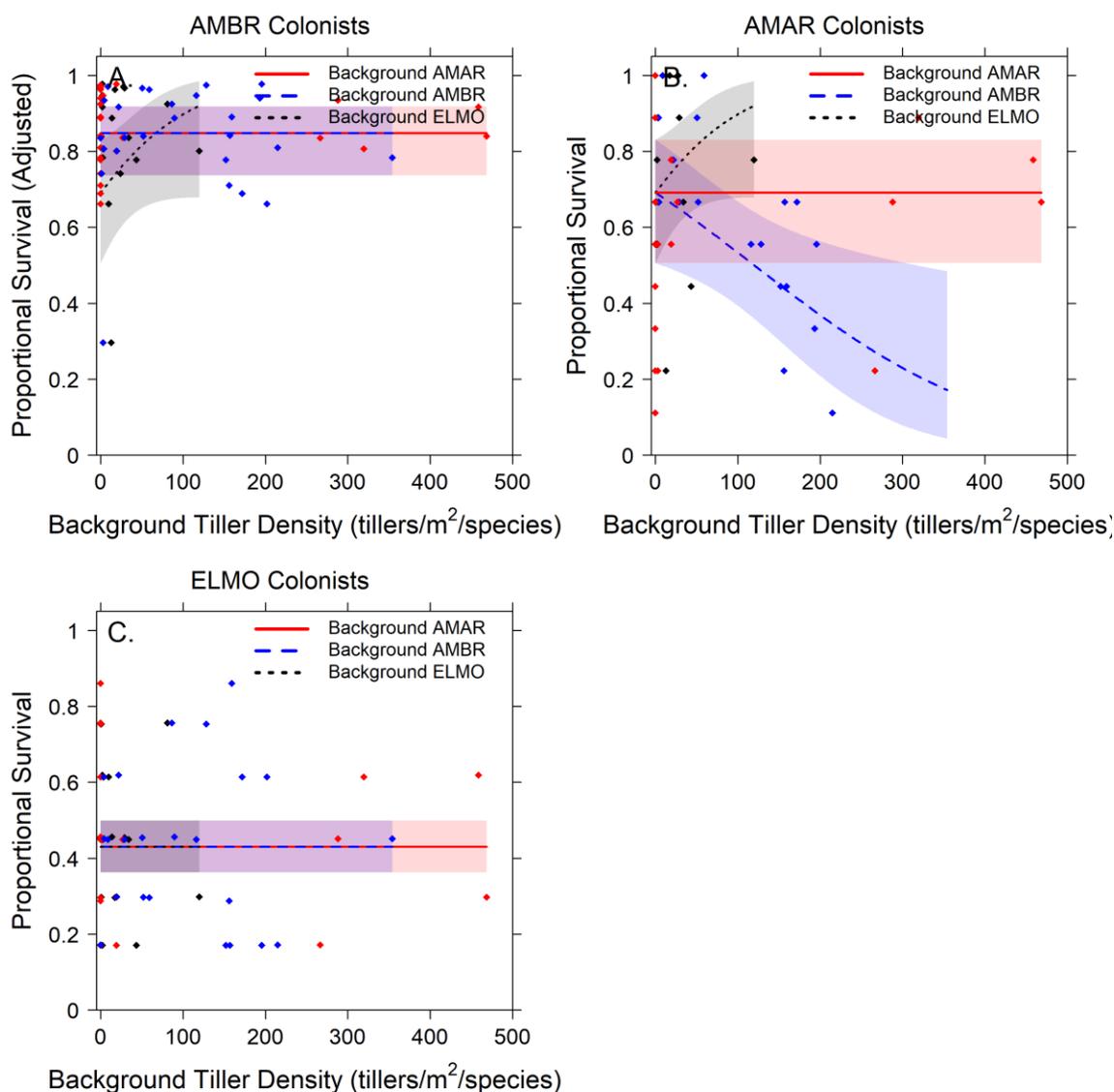


Figure 3.5. Relationships between colonist survival and species-specific tiller densities of invaded communities (A) for *A. breviligulata* (AMBR) colonists, (B) for *Ammophila arenaria* (AMAR) colonists, (C) for *E. mollis* (ELMO) colonists. Points show the effects of background tiller density of AMAR (red), AMBR (blue), and ELMO (black) within each plot (1 point per species per plot = 3 points per plot). Lines and bands show the fitted relationships and 95% confidence intervals, after adjusting for sand burial (panel A only).

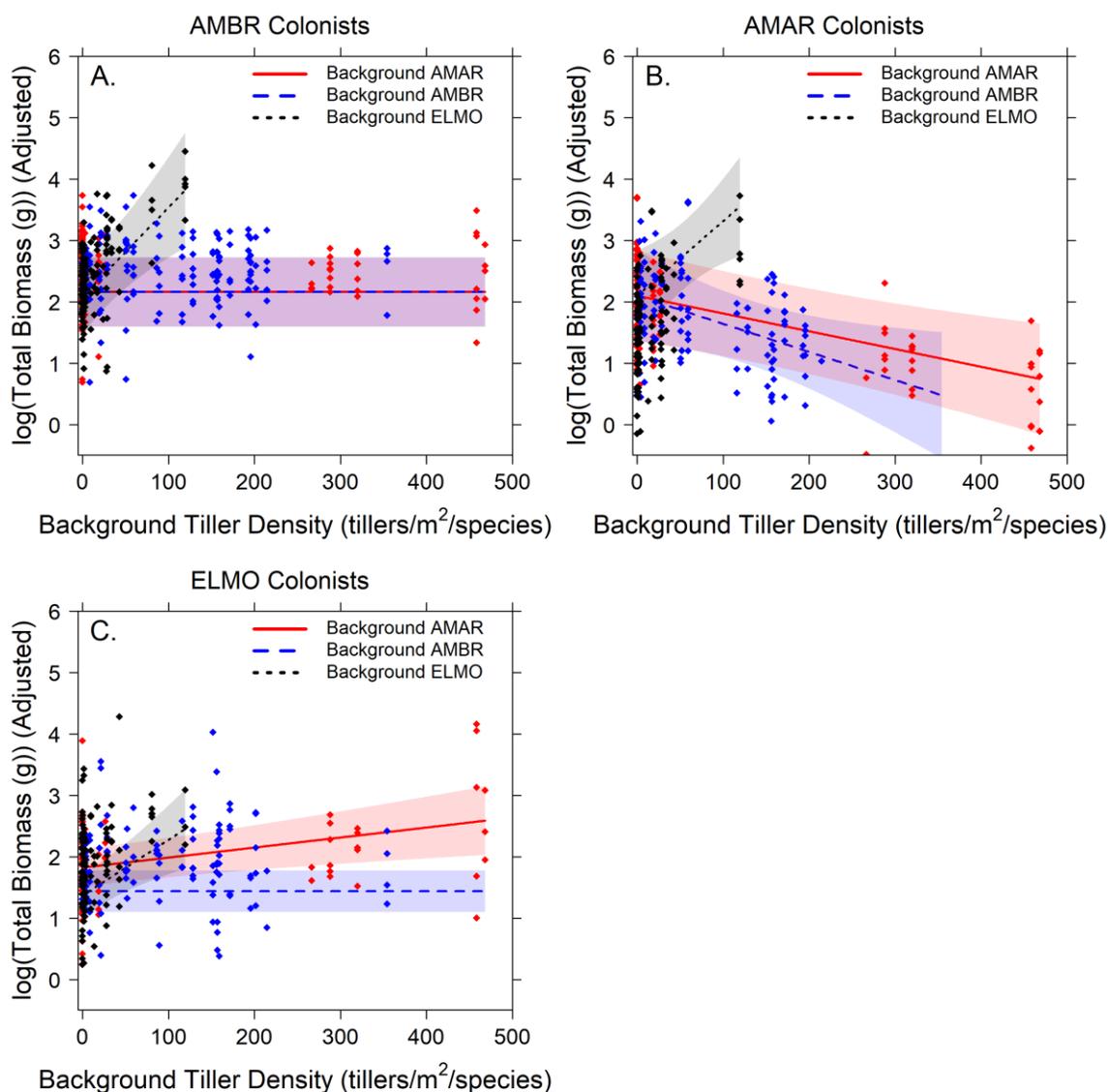


Figure 3.6. Partial residual plot illustrating relationships between colonist $\log(\text{total dry biomass})$ and species-specific tiller densities of invaded communities (A) for *A. breviligulata* (AMBR) colonists, (B) for *Ammophila arenaria* (AMAR) colonists, (C) for *E. mollis* (ELMO) colonists. Points show the effects of background tiller density of AMAR (red), AMBR (blue), and ELMO (black) within each plot (1 point per species per plot = 3 points per plot). Lines and bands show the fitted relationships and 95% confidence intervals, after accounting for initial biomass.

4. Climate change could alter the course of invasion and coastal vulnerability of Pacific Northwest dunes: temperature and sand burial affect the growth and species interactions of two invasive beach grasses

Reuben G. Biel and Sally D. Hacker

Abstract

Forecasting potential impacts of climate change on the distribution and abundance of invasive species is difficult because of numerous gaps in our ecological knowledge. Many invasive species exhibit introduced ranges that have distinct characteristics from their native range, in part because they may thrive under unique sets of environmental conditions and biotic interactions that vary in complex ways over environmental gradients. In this study, we examined how rising temperatures might alter the survival, growth, and biotic interactions of two invasive beachgrasses, *Ammophila arenaria* and *A. breviligulata*, along the U.S. Pacific Northwest coast. We wanted to understand how the current geographic ranges of these species might change as a consequence of physiological tolerances and changing species interactions under increasing temperatures and variable rates of sand deposition. Our results show that *Ammophila breviligulata* was less tolerant of elevated temperatures than *A. arenaria*, but the observed differences were generally small. High rates of sand burial also negatively affected *A. breviligulata*, which exhibited reductions in biomass production and tiller production, with few reductions in *A. arenaria* productivity. Nevertheless, under all experimental combinations of temperature and sand burial, *A. breviligulata* exerted a comparatively strong negative effect on *A. arenaria* tiller and biomass production (aboveground, belowground, and total biomass), while *A. arenaria* exerted a weaker negative effect on *A. breviligulata* on those same measures. Thus, although *A. breviligulata* is predicted to exclude *A. arenaria* across all experimental conditions, elevated temperatures and high rates of sand burial also increase the likelihood of coexistence between the two grass species. These differences in temperature and sand burial tolerance have significant implications for coastal management, conservation, and ecosystem services in the U.S. Pacific Northwest.

4.1. Introduction

Across North America average annual temperatures are predicted to increase by 2°C to 5°C by the end of the twenty first century with model projections showing that the average temperature found at any given location could shift 500-800 kilometers to the north (IPCC 2014). As such, ecologists have been increasingly interested in how climate change is and will continue to alter the distribution of species (e.g., Walther et al. 2002, 2009, Parmesan and Yohe 2003, Pearson and Dawson 2003, Chen et al. 2011). Evidence suggests that the physiological tolerances of species to climate-related abiotic conditions are a primary determinant of species distributions at limits of their geographic ranges (Sexton et al. 2009). Based on this pattern, many species distribution models (i.e., bioclimatic envelope models, ecological niche models, habitat-suitability models) utilize correlative relationships between patterns of species occurrence and environmental data to predict the distributions of species for the purposes of conservation planning, invasive species assessments, forecasting of the impact of climate change on species distributions, and other uses (e.g., Guisan and Thuiller 2005, Jeschke and Strayer 2008, Elith and Leathwick 2009, Araújo and Peterson 2012). However, the present-day distributions of species and their potential responses to environmental change depend upon numerous attributes, including historical distributions, modes of dispersal, environmental gradients, and biotic interactions. Of these, biotic interactions are perhaps the most complex, least understood, and oft-dismissed process that may influence species distributions at regional to global scales (Araújo and Luoto 2007, Gilman et al. 2010, Boulangeat et al. 2012, Blois et al. 2013, HilleRisLambers et al. 2013, Wisz et al. 2013).

Biotic interactions alter the local distribution and abundance of species via consumptive, competitive, and facilitative interactions. Theory and empirical examples show that differences in the types and strengths of species interactions can shape the species composition of biological communities through multiple mechanisms that promote coexistence (e.g., Paine 1969, Menge and Sutherland 1987, Hacker and Gaines 1997, Chesson 2000, Chase and Leibold 2003, Hubbell 2005, Leibold and McPeck 2006). Further, the relative importance of biotic interactions for structuring communities varies across environmental gradients of resources, disturbance, and stress (Menge and

Sutherland 1987, Hacker and Gaines 1997, Holmgren et al. 1997, Chesson 2000, Shea et al. 2004, He et al. 2013).

While biotic interactions are sometimes dismissed as being unimportant in influencing species ranges at large spatial scales (Pearson and Dawson 2003), numerous theoretical and empirical examples demonstrate that biotic interactions can alter species distributions, abundances, and assemblages across regional, continental, and global scales (Leibold et al. 2004, Chase and Myers 2011, Menge et al. 2015). Depending upon the nature of the interactions, they may contract (Davis et al. 1998, Case et al. 2005, Fitzpatrick et al. 2007, Beaumont et al. 2009) or expand (Bruno et al. 2003, Cavieres et al. 2005, He et al. 2013, McIntire and Fajardo 2014, Lany et al. 2017) species ranges (realized niche) beyond their physiological tolerances (fundamental niche). Biotic interactions that ameliorate stress, for example, may facilitate the survival and growth of species under abiotically stressful conditions, enabling them to expand their distribution beyond their solitary physiological limits (Hacker and Bertness 1999, Choler et al. 2001). Species invasions further provide evidence of biotic limits to species ranges, where environmental conditions within the non-native range of a species sometimes exceeds that of their native range (Fitzpatrick et al. 2007, Beaumont et al. 2009). Among many explanations, release from enemies may explain some range expansion in some non-native invasive species (Mitchell et al. 2006, Blumenthal et al. 2009). Finally, dispersal and metacommunity dynamics may further alter distributions by preventing species from occupying suitable sites, or by maintaining species in suboptimal habitat through immigration and source-sink dynamics (Holt 2009). However, accounting for biotic interactions in species distributions is especially challenging because they are often context dependent and may change in direction or strength across environmental gradients (Bertness and Callaway 1994, Holmgren et al. 1997, Bertness and Ewanchuk 2002, He et al. 2013, Chamberlain et al. 2014, Lany et al. 2017).

How might biotic interactions alter species responses to climate change? Gilman et al. (2010) assert that climate change will affect biotic interactions at every trophic level and across geographic scales. Not only will climate alter species fitness and geographic ranges, its effects will cascade through interacting species and the severity of those

effects will vary depending upon the characteristics of the interacting species, the sensitivity of interacting species to changes in climate forcing, and the potential for the formation of no-analog communities with novel interactions (Williams and Jackson 2007, Tylianakis et al. 2008, Gilman et al. 2010, Schleuning et al. 2016, Urban et al. 2017). Depending upon the interactions and contexts, biotic interactions may accelerate or slow climate tracking, either of which outcome would significantly alter management efforts (HilleRisLambers et al. 2013, Urban et al. 2013).

Relationships between species invasions and climate change add an additional layer of complexity. Plant invasions are frequently linked to changes in resource availability due to enrichment, novel disturbance, and spatiotemporal heterogeneity in resource supply or demand, among others (Davis et al. 2000). With increases in atmospheric CO₂ and other greenhouse gases, mean temperatures, nitrogen deposition, extreme weather events, and variable precipitation are creating novel environmental conditions that may benefit non-native species through changes in abiotic barriers to invasion and reductions in community invasion resistance (Dukes and Mooney 1999, Hellmann et al. 2008, Walther et al. 2009, Bradley et al. 2010). However, climate change may not universally benefit non-native invasive plants and is likely to produce range contraction and range shifting for some (Bradley et al. 2009, Allen and Bradley 2016, Merow et al. 2017). Predicting how a non-native invasive species might perform with a changing climate, though, proves especially difficult. Not only may invasive species occupy niche space in their invasive range that differs from their native range (Broennimann et al. 2007, Gallagher et al. 2010), their distribution in their invaded range may not be at equilibrium with the environment, may be limited by dispersal and colonization processes, and may also create novel interactions that remain uncharacterized (Hobbs et al. 2006, Bradley et al. 2010, Václavík and Meentemeyer 2012). Forecasting potential climate change impacts on invasive species in novel communities with unique interactions at disequilibrium with the environment requires an understanding of multiple mechanisms that may influence the distribution and abundance of those non-native invasive species.

Using the U.S. Pacific Northwest (PNW) coastal dune ecosystem as a case study, we examined how rising temperatures might alter the biotic interactions between two

invasive beachgrasses under varying sand deposition regimes. Pacific Northwest foredunes, defined as the seaward-most sand ridge running parallel to the shoreline, are presently dominated by two congeneric, non-native invasive beachgrasses: *Ammophila arenaria* and *A. breviligulata*. Their introduction and spread throughout the PNW has caused significant changes to the geomorphology, ecology, and supply of ecosystem services (Zarnetske et al. 2010, 2012, 2015, Hacker et al. 2012, Seabloom et al. 2013, Chapter 2). Ecologically and geomorphologically, the two beachgrasses have re-engineered 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 in numerous plants (e.g., *Abronia umbellata*, *Tanacetum bipinnatum*), insects, and shore-nesting birds (e.g., *Charadrius nivosus nivosus*, *Eremophila alpestris strigata*) (Slobodchikoff and Doyen 1977, Wiedemann 1984, USFWS 1993, 2010). 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, Zarnetske et al. 2012, 2015, Chapter 2), providing superior protection against winter coastal storms (Seabloom et al. 2013), while *A. breviligulata* more severely reduces endemic plant diversity (Hacker et al. 2012, David et al. 2015).

The present-day range of the two invasive *Ammophila* species, and forecasts for the future, hinge on knowing how a combination of historical introduction events, dispersal potential, abiotic tolerances, and biotic interactions affect their distribution and abundance. Regarding history, *A. arenaria* and *A. breviligulata* were introduced to the U.S. Pacific Northwest for sand stabilization in the early 20th century, but the spatial extent of plantings differed among 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). It is presently the dominant dune grass in Oregon and northern California,

and was historically more pervasive in Washington and British Columbia (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, USA in the 1930s. Since its introduction, *A. breviligulata* has expanded predominantly northward to Vancouver Island, BC, Canada (49°N), but also slightly southward into northern Oregon, displacing *A. arenaria* as the dominant beachgrass as far south as Seaside, Oregon (46°N) (Figure 4.1; Seabloom and Wiedemann 1994, Page 2001, Hacker et al. 2012, David et al. 2015). Nevertheless, small *A. breviligulata* extant populations were recently observed further south near Pacific City, OR (45°N) and San Francisco, CA (38°N) (Hacker et al. 2012, NPSpecies 2017). While the *Ammophila* species have spread since their initial introductions to the PNW, their present-day distribution in part simply reflects their respective planting histories.

However, the highly segregated distribution of the two congeners is also a consequence of several interacting factors, including species interactions, sand supply, dispersal limitation, and temperature. For example, in the north, where the two species were planted in succession, species interactions as well as sand deposition variability have played a critical role in their current relative dominance. 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 (Figure 4.1; Seabloom and Wiedemann 1994, Hacker et al. 2012, David et al. 2015). Further, manipulative experiments show that *A. breviligulata* is competitively dominant to *A. arenaria* and impedes its colonization and growth on PNW foredunes (Zarnetske et al. 2013, 2015, David et al. 2016, Chapter 3). However, these interactions can be mediated by sand deposition: *A. breviligulata* exhibits greater increases in both biomass and tiller production compared to *A. arenaria* in lower depositional regimes characteristic in the northern coast (Baye 1990, Zarnetske et al. 2012, 2015). Thus, *A. arenaria* and *A. breviligulata* are subject to a range of sand burial conditions that may influence their growth patterns, morphology, competitive interactions, and ultimately their distribution and abundance (Zarnetske et al. 2013, 2015, Chapter 3). Consequently, though *A.*

arenaria is still present in northern Oregon and southwest Washington, *A. breviligulata* has largely displaced *A. arenaria*, effectively limiting its northern extent (Figure 4.1).

Although the northerly distribution and abundance of *A. arenaria* may be limited by biotic interactions and sand supply, the present-day southerly range of *A. breviligulata* is likely dispersal limited because of oceanographic and geographic barriers to dispersal. *Ammophila* primarily invades new territory via establishment of rhizome fragments, and to a lesser extent via seed recruitment (Maun 1984, van der Putten 1990). When foredunes are subjected to wave action and erosion during storms, *Ammophila* rhizomes can fragment and be carried offshore and transported hundreds of kilometers via ocean currents (Baye 1990, Aptekar and Rajmanek 2000). The U.S. Pacific Northwest climate is conducive to this mode of long-distance dispersal, with one of the harshest wave climates in the world (Ruggiero et al. 2010). When combined with winter seasonal sea-level rise, winter storms erode foredunes, leading to rhizome fragmentation and the spreading of *Ammophila* when rhizome sprouting is at its peak (Pavlik 1983a, 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 (Figure 4.1; 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* germination, survival, photosynthesis, and primary production varies between 15°C and 30°C, depending on environmental as well as population genetic variability (Seneca and Cooper 1971, Yuan et al. 1993, Emery and Rudgers 2013). Some studies have shown that *A. breviligulata* begins exhibiting reductions in photosynthesis and belowground biomass as temperatures approach 20°C

(Seneca and Cooper 1971, Yuan et al. 1993). In contrast, *A. arenaria* grows in regions where temperatures regularly exceed 40°C and is known to survive frequent exposure to temperatures greater than 50°C without a reduction in its growth rate (Huiskes 1979).

Along the PNW coast where both species co-occur, mean maximum daily temperatures range from 16°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 (Appendix C, Table C1). 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 (Appendix C, Table C1). 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), potentially creating temperature conditions similar to the present-day climate at the southern distribution of *A. arenaria* in California.

Thus, while multidecadal observational surveys and manipulative experiments demonstrate that *A. breviligulata* effectively constrains the northern limit of *A. arenaria* by competitive displacement, it is unknown whether these interactions are sensitive to temperature, temperature related stresses (e.g., desiccation), or interact with other common foredune stressors (e.g., sand burial). Nevertheless, forecasting the potential climate response of the *Ammophila* species is essential because these two ecosystem engineers shape foredune ecology, geomorphology, and the supply of ecosystem services, but differ in their impact (Hacker et al. 2012, Seabloom et al. 2013, Chapter 2). Thus, changes to their distribution and abundance could significantly influence coastal management decision-making.

Here we examined the effects of elevated temperature and sand burial on the abundance, morphology, and competitive interactions of two dominant invasive *Ammophila* grasses on the U.S. Pacific Northwest coast. We wanted to understand how the current distributional ranges of the two species might change as a consequence of physiological tolerances and species interactions under increasing temperatures and under variable sand deposition. We wondered, could increased temperature, and its interaction

with sand deposition, decrease the production of *A. breviligulata*, thereby mediating or potentially reversing its competitive dominance over *A. arenaria*? Might this competitive reversal result in the extension of the northern distribution of *A. arenaria* and the restriction of the southern distribution of *A. breviligulata*.

To explore these possibilities, we used large sand-filled planters made of permeable geotextile bags to manipulated temperature, sand burial, and the relative abundances of *A. arenaria* and *A. breviligulata* to address the following questions. (1) Do temperature and sand burial alter plant productivity and morphological traits for each of the *Ammophila* species? Based on experiments in their native range, we hypothesized that *A. breviligulata* would exhibit higher sensitivity to temperature via reductions in biomass production, tiller production, and leaf area, while *A. arenaria* would exhibit little response. (2) Do temperature and sand burial conditions alter the direction and/or magnitude of *A. breviligulata* and *A. arenaria* interaction? 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* exhibited a negative response to elevated temperatures and/or sand burial, then we hypothesized that such changes might foster coexistence or 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*. Based on the results, we discuss how temperature and sand burial could influence current and future *Ammophila* distributions, and the potential knock on effects to U.S. Pacific Northwest dune ecology and geomorphology.

4.2. Methods

4.2.1. Experimental design

4.2.1.1. Grass species combinations

We assessed the growth response and species interactions of *Ammophila arenaria* and *A. breviligulata* under elevated temperature and varying sand deposition using a split-

split-plot common garden experiment at Hatfield Marine Science Center, Newport, OR USA. In Summer 2013, we placed 64 1m² (base) x 2m (height) permeable geotextile bags (Flexible Intermediate Bulk Container; Bag Corp, Richardson, TX) in an 8 x 8 grid (Appendix C, Figure C1). Each planter was then subdivided into four equal sized 0.25 m² quadrants (256 total) using clear greenhouse film (6 mil, 91% light transmission; International Greenhouse Company, Danville, IL), mounted to a wood frame and secured to the interior of each geotextile bag (Appendix C, Figure C2). The wood frame and greenhouse film functioned as a barrier to the exchange of sand, water, nutrients, and plant roots and rhizomes between quadrants of the bag.

To quantify density-dependent growth parameters and interaction between *A. arenaria* and *A. breviligulata*, we then planted four combinations of each species at varying densities in the four quadrants of each bag in September 2013: a monoculture of 6 *A. arenaria* plants, a monoculture of 6 *A. breviligulata* plants, a polyculture of 3 *A. arenaria* and 3 *A. breviligulata* plants, and a polyculture of 6 *A. arenaria* and 6 *A. breviligulata* plants (Appendix C, Figure C1, Appendix C, Figure C2). We defined a single plant as one rhizome with multiple attached tillers. Although the number of plants within each species combination was predetermined, the number of tillers per plant varied from 1 to 8 for *A. arenaria* and 1 to 6 for *A. breviligulata*. Quadrants with three *A. arenaria* and three *A. breviligulata* plants contained mean initial tiller densities of 12.5 ± 0.6 tillers/quadrant (mean \pm standard error) and 8.1 ± 0.5 tillers/quadrant (approximately 32.4 tillers/m²), respectively (Appendix C, Figure C3). Quadrants with six *A. arenaria* and/or six *A. breviligulata* plants contained mean initial tiller densities of 25.2 ± 0.9 tillers/quadrant (mean \pm standard error) and 14.3 ± 0.4 tillers/quadrant, respectively. In the Pacific Northwest, *A. arenaria* and *A. breviligulata* grow at respective mean tiller densities of 51 and 40 tillers/0.25 m² on the foredune (Zarnetske et al. 2012). Plants were well-watered until December 2013 and allowed to establish for nine months prior to the initiation of sand burial or temperature treatments in May 2014.

4.2.1.2. Sand burial treatment

To examine the growth response of *A. arenaria* and *A. breviligulata* to sand burial, we added sand to each quadrant of the bags from May 2014 to September 2015 at a rate

that reflected the natural range of sand deposition rates (typically less than 80 cm/yr.) in the U.S. Pacific Northwest (Ruggiero et al. in press, Chapters 2-3). Half of the bags received a single 4 cm sand addition event (low deposition) and the other half received multiple 4 cm sand addition events for the duration of the experiment, resulting in an overall 57 cm vertical accumulation after sand settling (high deposition treatment). As planters grew in height from sand additions, we attached additional dividers to maintain quadrant separation.

4.2.1.3. Heat treatment

To examine the growth response of the *Ammophila* congeners to elevated temperature, we divided the 8 x 8 common garden grid into four blocks, each consisting of two adjacent columns. We then applied a heat treatment to 4 columns of bags (32 bags) that was 3°C above ambient temperature, while adjacent control columns (32 bags) remained at ambient temperature (Appendix C, Figure C1). To maintain the temperature differential between heated and unheated bags within each block, we placed resistive heating cables (LT210 Self-Regulating Heater Cable, Nelson Heat Trace Systems, Tulsa, OK) woven between wire mesh 4 cm below the sand surface for all heat treatments (Appendix C, Figure C1, Appendix C, Figure C2). We similarly placed wire mesh within ambient temperature bags as a control. Before each sand addition event, we adjusted the wire mesh to ensure that the resistive heating cables remained within 4 cm of the surface of the sand. We used four differential temperature controllers with temperature probes (N321S Differential temperature controller, NOVUS, Miami, FL) (one temperature controller per block) to maintain a constant temperature differential between heated and unheated bags: when $T_{\text{heat}} - T_{\text{control}} < 2.9^{\circ}\text{C}$ within a block, the controller closed the circuit and began heating the heat treatment bags. When $T_{\text{heat}} - T_{\text{control}} > 3.1^{\circ}\text{C}$, the controller opened the circuit and stopped heating, thereby maintaining the 3.0°C temperature differential at the temperature probes (NTC thermistors). Independent measurements from HOBO temperature loggers (Onset Computer Corporation, Bourne, MA) placed centrally in each bag indicate that heating maintained a median temperature differential of 1.7°C to 2.8°C between paired bags, depending upon the block (Appendix C, Table C2).

4.2.1.4. Grass species biomass and morphology metrics

To estimate the total dry weight biomass of each species within the quadrants at the start of the experiment, we set aside 100 haphazardly chosen plants of each grass species before the grasses were planted to characterize initial plant biomass and morphology. We counted the number of tillers and measured the dry biomass (aboveground, belowground, total) of each plant. Aboveground biomass was defined as all biomass growing above 1 cm above the primary root node (the approximate location of the sand surface) and all buried leaf matter. Belowground biomass was defined as all root matter and rhizomes growing below the aforementioned primary node cutoff. We further counted the total number of tillers per species in the quadrants immediately after they were planted (September 2013) and again in May 2014, just prior to the initiation of heat and sand burial treatments (July 1, 2014). To estimate initial biomass/species/quadrant (aboveground, belowground, total) from observed initial tiller densities, we imputed the initial biomass per species for each quadrant based on species identity, initial beachgrass density (three or six plants per species; Appendix C, Figure C1), and observed initial tiller density per quadrant.

We ended the experiment in September 2015 and harvested the plants from each quadrant by cutting open the bags and pulling each plant, and as much of its roots and rhizomes as possible, from the sand. The plants were dried completely before we measured the tiller number and dry biomass (aboveground, belowground, total) per species within each quadrant. To estimate the leaf characteristics of individual plants, we haphazardly chose five plants per species per quadrant and measured the length of their longest tiller (from the primary root node to the longest leaf tip), the width of their widest leaf (measured at the base of the widest leaf), and counted all their leaves. We also calculated an index of total leaf area for each plant by multiplying half the tiller length x leaf width x leaf number.

4.2.2. Statistical analysis

The split-split plot design consisted of one whole plot treatment (ambient vs. elevated temperature; n=8), one split-plot treatment (low vs. high sand burial; n=64), and two split-split plot treatments (*A. arenaria* x *A. breviligulata* initial tiller density; n=256). To

assess density-dependent changes in grass tiller density, biomass, and morphology to heat, sand burial, and initial tiller densities of the congeners at the start of the experiment, we performed linear mixed effects models in R using the lme4 package. For each of the biomass metrics (i.e., aboveground, belowground, total), we calculated a log response ratio of biomass ($\log(\text{biomass}_{\text{Final}}/\text{biomass}_{\text{Init}})$). For quadrant scale measurements (i.e., biomass/species/quadrant, tillers/species/quadrant), we included a nested random intercept (1|whole plot/subplot) to account for the nested structure of our experimental design.

To assess how heat and sand burial affect tiller density, intraspecific interactions, and interspecific interactions in the two *Ammophila* species, we used linear mixed models to parameterize the Ricker model, a logistic, density dependent species interaction model, written as,

$$\begin{aligned}\log\left(\frac{N_{A, \text{Final}}}{N_{A, \text{Init}}}\right) &= r_A - \left(\frac{r_A}{K_A}\right)N_A - \left(\frac{\alpha_{AB}}{K_A}\right)N_B \\ \log\left(\frac{N_{B, \text{Final}}}{N_{B, \text{Init}}}\right) &= r_B - \left(\frac{r_B}{K_B}\right)N_B - \left(\frac{\alpha_{BA}}{K_B}\right)N_A\end{aligned}\quad (\text{Eqn. 4.1})$$

where A and B represented *A. arenaria* and *A. breviligulata*, respectively. Here, the response variable was the log ratio of the final (N_{Final}) to initial (N_{Init}) tiller density for each species. The intercept term (r_A in Eqn. 4.1) represented the intrinsic growth rate, K represents the carrying capacity, and α represented the effect of one species on the other. Environmental factors could also influence species interactions by exerting density-independent and/or density-dependent influence on growth:

$$\begin{aligned}\log\left(\frac{N_{A, \text{Final}}}{N_{A, \text{Init}}}\right) &= (r_A + \beta_1 \cdot \text{Temp} + \beta_2 \cdot \text{Sand}) - \left(\frac{r_A}{K_A} + \beta_3 \cdot \text{Temp} + \beta_4 \cdot \text{Sand}\right)N_A - \left(\frac{\alpha_{AB}}{K_A}\right)N_B \\ \log\left(\frac{N_{B, \text{Final}}}{N_{B, \text{Init}}}\right) &= (r_B + \beta_1 \cdot \text{Temp} + \beta_2 \cdot \text{Sand}) - \left(\frac{r_B}{K_B} + \beta_3 \cdot \text{Temp} + \beta_4 \cdot \text{Sand}\right)N_B - \left(\frac{\alpha_{BA}}{K_B}\right)N_A\end{aligned}\quad (\text{Eqn. 4.2})$$

In this potential model, heat and sand burial treatments each exerted both density-independent effects (β_1, β_2 in Eqn. 4.2) and density-dependent effects (β_3, β_4 in Eqn. 4.2) on growth. When depicted in linear mixed model form, this regression followed the form:

$$\begin{aligned}\log(N_{1, \text{Final}} / N_{1, \text{Init}}) &\sim \beta_0 + \beta_1 \cdot N_{1, \text{Init}} + \beta_2 \cdot N_{2, \text{Init}} + \beta_3 \cdot \text{Temp} + \beta_4 \cdot \text{Sand} + \\ &\quad + \beta_5 \cdot \text{Temp} \cdot N_{1, \text{Init}} + \beta_6 \cdot \text{Sand} \cdot N_{1, \text{Init}} + (1|\text{Wholeplot} / \text{Subplot}) + \varepsilon\end{aligned}\quad (\text{Eqn. 4.3})$$

Lastly, when analyzing individual plant morphometrics (i.e., tiller length, leaf width, total leaf area), we regressed each morphometric against heat treatments, sand burial

treatments, and the tiller density at the start of experimental treatments and included an additional nested random intercept term (1|whole plot/subplot/sub-subplot) to account for intra-quadrant non-independence.

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 4.1). For each set of models, we described which variables were included in substantially supported models ($\Delta\text{AIC}_c < 2$) and reported model coefficient estimates for the best-supported statistical model.

4.3. Results

4.3.1. Changes in grass biomass

Ammophila arenaria and *A. breviligulata* differed in their biomass response to intra- and inter-specific interactions, heat treatment, and sand deposition. For *A. arenaria*, mean total biomass (above and belowground biomass) increased by 52% (95% confidence interval (CI): 28%-80% increase) by the end of the experiment when grown in the absence of *A. breviligulata*. However, when grown with *A. breviligulata*, each tiller of *A. breviligulata* was associated with a 2.0% reduction (CI: 0.8%-3.2% decrease) in *A. arenaria* total biomass (log response ratio (LRR) < 0 when $N_{\text{AMBR}} > 20$ tiller/quadrant) (Figure 4.2, Appendix C, Table C3). Based on this and the other substantially supported models (Appendix C, Table C4), heat and sand burial treatments had negligible effects on the total biomass of *A. arenaria* (CI: 22% decrease-28% increase and 27% decrease-24% increase, respectively).

In contrast, for *A. breviligulata*, mean total biomass increased by 302% (CI: 218%-407% increase) when grown in the absence of *A. arenaria* and at low rates of sand burial. However, when grown with *A. arenaria*, each *A. arenaria* tiller was associated with a 1.1% reduction (CI: 0.4%-1.8% decrease) in total *A. breviligulata* biomass (LRR < 0 when $N_{\text{AMBR}} > 132$ tiller/quadrant; Figure 4.2, Appendix C, Table C3). Based on other substantially supported models, the effect of elevated temperature was negative but with high uncertainty, reducing *A. breviligulata* total biomass by 19.1% (CI: 45.2% decrease-

23.3% increase). Sand burial reduced *A. breviligulata* total biomass by an estimated 15% (CI: 30% decrease-0.1% increase; Figure 4.2, Appendix C, Table C3).

When aboveground and belowground biomass were considered separately, the two congeners exhibited differing responses to heat and sand burial (Figure 4.3). For *A. arenaria*, mean aboveground biomass increased by 27% (CI: 4%-55% increase) by the end of the experiment when grown in the absence of *A. breviligulata*. When grown with *A. breviligulata*, each tiller of *A. breviligulata* was associated with a 2.1% reduction (CI: 0.9%-3.4% decrease) in *A. arenaria* aboveground biomass (log response ratio (LRR) < 0 when $N_{AMBR} > 11$ tiller/quadrant) (Figure 4.3A, Appendix C, Table C3). Based on another substantially supported model, under low sand burial conditions, elevated temperatures were associated with a 44% increase (CI: 1%-111% increase) in *A. arenaria* aboveground biomass production relative to the ambient temperature, low sand burial condition ($\Delta AIC_c = 0.9$; Appendix C, Table C3). However, at high levels of sand burial, this gain in aboveground biomass disappeared (CI: 32% decrease-41% increase) relative to ambient temperature, low sand burial condition.

For *A. breviligulata*, mean aboveground biomass increased by 233% by the end of the experiment when grown in the absence of *A. arenaria* and under low sand burial conditions. However, when grown with *A. arenaria*, each tiller of *A. arenaria* was associated with a 0.8% reduction (CI: 0.2%-1.5% decrease) in *A. arenaria* aboveground biomass growth (LRR < 0 when $N_{AMAR} > 152$ tiller/quadrant under low sand burial conditions) (Figure 4.3B, Appendix C, Table C3). High rates of sand burial, though were associated with a 19% decline (CI: 4%-34% decrease) in aboveground biomass production relative to low sand burial conditions.

Ammophila arenaria belowground biomass increased by 102% throughout the experiment, when grown without *A. breviligulata* and under low sand burial and ambient temperature conditions. When present, *A. breviligulata* reduced belowground biomass growth by 2.3% per *A. breviligulata* tiller (CI: 1.1%-3.4% decrease; LRR < 0 when $N_{AMBR} > 30$ tillers/quadrant under ambient temperature, low sand burial conditions) (Figure 4.3C, Appendix C, Table C3). High sand burial under ambient temperatures was also associated with a 67% increase (CI: 17%-133% increase) in belowground biomass

production relative under ambient temperatures. However, when simultaneously exposed to both elevated temperatures and high sand burial, belowground biomass only increased by 10% (CI: 22% decrease-59% increase), relative to ambient temperature, low sand burial conditions.

Mean *A. breviligulata* belowground biomass increased by 807% (CI: 601%-1063% increase) when grown in the absence of *A. arenaria* and at ambient temperature. *Ammophila arenaria* decreased *A. breviligulata* belowground biomass by 1.8% per *A. arenaria* tiller (CI: 0.9%-2.6% decrease). Elevated temperature further reduced belowground biomass production by 36% (CI: 13%-56% decrease) (Figure 4.3D; LRR < 0 when $N_{AMAR} > 122$ and 98 tillers/quadrant under ambient and elevated temperatures, respectively). Sand burial had no significant effect on *A. breviligulata* belowground biomass production.

4.3.2. Changes in grass tiller density

Ammophila arenaria and *A. breviligulata* differed in their tiller production response to intra- and inter-specific interactions, sand deposition, and heat treatment (Figure 4.4, Table 4.2). Among quadrants with *A. arenaria* present at the initial time point (t_{init}), N_{AMAR} decreased by an average of 5.1 ± 11.6 tillers/quadrant. Analysis of the log-response ratio for tiller density [$\log(N_{AMAR,Final}/N_{AMAR,Init})$] between the initial and final time points indicates that both *A. arenaria* and *A. breviligulata* exerted negative density-dependent controls on the growth of *A. arenaria* tillers, reducing *A. arenaria* tiller production by 1.7% per $N_{AMAR,Init}$ (CI: 0.6%-2.6% decrease) and 1.2% per $N_{AMBR,Init}$ (CI: 0.3%-2.1% decrease). Based on the Ricker logistic equation, *A. breviligulata* exerted a strong negative effect on *A. arenaria* at both low and high temperatures and rates of sand deposition (Table 4.3). In contrast, based on other substantially supported models, sand burial (CI: 12% decrease-31% increase) and heat (CI: 22% decrease-31% increase) were poor predictors of *A. arenaria* tiller production ($\Delta AIC_c < 2$; Table 4.2).

Among quadrants with *A. breviligulata* present at the initial time point (t_{init}), N_{AMBR} increased by an average of 6.1 ± 13.5 tillers/quadrant. Both *A. arenaria* and *A. breviligulata* exerted negative density-dependent controls on the growth of *A. breviligulata* tillers, but the magnitude of density-dependence varied with sand burial. At

low rates of sand burial, initial tiller density of *A. breviligulata* reduced *A. breviligulata* tiller production by 6.3% per $N_{AMBR,Init}$ (CI: 3.7%-8.9% decrease) and initial tiller density of *A. arenaria* reduced *A. breviligulata* tiller production by 1.0% per $N_{AMAR,Init}$ (CI: 0.0%-2.1% decrease). At high rates of sand burial, though, the negative effect of initial *A. breviligulata* tiller density was lessened to a 3.3% reduction (CI: 1.2%-5.7% decrease) in *A. breviligulata* tiller production per $N_{AMBR,Init}$. Nevertheless, high rates of sand burial also reduced tiller production in *A. breviligulata* by 61% (CI: 24%-78% decrease). Thus, sand burial exerted both a negative and positive density-independent effect on *A. breviligulata* tiller production. Moreover, *A. arenaria* exerted a weak to moderate negative effect on *A. breviligulata* tiller production, whose interaction strength differed across rates of sand deposition (Table 4.3). Based on other substantially supported models, elevated temperature had a negative, but highly uncertain effect on *A. breviligulata* growth (estimate: 24% decrease; CI: 58% decrease-30% increase; $\Delta AIC_c < 2$; Table 4.2). However, our power to detect a significant heat treatment effect was limited by the low number of independent heat treatment replicates ($n=8$).

Based on the predictors of $\log(N_{AMAR,Final}/N_{AMAR,Init})$ and $\log(N_{AMBR,Final}/N_{AMBR,Init})$, we found that *A. breviligulata* exhibited a higher intrinsic growth rate (r), carrying capacity (K), and competition coefficient (α) when compared to *A. arenaria* (Table 4.3), and was competitively dominant to *A. arenaria* under all sand burial and heat treatment combinations (Figure 4.4). We predicted that under ambient temperature/low sand burial conditions, *A. arenaria* could infrequently coexist with *A. breviligulata* (3 of 16 bags; Figure 4.4), leading to more frequent displacement of *A. arenaria* by *A. breviligulata*. In contrast, under elevated temperature / low sand burial conditions, ambient temperature/high sand burial conditions and elevated temperature / high sand burial conditions, *A. arenaria* could coexist with *A. breviligulata* more often (6 of 16 bags, 7 of 16 bags, and 5 of 16 bags, respectively; Figure 4.4). Thus, these models suggest that elevated temperature and high rates of sand burial might result in the coexistence of the two *Ammophila* species (Figure 4.4)

4.3.3. Changes in leaf morphological characteristics

The leaf morphology of *A. arenaria* and *A. breviligulata* was influenced by the initial densities of *A. arenaria* and *A. breviligulata* within the quadrants (N_{AMAR} , N_{AMBR}), by sand burial, and to a lesser extent by temperature (Figure 4.5-Figure 4.6; Appendix C, Table C6, Appendix C, Table C7). Under high rates of sand burial *A. arenaria* total leaf area increased by 14% (CI: 5%-26% increase) relative to low burial conditions (Figure 4.5A). Although sand burial did not influence *A. arenaria* tiller length (Figure 4.5C), it increased leaf width by 23% (CI: 13%-32% increase; Figure 4.5E). High initial *A. arenaria* density, however, reduced the positive effect of sand burial on leaf width ($N_{AMAR} \times$ sand burial interaction; Figure 4.5E). Finally, elevated temperature had no effect on *A. arenaria* total leaf area or leaf width. Nevertheless, elevated temperatures increased median tiller length by 7.9% (CI: 1.4%-14.8% increase), although initial *A. breviligulata* density lessened the temperature effect on tiller length ($N_{AMBR} \times$ heat interaction).

In contrast, initial *A. breviligulata* tiller density had no observable effect on *A. arenaria* total leaf area (Figure 4.5B) or leaf width (Figure 4.5F). Initial *A. breviligulata* density, however, increased *A. arenaria* tiller length by 2.1% (CI: 0.2%-4.1% increase) for every 10 additional initial *A. breviligulata* tiller/quadrant under ambient temperature (Figure 4.5D). Under elevated temperatures, however, *A. breviligulata* density had no effect on *A. arenaria* tiller length.

The morphological response of *Ammophila breviligulata* to competitors, sand burial, and temperature treatments differed from *A. arenaria*. Although some *A. arenaria* leaf morphometrics varied with the initial tiller density of its congener, initial *A. arenaria* tiller density had no observable effect on *A. breviligulata* total leaf area, tiller length, or leaf width (Figure 4.6 B, D, E). *Ammophila breviligulata* also did not respond as positively to sand burial as *A. arenaria*. When initial *A. breviligulata* density is low, sand burial had a negligible effect on *A. breviligulata* total leaf area. However, for every 10 additional initial *A. breviligulata* tillers/quadrant, high sand burial increased total leaf area by 13% (CI: 1% decrease-28% increase; Figure 4.6A). Thus, sand burial was most beneficial when *A. breviligulata* occurred at high density. *Ammophila breviligulata*

subjected to high sand burial also exhibited a 3.2% decrease in median tiller length (CI: 5.8% decrease-0.8% increase; Figure 4.6 C, D) and a 13% increase in median leaf width (CI: 8% decrease-19% increase; Figure 4.6 E, F). Finally, elevated temperature had no effect on *A. breviligulata* total leaf area or tiller length. Nevertheless, elevated temperature reduced *Ammophila breviligulata* leaf width when *A. breviligulata* occurred at low initial densities. However, higher initial *A. breviligulata* density ameliorated the negative temperature effects on leaf width ($N_{AMBR} \times \text{heat}$ interaction).

4.4. Discussion

This study examined the effects of elevated temperature and sand burial on the abundance, morphology, and competitive interactions of the invasive beachgrasses *Ammophila arenaria* and *A. breviligulata* on the U.S. Pacific Northwest coast. Our goal was to understand how the current distributional ranges of the two species might change as a consequence of physiological tolerances and species interactions under climate change. We asked whether increased temperature, and its interaction with sand deposition, decrease the production of *A. breviligulata*, thereby mediating or potentially reversing its competitive dominance over *A. arenaria*. We predict that such a competitive reversal under climate change would result in the extension of the northern distribution of *A. arenaria* and the restriction of the southern distribution of *A. breviligulata*.

We found that *A. arenaria* responds more positively to sand burial and rising temperatures than *A. breviligulata* (Figure 4.2-Figure 4.6), but *A. breviligulata* still remains competitively dominant across the full range of experimental conditions (Figure 4.4). *Ammophila arenaria*, for example, exhibited few negative impacts of high rates of sand burial on production of biomass or tillers, but also increased belowground biomass production and total leaf area. In contrast, *A. breviligulata* exhibited reduced overall biomass, aboveground biomass, and tiller production under high rates of sand burial. However, sand burial also appeared to ameliorate some density-dependent intraspecific competition, as suggested by positive density-dependent effects of sand burial on tiller production and on total leaf area. Sand burial, then, had both positive and negative effects on *A. breviligulata* growth depending on its density.

This study found relatively weak effects of temperature on the biomass, tiller production, and morphology of the *Ammophila* congeners, although the data suggest that *A. breviligulata* is more sensitive to rising temperatures than *A. arenaria*. For *A. arenaria*, elevated temperatures had a neutral to positive effect on aboveground and belowground biomass, depending upon the rate of sand burial (Figure 4.3D, Appendix C, Table C3). Elevated temperatures further had no effect on *A. arenaria* tiller production or total leaf area (Appendix C, Table C5, Appendix C, Table C7). For *A. breviligulata*, elevated temperatures reduced the production of total biomass and belowground biomass (Figure 4.3D, Table 4.2).

Finally, *A. breviligulata* was competitively dominant to and was predicted to displace *A. arenaria* across all experimental conditions, although elevated temperature and high rates of sand burial increased the likelihood of coexistence (Figure 4.4). This change in competitive interactions was primarily attributable to reductions in *A. breviligulata* tiller production with high sand burial and with elevated temperatures rather than as a positive change in *A. arenaria* tiller production. When considered alongside the species-specific biomass trends discussed above, our model showed that high sand burial and elevated temperatures could increase the likelihood of coexistence by reducing the competitiveness of *A. breviligulata*.

4.4.1. Species-specific growth and morphological responses to elevated temperature

The difference in species interaction strength that we observed between the two congeners is a response to how they differentially deal with temperature and sand burial. Although we found that *Ammophila breviligulata* is less tolerant of elevated temperatures than *A. arenaria*, the observed differences were generally small with some uncertainty associated with our statistical estimates. For most metrics, both *Ammophila* species showed no response to elevated temperature. However, for belowground biomass production, the two species markedly differed: *A. breviligulata* exhibited a 36% reduction in belowground biomass production, while *A. arenaria* exhibited no such response. As a result, our findings are consistent in some respects with previous single-species *Ammophila* warming experiments (Seneca and Cooper 1971, Yuan et al. 1993, Emery and Rudgers 2013), but differ in other respects.

For example, *A. arenaria* biomass production appears insensitive to high temperatures, even when temperatures frequently exceeded 50°C in a greenhouse (Huiskes 1979). Thus, the lack of a temperature response in *A. arenaria* was consistent with previous work and our hypothesis. For *A. breviligulata*, the observed reductions in belowground biomass with rising temperatures also parallel observations by Seneca and Cooper (1971) and Emery and Rudgers (2013). For example, while both studies show decreased aboveground production at high temperatures, Seneca and Cooper (1971) found that reductions in aboveground production only became apparent at higher temperatures while belowground production decreased linearly across the range of temperature levels. Thus, reduced belowground biomass production appears to be an early response to rising temperatures in *A. breviligulata*.

The limited aboveground biomass response and tiller production of *A. breviligulata* may be related to several factors. In our study, the climate in the U.S. Pacific Northwest (PNW) is considerably more moderate than that of the Great Lakes and the U.S. Atlantic coast. For example, mean daily maximum air temperature at Hatfield Marine Science Center, Newport, Oregon, were 18°C to 20°C in June, July, August, and September (Appendix C, Table C1), and maximum daily air temperature rarely exceeds 30°C. At the soil surface, however, conditions may be more extreme: within unheated planters, average monthly maximum daily soil temperatures (4 cm below the surface) were 22°C and 27°C in unheated plots and 25°C and 29°C in heated plots during summer months (Appendix C, Table C2). Based on the results of these similar studies, it appears that *A. breviligulata* was experiencing some degree of heat stress in our study, but the mild regional climate of the PNW may allow *A. breviligulata* to continue to be a successful invader despite rising temperatures.

Temperature-associated reductions in *A. breviligulata* belowground biomass may have significant fitness ramifications. Foredune habitats are an abiotically stressful, xeric ecotone with low nutrient availability (Barbour et al. 1985, Pavlik 1985, Maun 2008, Wiedemann and Pickart 2008). Although expansive root systems are essential for obtaining resources, the reduction in belowground biomass production with temperature suggests that it may reduce the ability of *A. breviligulata* to secure water and nutrients,

both of which limit *Ammophila* productivity (Pavlik 1983a, 1985).

Correspondingly, Seneca and Cooper's (1971) finding that temperature limits rhizome production, when combined with our finding of lower tiller production with elevated temperatures, indicate that temperature may also inhibit clonal propagation in *A. breviligulata*.

The power of this study to detect temperature effects was likely hindered by a few factors. First, although we set up 64 planters (subplots), we were limited by the number of independent heating circuits we could deploy, which resulted in lower replication of the main plot treatment than we would have preferred (n=8). In addition, our experimental methods differed from those of others who have measured *A. breviligulata* sensitivity to temperature. We manipulated temperature by 3°C to match the predicted regional warming over a century time period (Mote and Salathé 2010) using buried heating cables in outdoor planters filled with sand (heating concentrated in soil), while past work with *A. breviligulata* manipulated temperature by 5°C or more using growth chambers (controlled, uniform heating throughout soil and canopy) (Seneca and Cooper 1971, Emery and Rudgers 2013). Consequently, we likely observed a lower magnitude but more realistic response to heating than past studies.

4.4.2. Species-specific growth and morphological responses to sand burial

Both *Ammophila* species are resilient to high rates of sand burial and even depend upon moderate rates of sand burial for growth. The *Ammophila* species, for example, can both survive in excess of one meter of sand burial per year, although with reduced growth and higher mortality at such extreme rates of sand burial (Huiskes 1979, Eldred and Maun 1982, Maun and Lapierre 1984, Zarnetske et al. 2012). At the other extreme, both *Ammophila* species exhibit reduced vigor under no sand burial conditions, although the explanation for this reduction in vigor is debated (Eldred and Maun 1982, Disraeli 1984, van der Putten et al. 1988, Little and Maun 1996).

Though the *Ammophila* congeners exhibit many similar responses to sand burial, they also differ in a few key aspects. For example, we found that high rates of sand burial caused no reductions 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 is repeatedly 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. 2012). For *A. breviligulata*, however, sand burial either did not alter tiller production (Maun and Lapierre 1984) or did not increase tiller production as much as *A. arenaria* (Baye 1990, Zarnetske et al. 2012); rather, sand burial caused significant *A. breviligulata* mortality, suffering 50% mortality at burial rates of <60cm/yr. (Maun and Lapierre 1984). Many of these studies, though, show that *A. breviligulata* increased in biomass in response to sand burial, despite limited production of tillers (Eldred and Maun 1982, Disraeli 1984, Maun and Lapierre 1984, Baye 1990, Zarnetske et al. 2012). Thus, both species generally increase productivity with sand burial, but *A. arenaria* responds via increased tiller production while *A. breviligulata* increases tiller biomass.

Multiple hypotheses have been proposed to explain why sand burial often stimulates growth and tiller production, including increased resource availability (Marshall 1965, Wahab and Wareing 1980), reduced interspecific competition (Huiskes 1980), 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* tiller production and total leaf area, but were unrelated to the density of competing *A. arenaria*. Thus, while sand burial was unrelated to the strength of interspecific competition (Eldred and Maun 1982), sand burial may ameliorate *A. breviligulata* intraspecific competition. This reduction in intraspecific competition could arise from higher sand burial-associated mortality (reduction in resource utilization), increased resource use efficiency with sand burial, increased resource availability with sand burial, or increased facilitative interactions among conspecifics that may offset competitive interactions (e.g., structural support enables higher survival).

4.4.3. Species interactions among congeners under varying temperature and sand burial

As has been shown before in Zarnetske et al. (2013), our experiment demonstrated that *A. breviligulata* is competitively dominant to *A. arenaria*, but the strength of that

interaction depended on environmental conditions. Under all four combinations of temperature and sand burial, *A. breviligulata* exerted a comparatively strong negative effect on *A. arenaria* tiller and biomass production (aboveground, belowground, and total biomass), while *A. arenaria* exerted a weaker negative effect on *A. breviligulata* on those same measures. Based on the fitted Ricker interaction models, we predict that *A. breviligulata* would exclude *A. arenaria* under nearly all experimental conditions. However, it remains possible that elevated temperature and high rates of sand burial can mediate coexistence between the *Ammophila* congeners. We found that *A. arenaria* was negligibly affected by elevated temperature and high rates of sand burial, while *A. breviligulata* tiller production decreased markedly with sand burial and temperature. Because high sand burial and elevated temperature disproportionately reduced *A. breviligulata* growth rates, our models showed that there was an increased but relatively low likelihood for stable coexistence to occur. For example, 30-45% of the elevated temperature/high sand burial bags were predicted to maintain a stable coexistence of both species, while less than 20% of bags under ambient temperature/low sand burial were predicted to maintain a stable coexistence (Figure 4.4). Thus, reductions in *A. breviligulata* performance under high rates of sand burial and elevated temperatures may allow *A. arenaria* to either stably coexist or may reduce its rate of displacement by reducing the growth of *A. breviligulata*.

4.4.4. Pacific Northwest dune ecology and geomorphology amidst invasion and a changing climate

Climate change is projected to increase temperatures along the U.S. Pacific Northwest coast by 3°C over a 100 year time-period (Mote and Salathé 2010). Similarly, sea-level rise, and changes to wave amplitude, periodicity, direction, and the frequency and intensity of storms is likely to alter rates of sand erosion and accretion on beaches and dunes. Nevertheless, *A. breviligulata* mostly displaces *A. arenaria* under present-day and projected temperature conditions and across a range of sand burial conditions. Consequently, rising temperatures and changes in sand deposition may reduce *A. breviligulata* invasiveness, thus altering the rate at which displacement occurs and occasionally fostering coexistence.

Ammophila breviligulata is currently dominant in the Columbia River Littoral Cell, a highly progradational region of open coastline near the mouth of the Columbia River (Figure 4.1). Because of the high sediment input from the Columbia River, much of this littoral cell's coastline is expanding seaward. Although counterintuitive, this high rate of beach building is associated with low vertical sand accretion, whereas more stable and erosive shorelines that are common in central to southern Oregon exhibit higher rates of vertical accretion (Hacker et al. 2012, Ruggiero et al. in press, Chapters 2-3). Thus, *A. breviligulata* dominance coincides with low sand burial conditions. As *A. breviligulata* expands its range southward, however, its capacity to displace *A. arenaria* could diminish. Because the shoreline change rates of central and southern Oregon are typically stable or mildly erosive (Ruggiero et al. 2013), rates of sand burial on central and southern Oregon foredunes may exceed those within the Columbia River Littoral Cell and impede further *A. breviligulata* expansion. *Ammophila breviligulata* colonists, for example, experience higher mortality under heightened sand burial conditions. Even after establishment, heightened sand deposition and warmer temperatures may impede *A. breviligulata* growth and tiller production as it spreads south. Because the success of *A. breviligulata* as an invader depends, in part, upon its ability to colonize, its rapid growth rate, and its capacity for clonal propagation, these temperature and sand-burial associated reductions in survival and growth are likely to reduce *A. breviligulata* invasiveness, with few mal-effects on *A. arenaria*. Thus, *A. arenaria* might experience some competitive release, permitting competitive coexistence among the *Ammophila* species.

Changes to the distribution and abundance of either *Ammophila* congener would also alter foredune community structure, geomorphology, and ecosystem services provided by foredunes. Ecologically, *A. breviligulata* is not only dominant to *A. arenaria*, it is a superior competitor to many native and endemic beach and foredune plant species. 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). Correspondingly, when *A. breviligulata* displaced *A. arenaria* as the dominant grass in the Columbia River Littoral Cell, it also reduced native richness and cover (Seabloom and Wiedemann 1994, Hacker et al. 2012,

David et al. 2015). Thus, further expansion of *A. breviligulata* range would likely portend further harm to endemic plants, but such an expansion might be moderated by temperature and sand burial conditions.

Geomorphologically, both *A. arenaria* and *A. breviligulata* are important dune-building species because of their abilities to induce aeolian sediment deposition. Here the capacity for beachgrasses to capture aeolian sediment is proportional to beachgrass density (Zarnetske et al. 2012), such that denser beachgrass growth may facilitate the formation of taller and narrower foredunes (Hesp 1989, Chapter 2). *Ammophila breviligulata* displacement of *A. arenaria*, though, may shorten and widen foredunes as a result of species-specific differences in morphology and growth form (Zarnetske et al. 2012, 2015, Chapter 2). Sand burial and rising temperature may also lessen *A. breviligulata* tiller density, resulting in reduced sand capture and ultimately shorter, wider foredunes. Because foredune height strongly influences the risk of coastal flooding and erosion during storm events (Ruggiero et al. 1996, Sallenger 2000, Stockdon et al. 2006), replacement of *A. arenaria* with *A. breviligulata* could substantially increase coastal hazard exposure, particularly with rising sea-level and changes in storminess (Seabloom et al. 2013).

4.4.5. Invasions, biotic interactions, and climate change

Forecasting potential climate change impacts on invasive species in novel communities requires an understanding of multiple invasion processes, including limitations to dispersal and both abiotic and biotic determinants of species distributions (Dukes and Mooney 1999, Hellmann et al. 2008, Walther et al. 2009, Bradley et al. 2010). Many invasions, however, place non-native species in new environments with novel, uncharacterized interactions (Hobbs et al. 2006, Bradley et al. 2010, Václavík and Meentemeyer 2012). Moreover, invasive species often grow better in invaded habitats than in native habitats (Parker et al. 2013), and even may occupy climate envelopes that differ from their native range (Broennimann et al. 2007, Gallagher et al. 2010). The *Ammophila* species, for example, are more pervasive and exhibit more vigorous growth in the Pacific Northwest than in their native range (Beckstead and Parker 2003, van der

Putten et al. 2005). Consequently, predicting how both abiotic and biotic factors may alter invasion requires observation and experimentation in their non-native range.

Predicting climate change impacts on species invasions adds additional challenges. Although both observational and experimental techniques may illuminate mechanisms that limit species ranges, invasive species are often at disequilibrium with their environment, due to dispersal barriers or due to the stage of invasion (Václavík and Meentemeyer 2012). When combined with differences in native and introduced range limits (Broennimann et al. 2007, Gallagher et al. 2010), estimating the potential distribution of an invasive species based on their native or introduced ranges alone may be misleading (Fitzpatrick et al. 2007, Gallien et al. 2012, Wisz et al. 2013). Experimental manipulations, then, provide an essential tool for investigating how invasive species might respond to climate change. From this and related studies, we show that novel biotic interactions arising from the dual invasion of the *Ammophila* congeners effectively constrain the northern distributional limit of *A. arenaria* in the Pacific Northwest, while dispersal may restrict the southern limit of *A. breviligulata*. However, we also show that the two species differed in their responses to rising temperatures and gradients in sand burial, and that changes in abiotic conditions altered their likelihood of coexistence. Thus, this study provides an important examination into how abiotic factors and biotic interactions might constrain the ranges of *A. arenaria* and *A. breviligulata* across environmental gradients and with climate change.

Consideration of climate change impacts on invasive species abundance may prove equally valuable (Hellmann et al. 2008, Yokomizo et al. 2009, Thiele et al. 2010). The invasiveness of non-native species often varies across environmental gradients, such that it may be invasive under some context, but not others (Alpert et al. 2000, Seabloom et al. 2003, Bradley et al. 2009). For the *Ammophila* congeners, their primary mode of impact on the foredune ecosystem is integrally related to their abundance: bioengineering of foredunes. Through stabilization of foredunes, the *Ammophila* congeners increase sand deposition on foredunes, but also reduce sand burial, sand scour, salt spray, and wave overwash on the backdune, thereby moderating backdune environments and facilitating backdune succession by salinity- and sand burial-intolerant species (Wiedemann and

Pickart 1996). Because beachgrass abundance partly controls rates of sand deposition and dune building (Zarnetske et al. 2012, 2015, Chapter 2), reductions in beachgrass vigor from climate and sand burial would not only affect beachgrass abundance, it could alter foredune geomorphology, foredune and backdune ecosystem processes, community structure, and ecosystem services (e.g., coastal protection, erosion control). Consequently, to holistically consider how climate change might alter invasive species effects, it is essential to consider not only distributional responses to climate change, but also abundance responses for predicting likely impacts and management needs.

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Table 4.1. *A-priori* hypothesized Ricker model variations for estimating tiller production responses ($\log(\text{final tiller density} / \text{initial tiller density})$) to heat, sand burial, and varying initial tiller densities of *Ammophila arenaria* ($N_{\text{AMAR, Initial}}$) and *Ammophila breviligulata* ($N_{\text{AMBR, Initial}}$). The effects of heat and sand burial on tiller production could be unimportant (---), independent of the density of either *A. arenaria* (AMAR) or *A. breviligulata* (AMBR) (i.e., density-independent effect), and/or dependent upon $N_{\text{AMAR, Initial}}$ or $N_{\text{AMBR, Initial}}$ (i.e., density-dependent effect).

Response Variable	$N_{\text{AMAR, Initial}}$	$N_{\text{AMBR, Initial}}$	Heat		Sand Burial	
			Density Independent	Density Dependent	Density Independent	Density Dep.
$\log\left(\frac{N_{X,\text{Final}}}{N_{X,\text{Initial}}}\right)$	---	---	---	---	---	---
	Yes	---	---	---	---	---
	---	Yes	---	---	---	---
	Yes	Yes	---	---	---	---
	Yes	Yes	Yes	---	---	---
	Yes	Yes	---	Yes ($N_{\text{AMAR, Initial}}$)	---	---
	Yes	Yes	---	Yes ($N_{\text{AMBR, Initial}}$)	---	---
	Yes	Yes	Yes	Yes ($N_{\text{AMAR, Initial}}$)	---	---
	Yes	Yes	Yes	Yes ($N_{\text{AMBR, Initial}}$)	---	---
	Yes	Yes	Yes	---	Yes	---
	Yes	Yes	---	Yes ($N_{\text{AMAR, Initial}}$)	Yes	---
	Yes	Yes	---	Yes ($N_{\text{AMBR, Initial}}$)	Yes	---
	Yes	Yes	Yes	Yes ($N_{\text{AMAR, Initial}}$)	Yes	---
	Yes	Yes	Yes	Yes ($N_{\text{AMBR, Initial}}$)	Yes	---
	Yes	Yes	---	---	Yes	---
	Yes	Yes	---	---	---	Yes ($N_{\text{AMAR, Initial}}$)
	Yes	Yes	---	---	---	Yes ($N_{\text{AMBR, Initial}}$)
	Yes	Yes	---	---	Yes	Yes ($N_{\text{AMAR, Initial}}$)
	Yes	Yes	---	---	Yes	Yes ($N_{\text{AMBR, Initial}}$)
	Yes	Yes	Yes	---	---	Yes ($N_{\text{AMAR, Initial}}$)
Yes	Yes	Yes	---	---	Yes ($N_{\text{AMBR, Initial}}$)	
Yes	Yes	Yes	---	Yes	Yes ($N_{\text{AMAR, Initial}}$)	
Yes	Yes	Yes	---	Yes	Yes ($N_{\text{AMBR, Initial}}$)	

Table 4.2. Substantially supported Ricker model results (based on AIC_c model comparison) of log-response ratios ($\log(N_{AMAR,Final}/N_{AMAR,Init.})$) of tiller density for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) using the predictors of *A. arenaria* (N_{AMAR}) and *A. breviligulata* (N_{AMBR}) initial tiller density, heat, and sand burial treatments.

Response	Fixed Predictors	df	L	AIC _c	Δ_i	W_i
Log($N_{AMAR,Final}/N_{AMAR,Init.}$)	$N_{AMAR} + N_{AMBR}$	6	-159.3	331.1	0.0	0.206
	$N_{AMAR} + N_{AMBR} + \text{Sand}$	7	-159.1	332.9	1.7	0.086
	$N_{AMAR} + N_{AMBR} + N_{AMBR} \times \text{Sand}$	7	-159.2	330.0	1.8	0.082
Log($N_{AMBR,Final}/N_{AMBR,Init.}$)	$N_{AMAR} + N_{AMBR} + \text{Sand} + N_{AMBR} \times \text{Sand}$	8	-225.8	468.5	0.0	0.268
	$N_{AMAR} + N_{AMBR} + \text{Heat} + \text{Sand} + N_{AMBR} \times \text{Sand}$	9	-225.3	469.6	1.1	0.156
	$N_{AMAR} + N_{AMBR} + \text{Sand}$	7	-227.6	469.8	1.3	0.137

Table 4.3. Predicted mean r , K , and α for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) under elevated and ambient heat and low and high sand burial combinations.

Heat Treatment	Sand Burial Treatment	Species	r	K	Competition Coefficient (α)
Ambient	Low	AMAR	0.27	15.9	$\alpha_{AB} = 0.70$
		AMBR	2.01	30.8	$\alpha_{BA} = 0.16$
	High	AMAR	0.27	15.9	$\alpha_{AB} = 0.70$
		AMBR	1.08	32.1	$\alpha_{BA} = 0.31$
Elevated	Low	AMAR	0.27	15.9	$\alpha_{AB} = 0.70$
		AMBR	1.74	26.6	$\alpha_{BA} = 0.16$
	High	AMAR	0.27	15.9	$\alpha_{AB} = 0.70$
		AMBR	0.81	24.1	$\alpha_{BA} = 0.31$

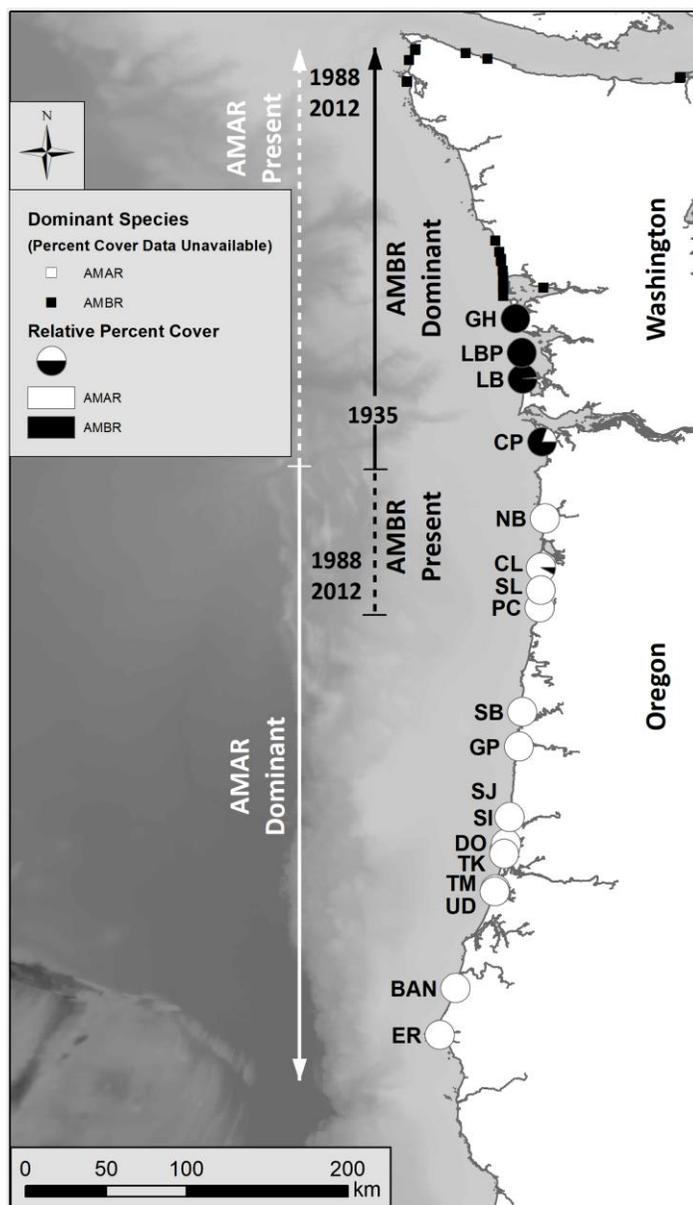


Figure 4.1. Distribution and relative percent areal cover of *Ammophila arenaria* (AMAR; white fill) and *A. breviligulata* (AMBR; black fill) along Pacific Northwest coast foredune sites (Grays Harbor (GH), Leadbetter Point (LBP), Long Beach (LB), Clatsop Plains (CP), Nehalem Bay (NB), Cape Lookout (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)). AMAR was dominant along the Oregon and Washington coasts by the 1950s (Seabloom and Wiedemann 1994). AMBR was first introduced to Clatsop Plains in 1935 and moved to its northern and southern locations shown on the map by 1988 (Hacker et al. 2012). Relative percent cover data from 2012 foredune community field surveys (Chapter 2).

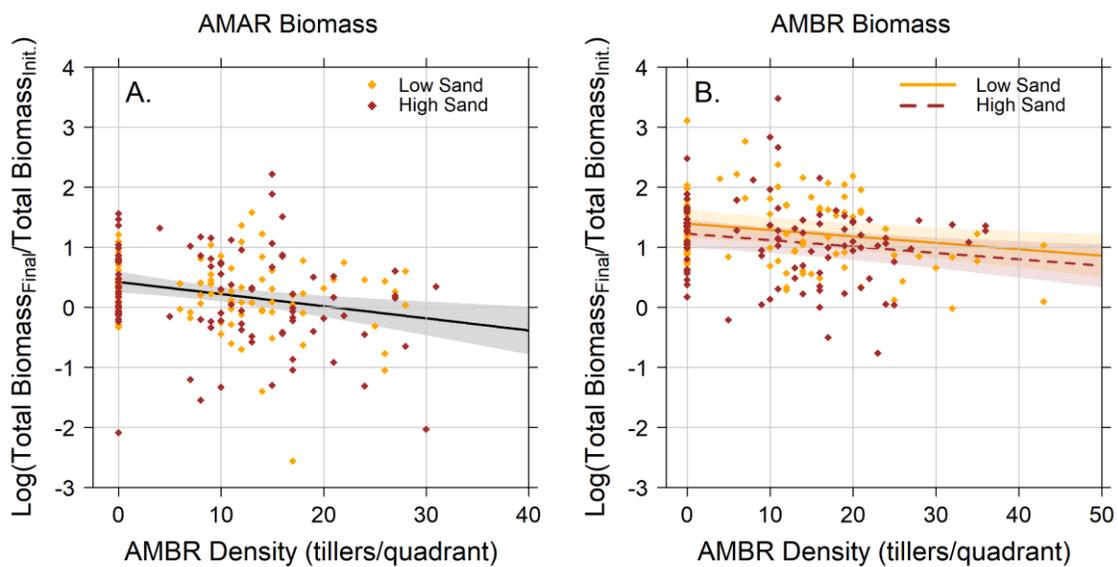


Figure 4.2. (A) Log response ratio ($\log(\text{Total Biomass}_{\text{Final}}/\text{Total Biomass}_{\text{Init}})$); LRR of *A. arenaria* (AMAR) total biomass associated with *A. breviligulata* (AMBR) initial tiller density. (B) LRR of AMBR total biomass associated with sand burial treatment levels and AMAR initial tiller density. LRR > 0 indicates biomass gain. Lines and bands represent LRR predictions and 95% confidence intervals based on linear mixed models.

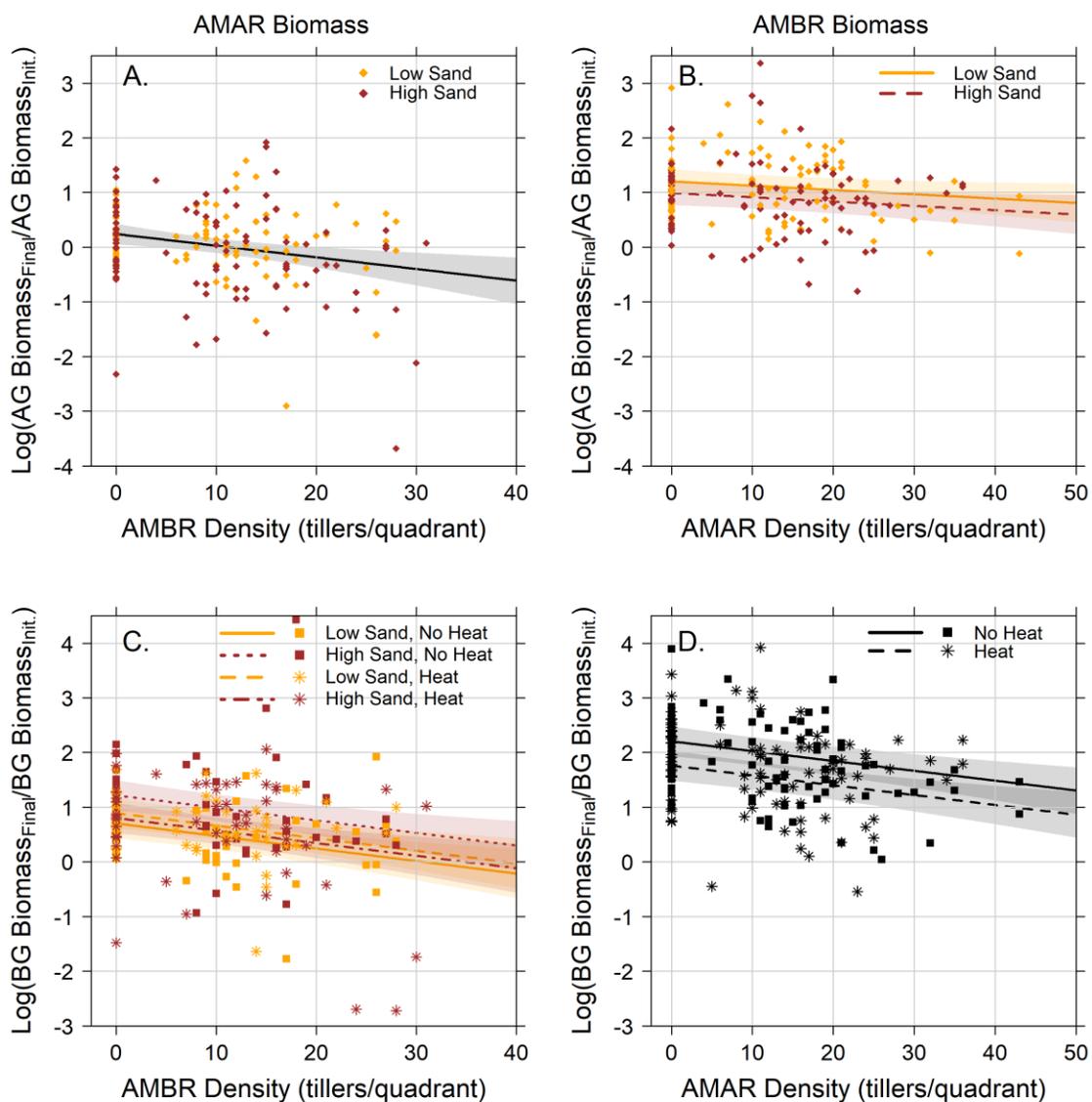


Figure 4.3. Log response ratio (LRR) of *A. arenaria* (AMAR) (A) aboveground (AG) biomass and (C) belowground (BG) biomass associated with sand burial treatment levels and *A. breviligulata* (AMBR) initial tiller density. LRR of AMBR (B) aboveground biomass and (D) belowground biomass associated with heat treatment levels and AMAR initial tiller density. LRR > 0 indicates biomass gain. Lines and bands represent LRR predictions and 95% confidence intervals based on linear mixed models.

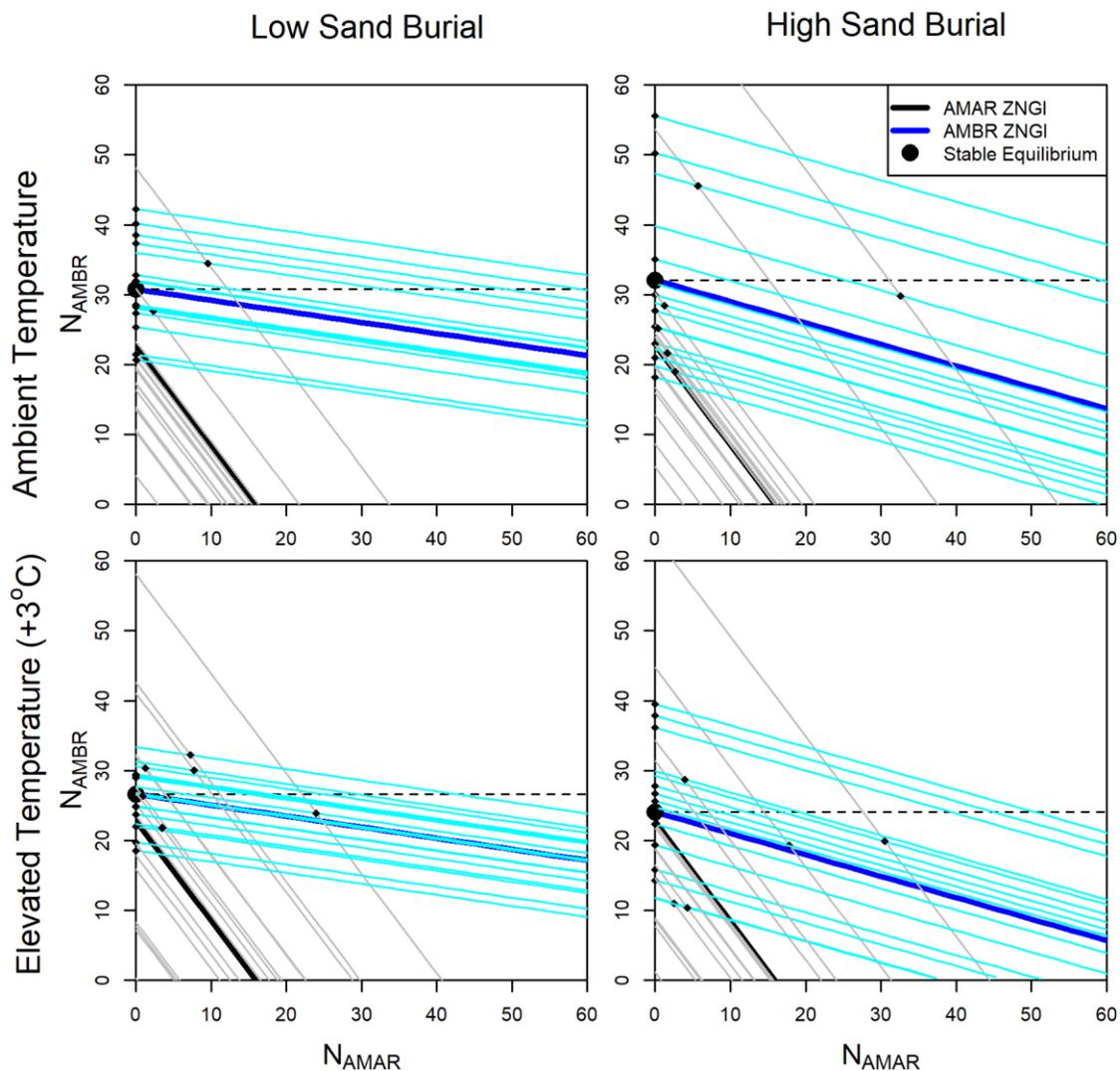


Figure 4.4. State space diagrams showing the zero-net growth isoclines (ZNGI) of *A. arenaria* (N_{AMAR} ; blue) and *A. breviligulata* (N_{AMBR} ; black) tiller density under varying heat and sand burial conditions. The thick lines depict the mean ZNGI among all bags, and the large black point shows the corresponding stable equilibrium point. Thin lines depict the estimated ZNGI for each bag (random intercept, corresponding to variation in species-specific intrinsic growth rates among bags), and the small black points show the corresponding stable equilibrium points for each bag.

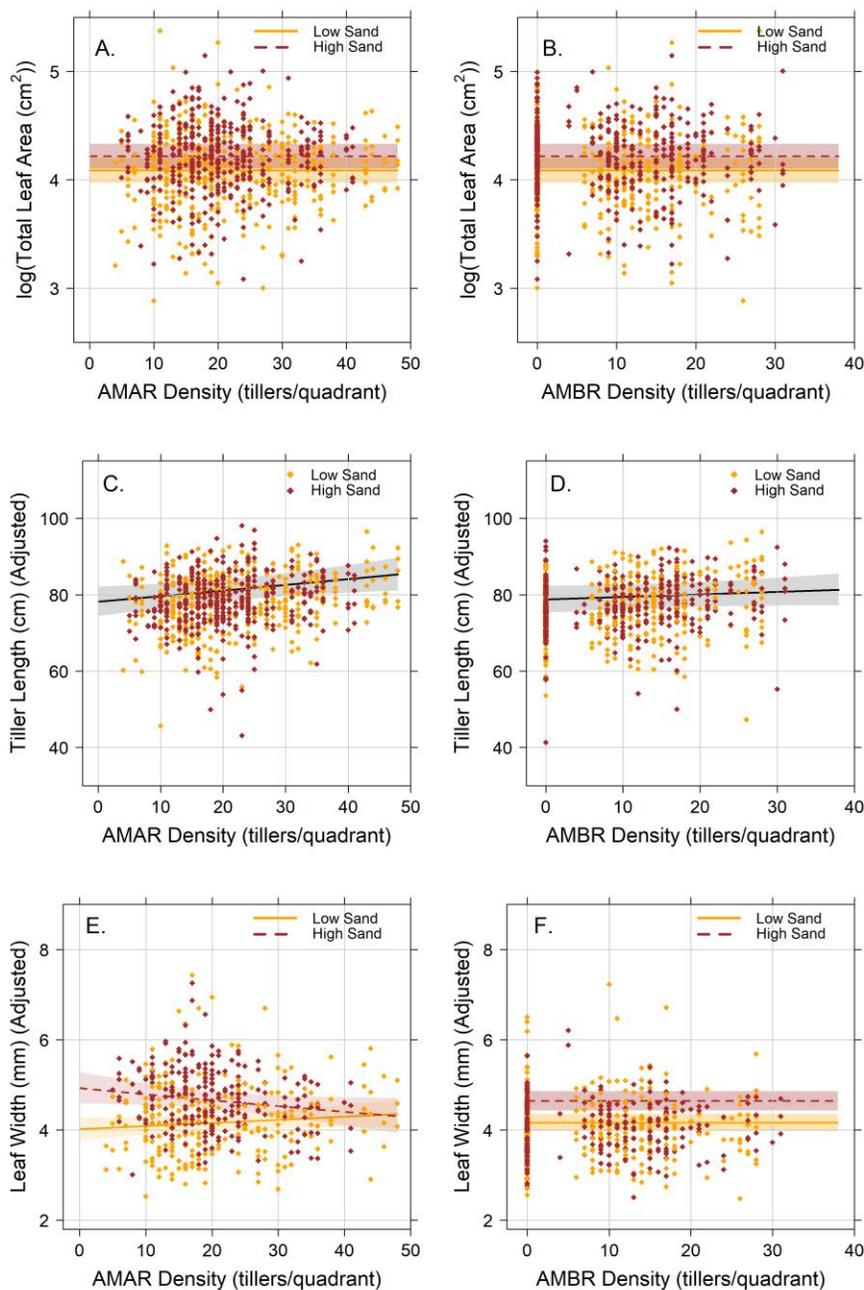


Figure 4.5. *Ammophila arenaria* leaf morphological responses to *A. arenaria* initial tiller density (A, C, E), *A. breviligulata* initial tiller density (B, D, F), and sand burial (all panels). (A-B) Log(total leaf area (cm²)). (C-D) Tiller length (cm), adjusted for all other covariates. (E, F) Leaf width (mm), adjusted for all other covariates. Points represent partial residuals of leaf 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 leaf morphometrics based on linear mixed models and associated 95% confidence intervals.

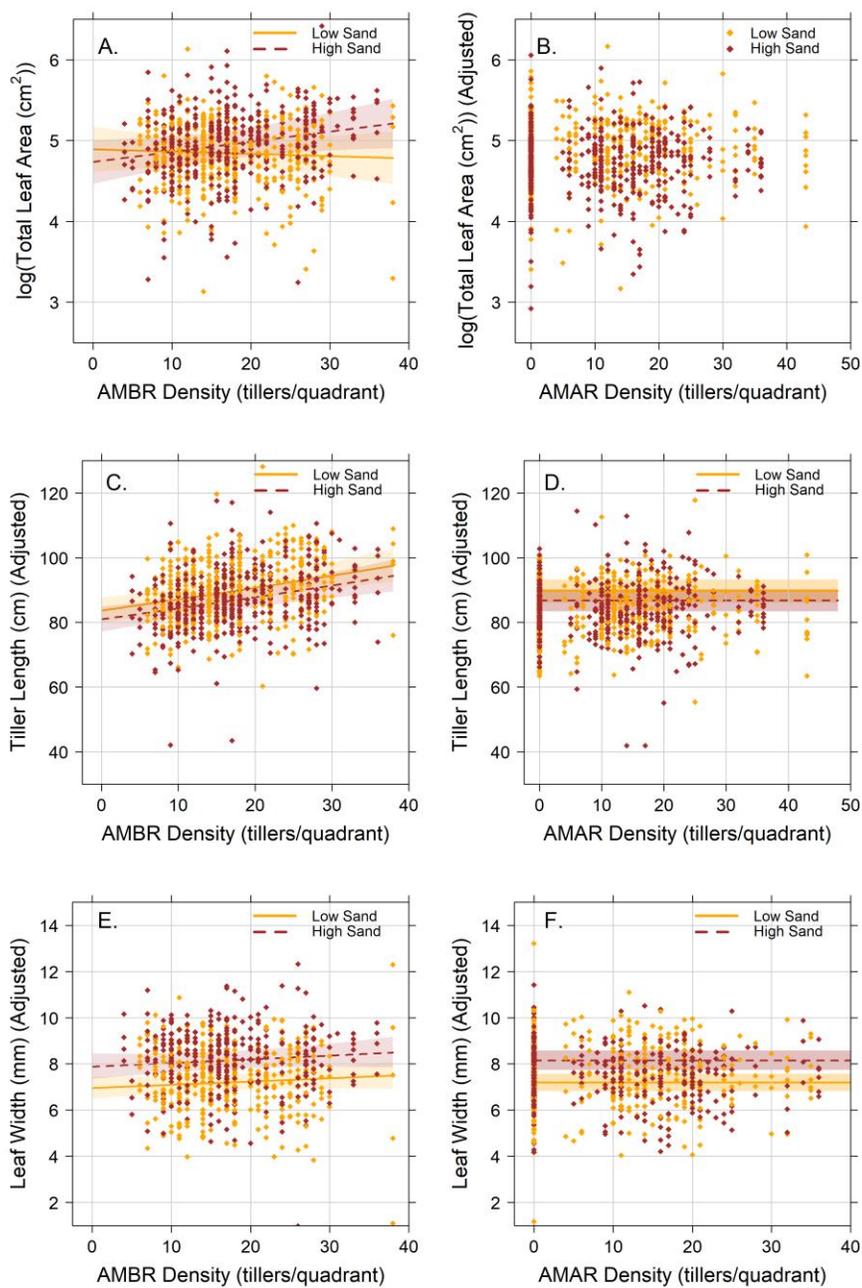


Figure 4.6. *Ammophila breviligulata* leaf morphological responses to *A. breviligulata* initial tiller density (A, C, E), *A. arenaria* initial tiller density (B, D, F), and sand burial (all panels). (A-B) Log(total leaf area (cm²)). (C-D) Tiller length (cm), adjusted for all other covariates. (E, F) Leaf width (mm), adjusted for all other covariates. Points represent partial residuals of leaf 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 leaf morphometrics based on linear mixed models and associated 95% confidence intervals.

5. Coastal protection and conservation on sandy beaches and dunes: context-dependent tradeoffs in ecosystem service supply

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Abstract

Managing multiple ecosystem services (ESs) across landscapes presents a central challenge for ecosystem-based management, because services often exhibit spatiotemporal variation and weak associations with co-occurring ESs. Further focus on the mechanistic relationships among ESs and their underlying biophysical processes provides greater insight into the causes of variation and covariation among ESs, thus serving as a guide to enhance their supply while preventing adverse outcomes. Here, we used the United States Pacific Northwest coastal dune ecosystem to examine how invasive beachgrass management affects three ESs: coastal protection, western snowy plover conservation, and endemic foredune plant conservation. At seven coastal dune habitat restoration areas, we observed spatial variation in the supply of each ES and further identified a tradeoff between western snowy plover conservation and coastal protection. While the ESs were collectively influenced by the invasive beachgrasses and the foredunes they create, the magnitude of the synergies and tradeoffs were influenced by numerous non-shared drivers, including nearshore geomorphology, changes in foredune shape as a result of restoration, and other management actions irrespective of restoration. Incorporation of these shared and non-shared drivers into future coastal management planning may reduce tradeoffs among Pacific Northwest dune ESs. With better understanding of ES relationships, it becomes possible to identify management actions that may enhance synergies and mitigate tradeoffs, leading to better decisions for nature and people.

5.1. Introduction

Throughout human history, ecosystems have been manipulated to provide goods and services that enhance human wellbeing. However, a confluence of factors, such as population and economic growth, has created a rising demand for ecosystem services (ESs). In some cases, this demand is unmet because of misallocation of resources, ecosystem mismanagement, and habitat degradation and destruction (MEA 2005). To improve the efficiency of ES management, multiple studies have called for more research

on common patterns and relationships among ESs (Bennett et al. 2009, Lester et al. 2013, Needles et al. 2015).

Ecosystems are often managed to maximize individual ESs, most commonly provisioning services such as food, fuel, and timber production (MEA 2005). While these strategies boost target ESs, they often cause unintended, and sometimes unexpected, losses to non-target ESs due to coupling of target and non-target ESs (Gordon et al. 2008, Pejchar and Mooney 2009, Bullock et al. 2011, Needles et al. 2015). To optimize ES supply, it may be important to consider how multiple ESs individually vary and jointly covary across landscapes. This multi-service approach may benefit natural resource, conservation, and invasive species management planning, which often focus on single species or ESs. For example, invasive species represent one of the greatest threats to biodiversity and reduces provisioning of many goods (e.g., agricultural products) and services (e.g., carbon sequestration, erosion control). However, invasive species sometimes provide valuable services to local communities and may support essential ecosystem processes (Ewel et al. 1999, Hershner and Havens 2008, Pejchar and Mooney 2009, Lampert et al. 2014). Similarly, ecological restoration practitioners frequently pursue multiple restoration objectives that might include improvements to target species, restoration of ecosystem processes, structure, and function, and/or recovery of ecosystem services. Although restoration objectives are frequently complementary, situations also arise in which ecosystem management goals conflict (e.g., endangered species conservation threatened by invasive species eradication (Lampert et al. 2014); ecological and socio-economic goals of public forests under multiple-use mandates (Vogler et al. 2015)). Therefore, while invasive species removal and ecosystem restoration often benefit both biodiversity and other important ESs, it can also produce ES tradeoffs (Bullock et al. 2011) and conflicts among stakeholders (Bode et al. 2008, Buckley and Crone 2008). Consideration of multiple ESs and their interactions, then, may improve ES management by revealing which interventions are likely to yield net-positive effects (White et al. 2012, Needles et al. 2015), and allow managers and stakeholders to identify and allay potential conflicts (Abelson et al. 2016).

To provide a comprehensive understanding of ESs, recent work has explored whether groups of ESs exhibit consistent spatial patterns and interactions (Bennett et al. 2009). When examining ES covariation, multiple ESs may positively covary as “synergies” or negatively covary as “tradeoffs” (sensu Bennett et al.; 2009) along physical or ecological gradients, or in response to management actions. ES covariation indicates two possible relationships among covarying ESs. If ESs share a common driver, then they may jointly respond to any changes in the shared driver. Alternatively, if one ES directly modifies the biophysical value of another ES, then any modifications to the former ES causes a corresponding change to the latter ES (Bennett et al. 2009). Although some studies have investigated ES co-occurrence and correlation patterns and clustering of ESs within landscape types (Egoh et al. 2008, Raudsepp-Hearne et al. 2010, Martín-López et al. 2012), few explicitly examine how ecosystem processes influence ES interactions (but see (Cademus et al. 2014, Lamarque et al. 2014)). Moreover, ES correlational patterns alone cannot accurately predict ES provisioning under different management strategies, because ESs often exhibit weak to moderate correlation (Egoh et al. 2008, Raudsepp-Hearne et al. 2010), show nonlinear relationships (Koch et al. 2009), and vary spatiotemporally (Koch et al. 2009, Barbier 2012). To better incorporate ES interactions into management planning, we suggest that focusing on mechanistic relationships among ESs and their underlying biophysical processes may 1) provide insight into causes of variation and covariation among ESs, and 2) illuminate management actions that can enhance ES supply while preventing non-target, adverse outcomes.

In this study, we examined interactions among three ESs within the context of invasive species management and ecosystem restoration in the U.S. Pacific Northwest coastal dune system: coastal protection, conservation of the federally threatened western snowy plover (*Charadrius nivosus nivosus*; hereafter, plover), and conservation of endemic beach and foredune plants (e.g., Pink sand verbena, *Abronia umbellata*). Western snowy plovers and endemic dune plants provide cultural and supporting ecosystem goods and services. They support both non-consumptive direct use values (e.g., education, tourism and recreation) and indirect use value (e.g., maintenance of wildlife (Giles-Johnson and Kaye 2014)). Moreover, as threatened species, they have

significant existence and bequeath value and are targets of intensive restoration efforts (USFWS 2007, Giles-Johnson and Kaye 2014).

The coastal dunes of the Pacific Northwest present a useful study system for looking at interactions among ESs. In the early 20th century, two dune-building plants, *Ammophila arenaria* (L.) Link (European Beachgrass) and *A. breviligulata* Fernald (American Beachgrass) were intentionally introduced to facilitate dune stabilization, and their proliferation transformed the historical backshore landscape from an open sand habitat to a stabilized dune system of tall, vegetated foredunes (seaward-most dune ridge parallel to the shoreline) (Cooper 1958, Wiedemann and Pickart 2008). Although these tall foredunes reduce coastal erosion and flooding during storm events (Seabloom et al. 2013, Mull and Ruggiero 2014), beachgrass colonization eliminated upper beach habitat, resulting in population declines of endemic plants (e.g., *Abronia. umbellata*) and shorebirds (e.g., *C. nivosus nivosus*) (Wiedemann and Pickart 2008).

To prevent plover extinction, in the 1990s, U.S. federal and state agencies began dune habitat restoration activities, including foredune and beachgrass removal, predator management, and recreational beach restrictions (USFWS 2007). These efforts produced foredune denudation and shortening, and increased plover abundance (Zarnetske et al. 2010, Pearson et al. 2016) but also precipitated concerns about the loss of coastal protection and recreational beach access (Allan 2004, USFWS 2007, 2012). Nevertheless, few studies have quantified the impact of beachgrass removal on coastal exposure to flooding and erosion. Additionally, although beachgrass removal, beach use restrictions, and predator controls have facilitated plover recovery, beachgrass removal methods appear to reduce endemic plant diversity, suggesting that some restoration methods may hinder holistic dune habitat function, and ultimately, recovery (Zarnetske et al. 2010).

Given the impacts of beachgrass on foredune geomorphology and community structure, we assessed the effects of U.S. Pacific Northwest foredune restoration on exposure to coastal flooding under present-day and possible future extreme storm conditions, on plover conservation, and on endemic plant community conservation. In this study, we address the following questions: 1) Does beachgrass and foredune removal create synergies or tradeoffs (i.e., positive or negative covariation) between three Pacific

Northwest dune services: coastal protection, plover conservation, and endemic plant conservation? 2) Which biophysical processes and interventions produce ES interactions, and do these interactions vary among sites?

To evaluate the potential tradeoffs among ESs, we characterized dune geomorphology and plant community patterns at seven Habitat Restoration Areas (HRAs) and nearby reference sites in Oregon and Washington. A coastal change model, XBeach (Roelvink et al. 2009), was used to assess how geomorphology and beachgrass removal affects flooding and erosion during several extreme storm scenarios. Finally, we analyzed how management interventions (e.g., beachgrass removal, plover predator control) affect plover productivity and plant community composition.

5.2. Methods

5.2.1. Habitat restoration areas

We surveyed seven foredune habitat restoration areas (HRAs) in Oregon and southern Washington, USA in summer and fall 2012 (Figure 5.1, Appendix D, Table D1). Within the HRAs, we established 58 cross-shore transects at beachgrass removal and nearby reference locations (6-14 per HRA) and near sites used by Zarnetske et al. (2010) (Figure 5.1, Appendix D, Table D1). Beachgrass removal was conducted one to three years prior to conducting the surveys, using bulldozing, discing, herbicide, hand pulling, or burning (Appendix D, Table D2; Zarnetske et al. 2010, Lauten et al. 2012, Pearson et al. 2013).

5.2.2. Cross-shore topobathymetric profiles

At each transect location, we measured topography in three cross-shore replicate transects using Network Real-Time Kinematic Differential Global Positioning Systems (Network RTK DGPS). Each of the three replicate transects were run perpendicular to the foredune and parallel to neighboring replicate transects at 10 m alongshore spacing (Figure 5.1; 174 replicates within 58 transects). Topographic beach and foredune profiles were then measured along each replicate between the waterline and the landward edge of the dune field, at sub-decimeter accuracy (Figure 5.2) (Ruggiero et al. 2005).

Corresponding bathymetric profiles were reconstructed between the shoreline and the 18

m isobaths from the best available data sources (Ruggiero et al. 2005, Carignan et al. 2009a, 2009b, Stevens et al. 2012, Di Leonardo and Ruggiero 2015).

5.2.3. Nearshore and foredune metrics and statistics

We classified each topobathymetric transect using metrics of nearshore and foredune morphology. Nearshore morphology was classified into nearshore slope, the mean slope between the horizontal locations of the 18 m isobaths and mean low water (MLW); foreshore slope, mean slope between MLW and mean high water (MHW); and backshore slope, mean slope between MHW and the 4 m contour above local mean sea level (MSL). Foredune morphology was also classified into foredune toe (d_{toe}), foredune crest (d_{crest}), and foredune heel (d_{heel}) elevations and positions (Figure 5.2) using methods described by Mull and Ruggiero (2014), where d_{crest} is the maximum foredune elevation; d_{toe} is the inflection point between the concave-up backshore and concave-down foredune and approximates the most-seaward vegetation line; and d_{heel} is the landward extent of the foredune.

To assess the effects of beachgrass treatment and HRA site on foredune morphology, we modeled d_{toe} and d_{crest} elevation response variables as functions of treatment nested within HRA using R v3.1.2 (R Core Team 2014) and nlme v3.1 (Pinheiro et al. 2014). Because of our nested sampling design, transect was treated as a random intercept, and we included a constant variance function to account for heteroskedasticity among HRA sites and treatments.

5.2.4. XBeach model and extreme storm scenarios

XBeach is a process based numerical model of wave propagation, sediment transport, and nearshore, beach, and dune morphological change (Roelvink et al. 2009). To assess storm-related flooding and erosion exposure, we developed a 1-dimensional cross-shore XBeach model for each of the topobathymetric cross-shore profiles. We employed a variable cross-shore grid resolution of 25m to 1m, with increasing grid resolution near foredunes, and incorporated median sediment grain size estimates from a regional database of physical shoreline characteristics (Peterson et al. 1994) as non-default

parameters in XBeach simulations. All other XBeach model parameters were set to default values. Upon running model simulations, we stored values of bed level and wave height for each 56 hour storm scenario.

To simulate possible changes to regional extreme storms, we considered nine storm scenarios with three levels of significant wave height (SWH) and peak wave period (T), and three levels of storm surge. For a present-day approximately 30-year return level storm event (Mull and Ruggiero 2014), we utilized a 56 hour storm hydrograph from the ‘storm of record’, the March 2-3, 1999 extratropical storm (SWH, T, tide, and surge). Based on wave buoy and tide gauge measurements, the March 2-3 storm event produced SWH = 13.3m, T = 16.7s, and a maximum storm surge = 1.6m. To simulate possible changing storminess patterns on extreme storms, we varied maximum SWH by -1.5m to +2m (11.8 to 15.3m), T by ± 3 s (13.7 to 19.7s; see Seabloom et al. (2013)), and storm surge by ± 0.5 m (1.1 to 2.1m).

5.2.5. Coastal protection metrics and statistics

Using XBeach model outputs, we measured foredune flooding incidence, foredune erosion volume, and foredune retreat distance metrics between pre- and post-storm cross-shore profiles as metrics of flooding and erosion exposure (Figure 5.2). Foredune flooding was identified by the incidence of sediment transport landward of the d_{crest} position, indicating wave overtopping of d_{crest} . Foredune erosion volume represents the change in sediment volume above the 4m contour relative to MSL in pre- and post-storm profiles. Foredune retreat distance denotes the change in the 4m contour’s cross-shore position between the pre- and post-storm profiles. The 4m contour approximates the location of d_{toe} , delineating the beach (< 4 m elevation) from the foredune (≥ 4 m elevation).

To examine how flooding incidence relates to nearshore morphometrics (nearshore, foreshore, and backshore slope), foredune morphometrics (d_{toe} elevation, d_{crest} elevation), and storm characteristics (SWH, T, surge), we modeled flooding incidence against these metrics using a mixed-effects binomial regression model using lme4 v1.1-9 (Bates et al. 2015). Transect was included as a random-intercept to account for the nested sampling

design. To assess multicollinearity among explanatory variables, we calculated the variance inflation factor (VIF) and removed highly multicollinear variables ($VIF > 5$) from the model. To similarly examine how foredune retreat relates to nearshore morphometrics, foredune morphometrics, beachgrass removal, and storm characteristics, we modeled foredune retreat distance against these metrics using a linear mixed model (nlme v3.1). We included a random intercept of replicate-transect nested within transect to reflect the nested sampling design, and a constant variance function to account for heteroskedasticity among HRA-site X treatment combinations.

To examine how flooding and erosion exposure varied among HRAs and with beachgrass removal, we also modeled flooding incidence and foredune retreat against HRA-site, beachgrass removal, and storm characteristics, and excluded multicollinear geomorphology explanatory variables. For flooding incidence, we performed a binomial mixed model with HRA-site, beachgrass removal, and storm characteristics as fixed effects, and transect as a random intercept (lme4 v1.1-9). For foredune erosion volume and retreat distance, we performed linear mixed models with HRA-site, beachgrass removal, and storm characteristics as fixed effects, replicate-transect nested within transect as a random intercept, and a constant variance function to account for heteroscedasticity among HRA-site by treatment combinations (nlme v3.1). For all models, we considered AIC_c and BIC metrics to find the most parsimonious model.

5.2.6. Western snowy plover conservation analysis

To assess plover productivity at each HRA, we obtained data on counts of adult breeding males, counts of fledglings, and whether predator controls were applied for each HRA and year (1992 to 2014) from annual plover population monitoring reports (Lauten et al. 2014, Pearson et al. 2015). Monitoring of breeding plover populations in Oregon and Washington occurs at all sites where plover nesting activity has been detected. Data were visually assessed for temporal autocorrelation using autocorrelation function (ACF) plots. We performed a Bayesian hierarchical Poisson regression using a log link-function with fledgling count as the response variable, $\log(\text{count of breeding males})$ as an offset, and HRA-level intercept and predator management as explanatory variables in rstan

v2.5.0 (Stan Development Team 2014). MCMC parameters were thinned and 95% posterior intervals calculated.

5.2.7. Endemic foredune plant conservation analysis

To assess the effects of beachgrass removal on the dune plant community, we visually estimated percent areal cover of all plant species using 0.25 m² quadrats at 5 m intervals along the cross-shore replicate transects (Figure 5.1). Measurements extended from the seaward vegetation line to d_{heel} . To explore effects of beachgrass removal on plant community composition, we compared plant species richness and abundance between beachgrass removal and reference areas for endemic foredune plants, exotic foredune plants, native backdune plants, and exotic backdune plants (Appendix D, Table D3) using a Bayesian Poisson regression model with HRA-site as a random effect. Richness estimates were rarefied with a bootstrap function (`vegan::specpool`) and rounded to the nearest integer prior to modeling (Oksanen et al. 2013). We further estimated impacts of beachgrass removal on beachgrass and native dune grass percent cover using a Bayesian beta regression model with a non-informative prior. Finally, we assessed responses of individual species incidence to beachgrass removal using a Bayesian logistic regression model with a weakly informative prior Cauchy(0, 2.5) distribution to manage complete separation at some HRA-sites (Gelman et al. 2008).

5.3. Results

5.3.1. Coastal protection service

Nearshore, beach, and foredune morphology are important determinants of coastal hazard exposure, and significantly contribute to differences in flooding and erosion exposure among HRA sites and with beachgrass removal. The seven HRA sites examined in this study had variable nearshore and foredune geomorphology. Nearshore slope, foreshore slope, and backshore slope varied by HRA (Figure 5.3; Appendix D, Table D4–Appendix D, Table D5) and generally increased from northern to southern HRAs. Mean foredune toe (d_{toe}) and crest (d_{crest}) height also varied among sites and with beachgrass removal (Appendix D, Table D6). Consequently, the northernmost HRA, Leadbetter Point,

exhibited a shallow-sloping nearshore extent with comparatively short reference area foredunes, while southerly sites exhibited steeper-sloping nearshore extents with taller reference area foredunes. Among the seven HRAs, beachgrass removal significantly reduced mean d_{toe} and d_{crest} heights relative to reference areas at many HRAs, by an average of 30% (\pm SE: 62% – 80%) for the d_{toe} and 2.2 ± 0.5 m for the d_{crest} . However, the degree of shortening varied considerably among HRAs (Fig 3).

The among-site variation in nearshore morphology and within-site elevation differences alters flooding and erosion exposure to present-day and possible future extreme storm conditions. For flooding exposure, the odds of backdune flooding (wave overtopping of d_{crest}) was positively associated with nearshore slope ($p < 0.0001$) and storm surge ($p < 0.0001$), negatively associated with d_{crest} elevation ($p < 0.0001$) with d_{crest} elevation x surge ($p = 0.058$) and d_{crest} elevation x nearshore slope ($p < 0.0001$) interactions, and not associated with d_{toe} elevation ($p = 0.31$), indicating that steeper sloping nearshore extents, shorter foredunes, and higher storm surge increase the odds of flooding (Figure 5.4). Similarly, foredune retreat (landward retreat of the 4m contour; Figure 5.2) during XBeach simulations was also associated with geomorphology, storm wave intensity (SWH, T), and surge. Foredune retreat distance was positively associated with nearshore slope ($p < 0.0001$), foreshore slope ($p < 0.0001$), backshore slope ($p < 0.0001$), storminess ($p < 0.0001$), and surge ($p < 0.0001$). Foredune retreat was further influenced by interactions between numerous variables, including d_{crest} elevation x backshore slope ($p = 0.019$), d_{crest} elevation x storminess ($p < 0.0001$), and d_{crest} elevation x surge ($p < 0.0001$), indicating that stronger storms, steeper sloped profile, and lower foredunes increased foredune retreat distances (Figure 5.5).

When examining flooding and erosion exposure within and among HRA-sites, we found that the odds of backdune flooding differed among HRA site ($p = 0.0007$), with beachgrass removal ($p = 0.0006$), and with storm surge ($p < 0.0001$; Figure 5.6). Specifically, during a present day extreme storm, the odds of overtopping range from 0.002 (± 1 SE: 0.0006–0.004) to 0.06 (0.03–0.12) at each HRA site. When reframed in terms of absolute risk of overtopping (i.e., expected proportion of overtopped transects during an extreme storm event), overtopping risk ranged from 0.002 (± 1 SE: 0.0006–

0.004) to 0.06 (0.03–0.11) at each HRA site. Beachgrass removal and elevated storm surge further increased the relative odds of overtopping by 6.9 fold (4.0–12.6) and 4.2 fold (3.4–5.3), respectively, relative to the present-day storm scenario. Foredune retreat exhibited similar patterns, where retreat distance varied among HRA sites ($p < 0.0001$), and increased with wave intensity ($p < 0.0001$), surge ($p < 0.0001$), and with beachgrass removal ($p < 0.0001$), with significant HRA-site x wave intensity ($p < 0.0001$), HRA-site x surge ($p < 0.0001$), beachgrass removal x surge ($p < 0.0001$), and wave intensity x surge interactions ($p < 0.0001$). For foredune retreat, a present-day extreme storm caused between 3.0 m (± 1 SE: 2.6–3.3 m) and 26.0 m (23.4–28.9 m) of foredune retreat (mean retreat distance: 13.7 ± 0.3 m), depending upon the HRA site. Stronger wave intensity increased retreat by 14% (9–20%) to 23% (22–24%), while higher surge increased retreat by 17% (16–18%) to 29% (27–31%) at six HRA sites (mean increase: $24 \pm 2\%$), and by 149% (137–162%) at Leadbetter Point. Beachgrass removal further boosted foredune retreat by 26% (19–35%), while higher surge intensified retreat at removal areas by 6% (5–7%).

5.3.2. Plover conservation service

Western snowy plover productivity (fledglings per breeding adult male) responded positively to beachgrass removal and predator control interventions, although this varied among HRA sites (Figure 5.7). Among the HRAs examined, mean productivity ranged from 0.4 (Bandon SPMA; 95% posterior interval: 0.3, 0.6) to 0.9 fledglings per male (Ten Mile Creek; 0.7, 1.1) in years prior to predator management. During years with lethal predator controls, mean plover productivity at HRAs rose by 1.4- to 2.2-fold. No plovers have been observed nesting at Elk River since monitoring began (Lauten et al. 2014).

5.3.3. Endemic dune plant conservation service

Endemic dune plant metrics differed in restored versus reference areas. Beachgrass removal was associated with an 84% decrease in native backdune plant richness (95% posterior interval: 75 – 91% decrease), a 49% decrease in exotic backdune plant richness

(27 – 70% decrease), and no change in either endemic beach and foredune plant richness (42% decrease – 57% increase) or exotic beach and foredune plant richness (11% decrease – 110% increase). As expected, invasive beachgrass removal reduced beachgrass cover, although the magnitude of reductions varied by site (Figure 5.8; Appendix D, Table D7). However, among historically important beach and foredune plant species, beachgrass removal also significantly reduced native dune grass cover (*Elymus mollis*) at most HRA sites (Figure 5.8), and did not affect the incidence of the native forbs *Abronia latifolia*, *Ambrosia chamissonis*, and *Calystegia soldanella* (Appendix D, Table D7). Nevertheless, for the threatened pink sand verbena, beachgrass removal areas were associated with up to an 8.7 fold increase in the odds of incidence when compared to reference areas, depending upon the HRA site (Figure 5.8; Appendix D, Table D7).

5.3.4. Biophysical valuation of tradeoffs

We examined variation and covariation among the three ESs in response to foredune restoration. Coastal protection metrics exhibited tradeoffs with plover productivity, where foredune restoration reduced coastal protection and increased plover productivity. However, the strength of the tradeoff varied both among sites and among coastal protection metrics (Figure 5.9). In contrast, most plant conservation metrics (e.g., richness, incidence of endemic species) exhibited no relationship with either plover productivity or coastal protection (Figure 5.9H), although *Abronia umbellata* incidence positively co-varied with plover productivity (Figure 5.9I) and negatively co-varied with coastal protection metrics. Although quantification of demand for ESs was beyond the scope of this study, see Appendix E for a discussion of demand for coastal protection and conservation ESs in the Pacific Northwest coastal dune system.

5.4. Discussion

Recent reviews on the science of ecosystem services (ESs) call for an improved understanding of their patterns and processes to benefit natural resource and conservation management (MEA 2005, Bennett et al. 2009). As researchers identify more ESs and

their interactions, managing individual ESs within a complex ES network quickly becomes untenable. Moreover, because of this interconnectedness among ESs, management of individual ESs in isolation increases the chance for negative impacts on non-target ESs. Consequently, systematic assessments can help to avoid or mitigate negative externalities and to identify possible interventions that improve provisioning of multiple ESs for multiple users (Lester et al. 2013, Needles et al. 2015).

Methodologically, ES interactions may be identified by examining potential covariation among ESs and their underlying drivers (i.e., ecosystem processes or functions).

Covariation among ESs indicates either the presence of a shared driver (i.e., an ecosystem processes that affects multiple ESs) or a direct modification of one ES by another (Bennett et al. 2009). While shared drivers provide leverage points for altering ES supply, non-shared drivers and context-dependent relationships are also important for ES management.

5.4.1. Shared drivers: Plover-coastal protection tradeoff

Manipulation of shared drivers provides an opportunity to alter ES synergies and tradeoffs: when ESs positively covary, alteration of shared drivers has the potential to boost both ESs, creating “win-win” management opportunities; in contrast, for negatively covarying tradeoff ESs, alteration of a shared driver may deepen a “win-lose” situation by enhancing one ES over another. The plover-coastal protection tradeoff represents the latter case, where invasive beachgrasses, the shared driver, inhibit plover nesting, but also provide coastal protection.

Invasive beachgrasses harm plover productivity, yet build foredunes that reduce risk of wave overwash and erosion. Plovers preferentially select nesting habitat with low vegetation cover (1-18% (Zarnetske et al. 2010)) and in areas with $\geq 100\text{m}$ of open space, possibly to facilitate courtship and early predator detection (Muir and Colwell 2010, Pearson et al. 2016). Throughout the U.S. Pacific Northwest, though, beachgrass cover exceeds 25% across the foredune itself, with near-complete monopolization of space near the foredune crest (Hacker et al. 2012). This elimination of open space by beachgrasses not only inhibits plover nest initiation, but also provides habitat for multiple mammalian

and avian predators. In turn, beachgrass removal has re-created open nesting habitat and remains essential for plover productivity and recovery (Figure 5.9A) (USFWS 1993, 2007, Muir and Colwell 2010, Zarnetske et al. 2010, Dinsmore et al. 2014, Pearson et al. 2016).

Beachgrasses also increase coastal protection ES by creating foredunes via sand accretion (Hesp 1989, Zarnetske et al. 2012). In the Pacific Northwest, invasive *Ammophila* spp. effectively capture sand, leading to development of tall, stable foredunes that range from 3–18 meters in height (Hacker et al. 2012). Correspondingly, mechanical beachgrass removal reduces both invasive beachgrass abundance (Figure 5.8) and foredune height (Figure 5.3), resulting in a 6.9-fold increase in the odds of flooding and a 26% greater foredune retreat distance for a representative 30-year return level storm event (Figure 5.6). Consequently, both plover conservation and coastal protection ESs share a common driver of beachgrasses that unavoidably creates an ES tradeoff.

5.4.2. Non-shared drivers: Plover-coastal protection tradeoff

Even though ESs may covary, they are often also affected by non-shared drivers, ecosystem processes that only affect one ES in a pairwise relationship. These non-shared drivers may provide an opportunity for mitigating tradeoffs by permitting manipulation of one ES without cost to the other. For the coastal protection-plover tradeoff, while beachgrass removal and foredune shortening function as a shared driver in the coastal protection-plover productivity tradeoff, tradeoff intensity differed among the seven restoration areas (Figure 5.9F-G). This variation was the consequence of important non-shared drivers that produce spatial variation in coastal protection and plover production.

For coastal protection, nearshore geomorphology mediates the intensity of flooding and erosion exposure (Figs. 3-4), but does not affect plover productivity. Regions with shallow sloping nearshore environments and wide beaches (i.e., dissipative beaches (Wright and Short 1984)) provide greater area for wave energy dissipation to occur than regions with moderate to steep-sloped nearshore environments and narrow beaches (i.e., intermediate and reflective beaches). Thus, under comparable wave conditions, dissipative beaches typically experience lower wave runup elevations than reflective

beaches (Stockdon et al. 2006). If beaches do not dissipate all the wave energy they experience, foredunes provide a second line of defense by reflecting or dissipating residual wave runup and by widening beaches via sediment erosion from the foredune to the beach (Larson et al. 2004, Roelvink et al. 2009).

In our study, HRAs on dissipative beaches (e.g., Leadbetter Point) exhibited little flooding and erosion exposure as compared to HRAs on intermediate and intermediate-reflective beaches (e.g., Bandon SPMA, Elk River). Moreover, while beachgrass removal and associated dune shortening on dissipative beaches increased flooding and erosion exposure slightly, similar shortening on intermediate and intermediate-reflective beaches produced sizeable increases in exposure (Figure 5.6). These results suggest that nearshore geomorphology, a non-shared driver, may significantly alter each site's coastal hazard exposure, and that nearshore geomorphology may also mediate the effects of dune shortening on coastal hazard exposure (Figs. 4-5). Thus, managers can mitigate tradeoffs between plover productivity and coastal hazard exposure by incorporating nearshore geomorphological information into HRA site selection processes. Although not examined in this study, managers can also minimize vulnerability to coastal hazards by locating restoration sites in areas where flooding and erosion events would have tolerable impacts on coastal development and ecosystem service supply (see Appendix E).

Similarly, for plover conservation, numerous non-shared drivers influence plover productivity, without influencing coastal protection. In addition to beachgrass cover, plover productivity is significantly affected by predation pressure, recreational beach use, habitat quality, and plover behavior (USFWS 1993, 2007, 2012, Lafferty et al. 2006, Colwell et al. 2011, Pearson et al. 2016). Predators affect plover productivity at multiple stages throughout nesting, causing nest abandonment and depredation of eggs, chicks, and adults. In response, plover managers have employed numerous predator control methods, including predator exclosures and both non-lethal and lethal predator removal (Pearson et al. 2016). At this study's seven HRAs, each of these predator controls have been employed in varying intensity, and predator exclosures have significantly improve nest survival (Zarnetske et al. 2010, Pearson et al. 2016). Although we did not control for predator exclosure intensity in our analysis, plover productivity appreciably rose during

years when lethal predator controls were employed, although its efficacy varied among sites (Figure 5.9). While predator exclosures may partly explain differences in site-specific responses to lethal predator controls, it is also likely that predation pressure varied among sites (Hardy and Colwell 2012, Pearson et al. 2016) and may have produced site-specific responses to predator controls.

Social cues may also partly explain observed differences in nesting patterns, particularly at the Elk River HRA. Plovers nest at sites where conspecifics have previously nested and often return to those same sites in subsequent years (Nelson 2007). Because plovers often require social stimulation to settle new sites, this site-faithfulness may produce long time-lags between construction of suitable nesting habitat and observed plover responses. The Elk River region, for example, does not appear to have supported any nesting plovers since 1978 (Page et al. 1991). Moreover, the Elk River HRA, established in 2006, is the newest plover HRA in the Oregon and Washington region and has yet to support nesting plovers (Lauten et al. 2014). Finally, habitat quality (Colwell et al. 2011) and disturbance from recreational beach use (Lafferty et al. 2006) may also differ among sites, but both habitat quality and recreational pressures were beyond the scope of this study.

5.4.3. Context dependence: Endemic plant conservation relationships

While shared and non-shared drivers are important sources of ES variation and covariation, context dependence may also control ES interactions. Context dependent ES interactions may arise when additional covariates interact with shared drivers to alter the sign or magnitude of ES relationships. Consequently, ESs may exhibit neutral or weak interactions under one set of conditions and strong interactions under different conditions. Context may include, but is not limited to, spatial or temporal conditions, disturbance regimes, and abiotic or biotic conditions (Koch et al. 2009). In Pacific Northwest dunes, endemic plant conservation typifies this relationship because endemic plant decline likely was driven by direct competition with beachgrasses and indirect effects of beachgrass ecosystem engineering (e.g., altered sand burial, sand scour, and salt spray regimes (Wiedemann and Pickart 2008)). Yet beachgrass removal had no effect on the incidence

or abundance of many historically important endemic foredune plants (e.g., *Abronia latifolia*, *Ambrosia chamissonis*, *Calystegia soldanella*; Figure 5.9D, Appendix D, Table D7). Although beachgrass removal creates habitat for endemic plants, we hypothesize that seed dispersal limitation is largely responsible for their lack of recovery.

Endemic beach and foredune plant community re-establishment can occur through vegetative growth, establishment from a seed bank, or through seed dispersal. Because few endemic beach and foredune plants occur near removal areas and removal areas are frequently bulldozed, re-establishment via vegetative growth is unlikely. Although seed banks may facilitate plant re-establishment, seedbanks on foredunes are typically poorly developed with variable composition and germination rates (Leicht-Young et al. 2009). Moreover, since beachgrasses have dominated these HRAs for more than five decades, it is likely that few endemic plants have contributed to the seed bank in recent decades. When combined with mechanical beachgrass removal that produces extreme sediment redistribution, seed banks alone are unlikely to produce holistic foredune habitat restoration.

Consequently, seed dispersal provides the most probable method for endemic plant re-establishment. However, because beachgrasses monopolize adjacent areas and severely reduce the abundance of endemic plants, few parent plants exist to provide seed to removal areas. Enhanced granivory pressures within beachgrass-dominated dunes may further depress seed availability (Dangremond et al. 2010). Consequently, few seeds likely reach removal areas, producing the observed lack of recovery in endemic plants following beachgrass removal.

Pink sand verbena (*Abronia umbellata*), however, deviates from this pattern. It positively covaries with plover conservation (Figure 5.9I) and negatively covaries with coastal protection. Unlike other endemic species, pink sand verbena's success arises from a combination of beachgrass removal, increased disturbance (from both beachgrass removal activities and from wave overwash), seed additions, and targeted protection of overwintering plants from discing and herbicide. Through these actions, managers have alleviated beachgrass competition and dispersal limitation, and facilitated increases in pink sand verbena abundance (Figure 5.8) (Giles-Johnson and Kaye 2014).

Consequently, a synergistic relationship exists between plover conservation and pink sand verbena conservation, due to beachgrass removal (shared driver) and reduced dispersal limitation (context dependence). For other endemic foredune plants, it is unlikely that a similar synergistic relationship would develop without seeding interventions.

5.4.4. Optimizing ecosystem service management

With better understanding of the mechanisms that drive ES covariation, natural resource and restoration managers can better predict how synergistic or tradeoff ESs might respond to interventions (Bennett et al. 2009), and to ecological and socio-economic responses to environmental change (Lamarque et al. 2014). When ESs exhibit synergistic interactions, then facilitation of shared drivers has the potential to augment supply of both ESs. However, when tradeoffs arise, manipulation of shared drivers may exacerbate ES conflicts; thus, management of context dependent and non-shared drivers may provide an alternative avenue for achieving management objectives while lessening conflict. For example, while restoration of the western snowy plover requires beachgrass removal, appropriate site selection criteria could help to alleviate plover-coastal protection tradeoffs. Future restoration efforts could be targeted to dissipative beaches, where beachgrass and foredune removal would produce little additional flooding and erosion risk (Figs. 4-5). Alternatively, if restoration occurs on intermediate to reflective beaches, then managers could either limit reductions in foredune height to reduce flooding exposure or plan for possible severe flooding and erosion events. Lastly, to realize the potential synergy between endemic foredune plants and plover conservation, managers likely need to engage in seeding to reduce dispersal limitation.

In other systems, ES supply can also be optimized by exploiting context dependence and non-shared drivers. In Thailand, mangroves provide coastal protection, but are often irreversibly converted to shrimp aquaculture ponds, creating a tradeoff between coastal protection and shrimp aquaculture. Spatial planning of shrimp aquaculture pond placement, though, can alleviate this tradeoff: while placement of ponds at the seaward fringe of mangroves creates a strong ES tradeoff, pond placement near the inland

boundary of mangrove areas causes little reduction in coastal protection and may further enhance shrimp production (Barbier 2012). Similarly, although agriculture production ESs commonly tradeoff with water quality, placement of targeted riparian buffers can significantly diminish tradeoff intensity by minimizing sediment erosion and nutrient loading (Polyakov et al. 2005).

For natural resource, conservation, and restoration management, recognition and mitigation of ES tradeoffs may help managers meeting multiple management objectives. Although not of large concern for most HRAs examined in this western snowy plover case study (see Appendix E), conservation and restoration projects that fail to consider negative socioeconomic and socio-ecological impacts of conservation policies can alienate local communities and stakeholders, cause disenfranchisement and loss of livelihood to local communities, deprive conservation groups with political allies and local enforcement, and inefficiently use limited financial resources (Adams et al. 2004, Aronson et al. 2006, Naidoo and Iwamura 2007). For some projects, these oversights may impair the efforts to conserve or restore ecosystems and may ultimately lead to project failure, as has occurred in both developing and developed countries (Bode et al. 2008, Buckley and Crone 2008, Abelson et al. 2016). Consideration and amelioration of ES tradeoffs not only ensures that an ecosystem's finite resources are managed efficiently (Naidoo and Ricketts 2006, Naidoo and Iwamura 2007), it also provides a framework for facilitating local community and stakeholder engagement and support when establishing ecological reserves and managing resources for multiple users (Davenport et al. 2010, Marttila et al. 2016, Abelson et al. 2016).

Identification of potential management solutions that augment synergies and mitigate tradeoffs requires a better understanding of the physical, ecological, and social processes that produce ES interactions. Examining ES interactions through the lens of shared and non-shared drivers will enable resource managers to recognize interventions that may alter the supply of multiple ESs. By comprehensively characterizing impacts of management actions, managers can identify which interventions are likely to yield net-positive effects, and further facilitate stakeholder engagement to exploit synergies and allay potential conflicts over tradeoffs.

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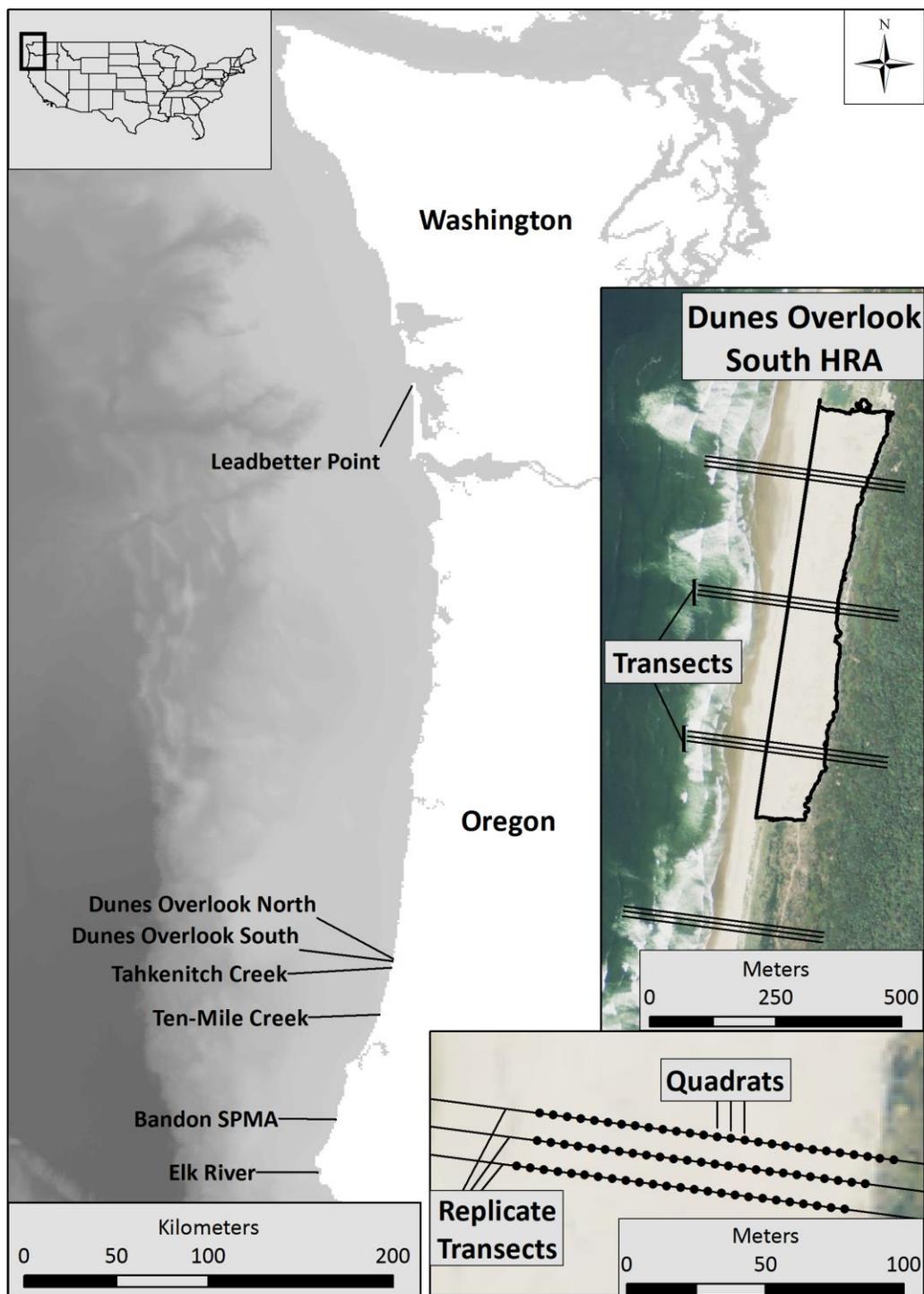


Figure 5.1. Dune habitat restoration areas (HRAs) in Oregon and southern Washington, USA and survey design (Appendix D, Table D1). Aerial photo of Dunes Overlook South shows transect placement within beachgrass removal and nearby reference locations. Black lines show transects; points indicate vegetation survey quadrats.

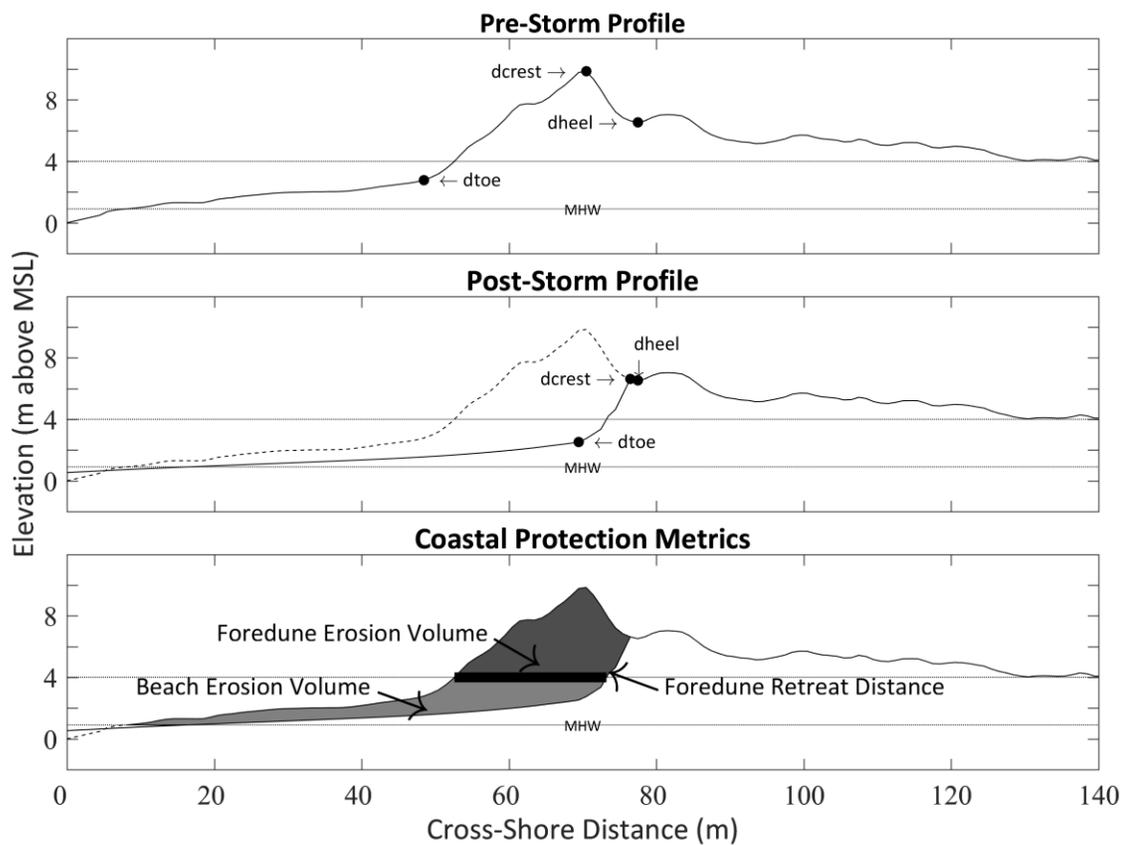


Figure 5.2. An example of pre- and post-storm cross-shore profiles at a Ten-Mile Creek HRA. Foredune toe (d_{toe}), foredune crest (d_{crest}), and foredune heel (d_{heel}) positions are indicated for both the pre-storm and post-storm profiles. Shading indicates the cross-sectional area eroded during the simulated storm (dark gray = foredune erosion volume; medium gray = beach erosion volume; black line = foredune retreat distance).

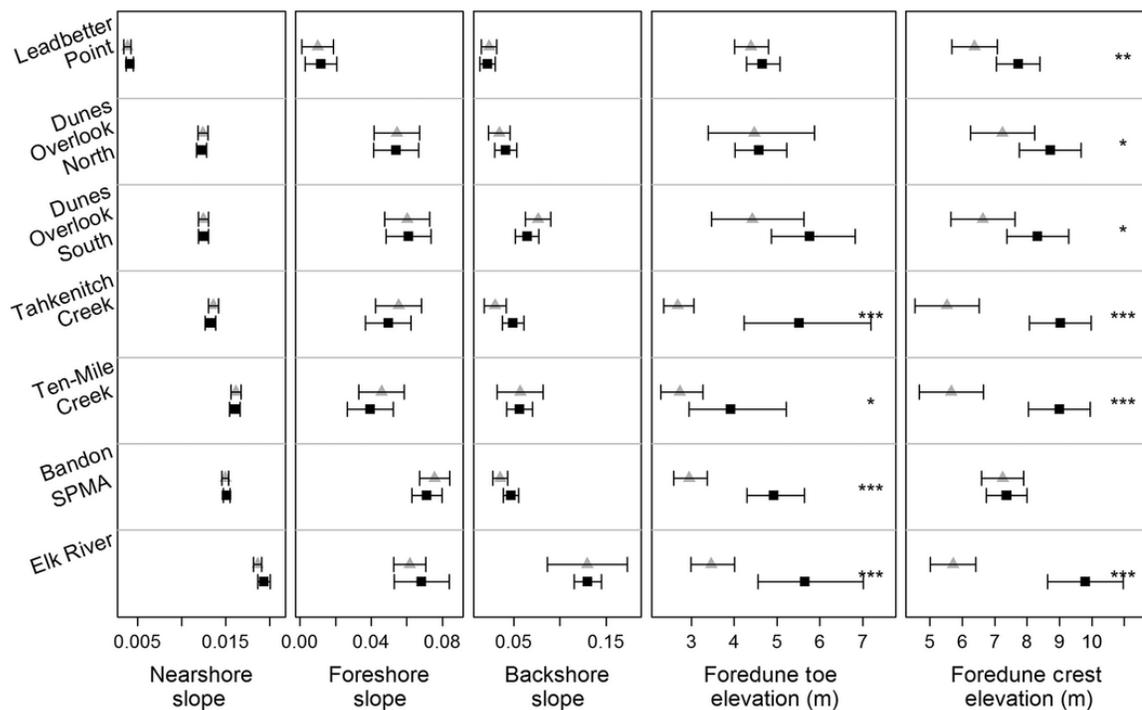


Figure 5.3. Dune geomorphology at beachgrass removal (gray triangles) and reference (black squares) areas at seven HRA sites (Figure 5.1, Appendix D, Table D1). Error bars indicate 95% confidence intervals. Asterisks indicate significant difference within HRA sites: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

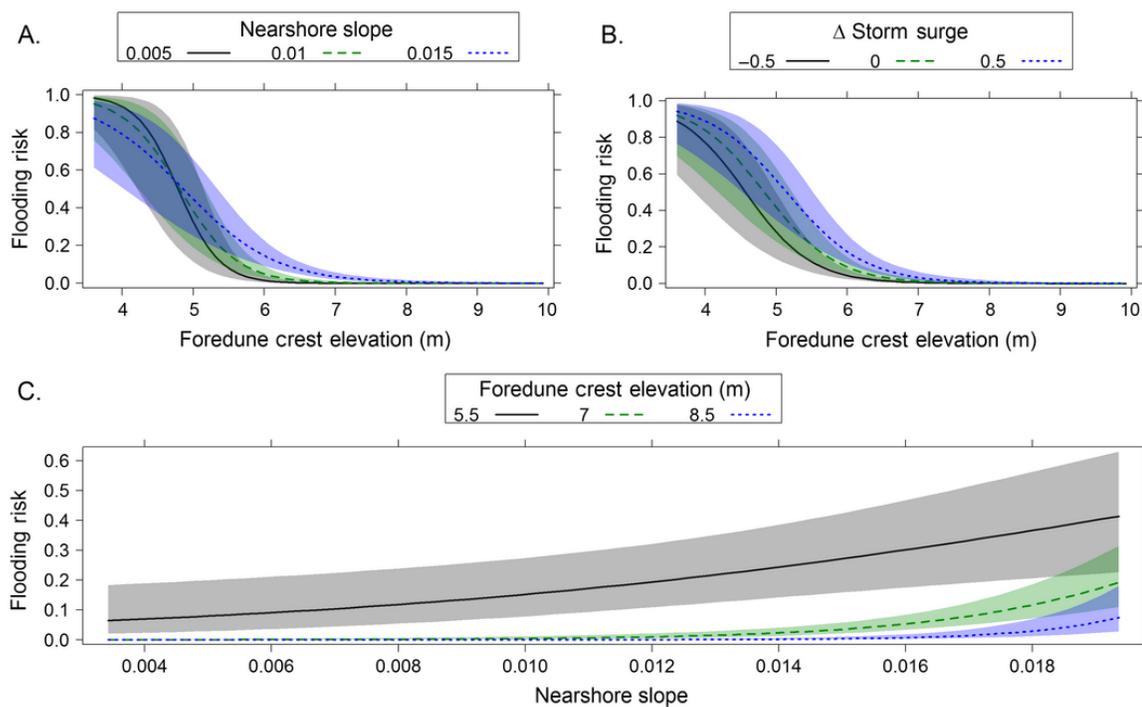


Figure 5.4. Interactive effect of (A, C) nearshore slope \times d_{crest} elevation and (B) Δ storm surge \times d_{crest} elevation on absolute flooding risk. Bands indicate confidence intervals.

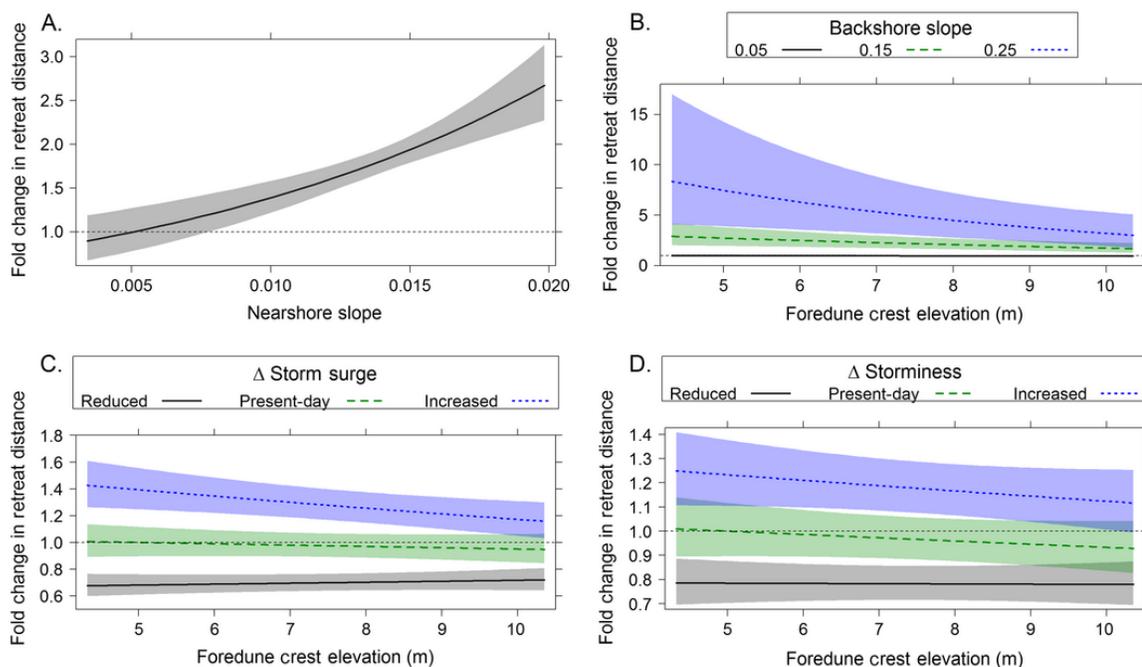


Figure 5.5. (A) Main effect of nearshore slope on foredune retreat distance. Interactive effect of (B) backshore slope \times d_{crest} elevation, (C) Δ storm surge \times d_{crest} elevation, and (D) Δ storminess \times d_{crest} elevation on foredune retreat distance. Fold-change in foredune retreat distance measures the relative amount of retreat for foredunes under different conditions as compared to a reference condition (conditions with a predicted 1x-fold change). Bands indicate confidence intervals.

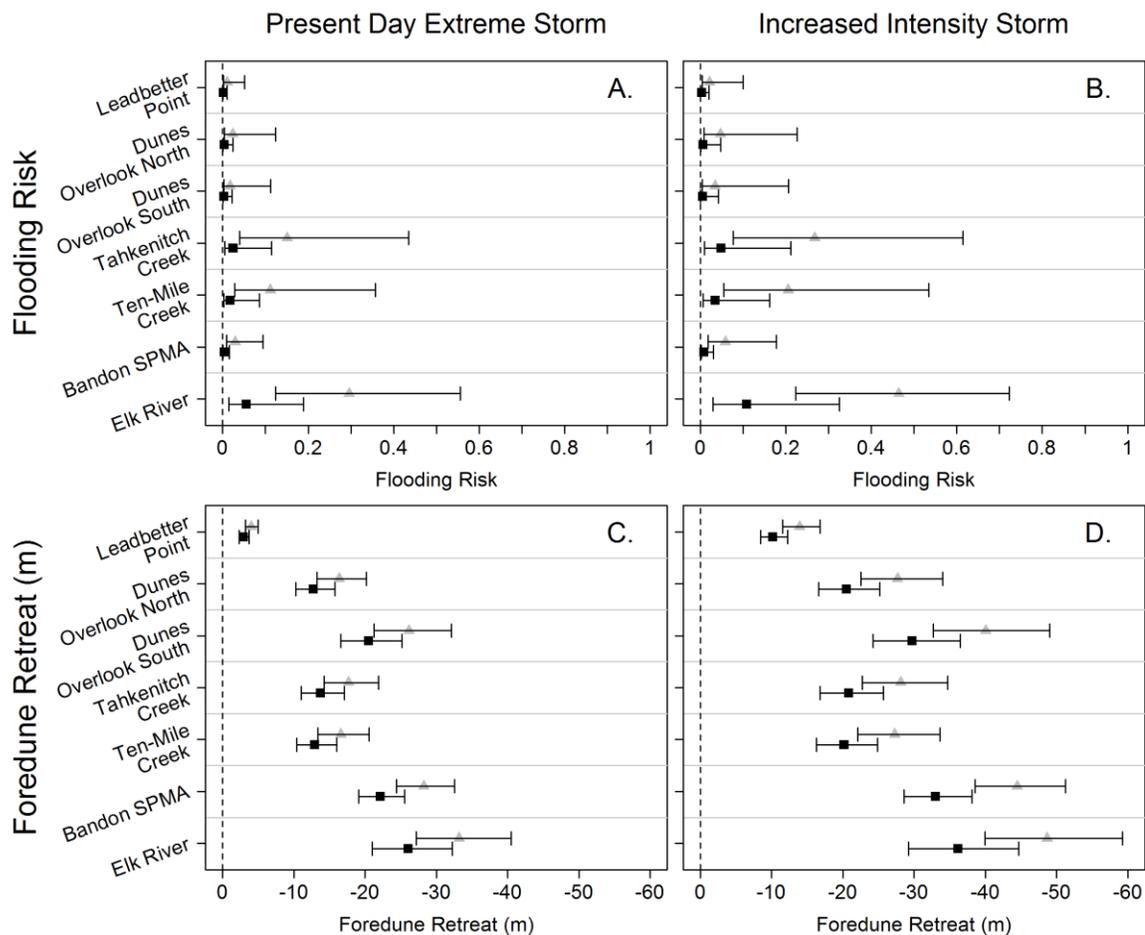


Figure 5.6. (A-B) Flooding risk (probability of flooding) at beachgrass removal (gray triangles) and reference (black squares) sites under (A) a present-day extreme storm scenario and (B) an increased wave intensity and surge extreme storm scenario. (C-D) Predicted foredune retreat at beachgrass removal and reference areas under (C) a present-day extreme storm scenario and (D) an increased wave intensity and surge extreme storm scenario. Error bars indicate 95% confidence interval.

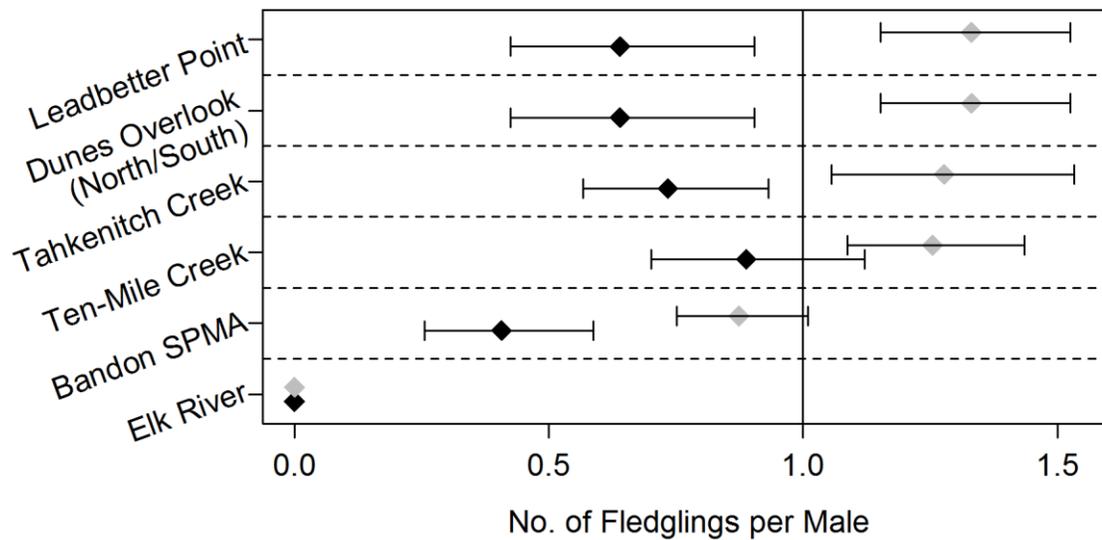


Figure 5.7. Plover productivity at HRAs during years without predator removal (black diamonds) and with plover predator removal (gray diamonds). Error bars indicate 95% posterior intervals. Dunes Overlook plover productivity encompasses both the Dunes Overlook North and South sites.

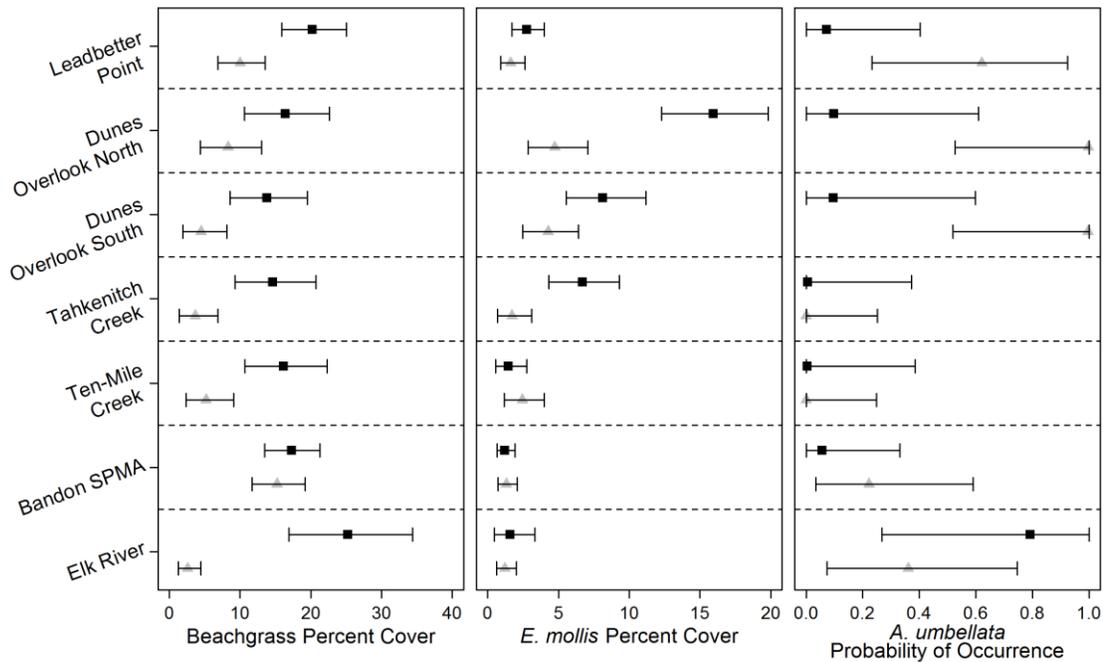


Figure 5.8. (A) Beachgrass percent cover; (B) native dune grass percent cover; and (C) pink sand verbena probability of occurrence at beachgrass removal (gray triangles) and reference (black squares) areas at seven HRA sites (Figure 5.1, Appendix D, Table D1). Points indicate median posterior estimates; error bars indicate 95% posterior intervals.

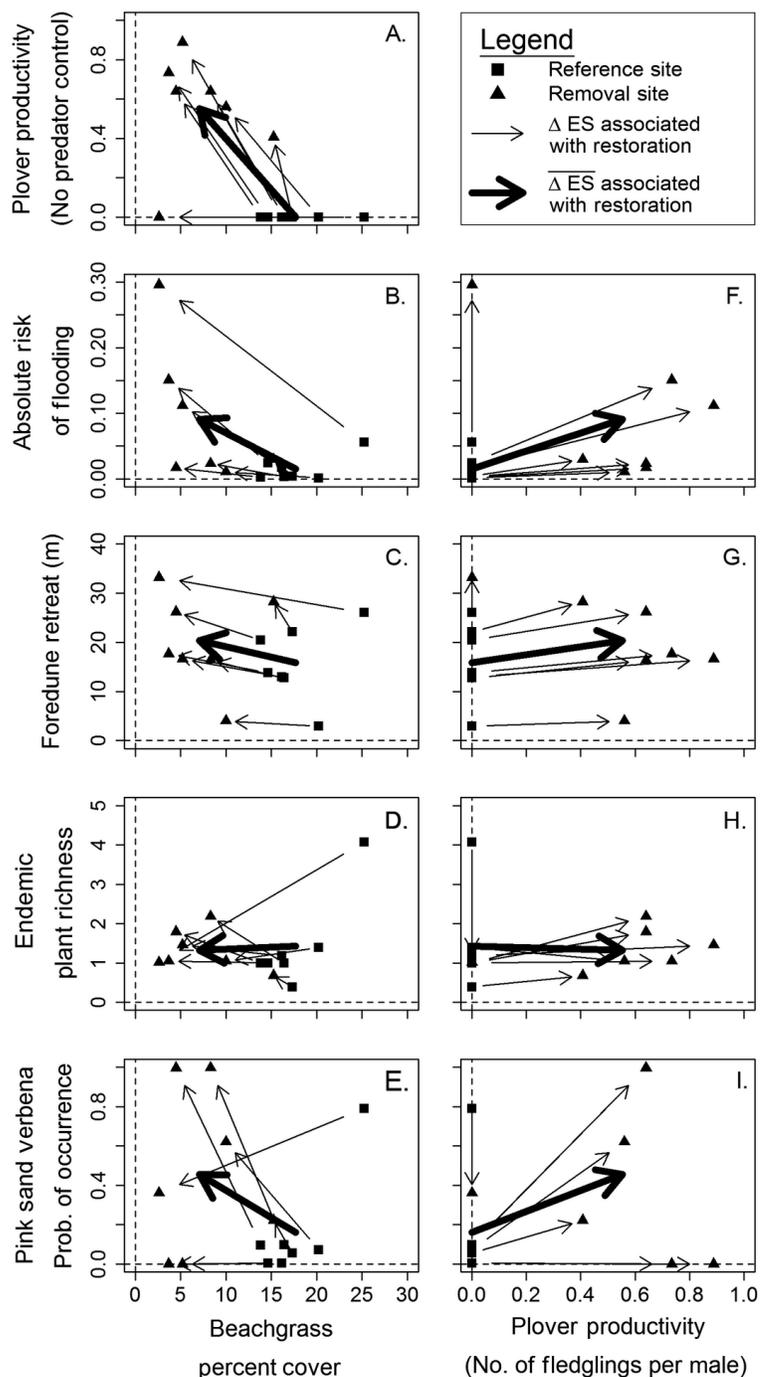


Figure 5.9. (A-E) Comparison of ecosystem service (ES) metrics with beachgrass percent cover at paired beachgrass removal (black triangles) and reference (black squares) areas at seven HRA sites (Figure 5.1, Appendix D, Table D1). (F-I) Pairwise comparison of plover productivity with coastal protection and endemic plant conservation ES metrics. Thin arrows indicate Δ ES supply at each site. Bold arrows indicate mean change in ES ($\overline{\Delta}$ ES) metric between removal and reference areas.

6. Conclusion

My dissertation research used an interdisciplinary approach to study the interactions and impacts of two invasive beachgrasses across environmental gradients of sand supply and wave climate. Through the study of *Ammophila arenaria* and *A. breviligulata*, this work will improve predictions and management of the future of the Pacific Northwest coastal dune system amidst biological invasions and a changing climate. This research was guided by several themes.

First, biological invasions by ecosystem engineers have profound impacts on ecological communities, on ecosystem processes, and on the services that they provide (Cuddington and Hastings 2004, Ehrenfeld 2010, Simberloff 2011). Within my dissertation, several chapters elucidated the impacts of the two *Ammophila* species on dune biophysical processes, on ecosystems, and on society. Previous research in this system has shown that *A. arenaria*-dominated foredunes are typically taller and narrower than *A. breviligulata*-dominated counterparts (Seabloom and Wiedemann 1994, Hacker et al. 2012, Zarnetske et al. 2015), that species-specific differences in density may provide one-such mechanism for this disparity (Zarnetske et al. 2012), and that these species-specific differences in foredune morphology can alter risks of flooding during storm events (Seabloom et al. 2013). The Bayesian networks of Chapter 2 confirmed that both *Ammophila* species alter foredune morphology under higher stem densities and produce taller foredunes as a consequence. Moreover, even after accounting for sand supply and beach geomorphology, *A. arenaria*-dominated foredunes remained taller and narrower than *A. breviligulata*-dominated foredunes. Based on these analyses, the disparity in foredune morphology arises because species-specific differences in growth form produce patterns of sand accretion that are unique to each species: the lateral growth form of *A. breviligulata* induces sand deposition along the seaward margin of the foredune, resulting in lateral dune growth. In contrast, the slow rate of lateral growth in *A. arenaria* produces greater sand deposition near the foredune crest, resulting in vertical dune growth. Consequently, the Bayesian network analyses empirically support prior research that *A. arenaria* produces taller and narrower foredunes than *A. breviligulata*, and indicate how density and growth form mechanistic influence foredune shape.

Second, the causes of invasion success, species invasiveness, and community invasibility are widely debated in the literature (e.g., Hobbs and Huenneke 1992, Alpert et al. 2000, Davis et al. 2000, Richardson and Pyšek 2006, Pyšek and Richardson 2010). As biological invasions increase in frequency and magnitude, prediction, prevention, and mitigation of biological invasions requires a better understanding of the determinants of invasion success. In Chapter 3, I assessed the relative survival and productivity of the three dune grass species, and the relative invasibility of the communities in which they dominant, all across a sand burial gradient. This work demonstrated that both species invasiveness and community invasibility influence invasion success. Notably, species interactions significantly altered invasion success, such that *E. mollis* facilitated survival and growth of the grass colonists. Sand deposition further mediated these relationships by reducing the survival, but increasing the productivity, of the grass colonists. Both facilitation of invasion by a native species and the contrasting influence of sand burial on the survival and growth of invading species have important implications for invasive species management in the Pacific Northwest. Chapter 3 further illustrated the utility of reciprocal invasion trials for understanding the influence of both species invasiveness and community invasibility on invasion success.

Third, the impacts of climate change on biological invasions is of growing interest because of the rising threats to ecosystem services (MEA 2005). Invasive species responses to climate change, though, are uncertain and species-specific. While most invasive species are likely to benefit from climate change (Dukes and Mooney 1999, Hellmann et al. 2008, Thuiller et al. 2008, Walther et al. 2009, Bradley et al. 2010), it may reduce the invasion risk for others and potentially unlock opportunities for conservation (Bradley et al. 2009, Allen and Bradley 2016). In Chapter 4, I examined possible climate change impacts on the distribution and abundance of *A. arenaria* and *A. breviligulata* using a split-split-plot common garden experiment. By subjecting these plants to varying levels of heat, sand burial, and initial densities of *A. arenaria* and *A. breviligulata*, I showed that *A. breviligulata* is competitively dominant but is less tolerant of elevated temperatures and high rates of sand burial than *A. arenaria*. Through this experiment, I demonstrated rising temperatures and high rates of sand deposition

increased the likelihood of coexistence between the two species. These results suggest that *A. breviligulata* is likely to continue its range expansion south, but climate change, in conjunction with latitudinal gradients in temperature and sand burial may temper its spread.

Finally, management of invasive species can present both logistical and socio-ecological challenges. While many biological invasions cause significant ecological and economic harm, invasive species sometimes support essential ecosystem processes and provide valuable goods and services to local communities (Ewel et al. 1999, Hershner and Havens 2008, Pejchar and Mooney 2009, Lampert et al. 2014). In Chapter 5, I examined both the negative and the positive impacts of the *Ammophila* invasions and their management on foredune communities and their ecosystem services. Foremost, the *Ammophila* species have severely harmed the endemic foredune community, resulting in lower abundances of endemic plants and animals (Hacker et al. 2012). Although intensive management of the western snowy plover has taken these birds away from the brink of extinction, *Ammophila* management actions are still insufficient for restoring the endemic plant community. I further showed that the degree of protection against flooding and erosion hazards is dependent on foredune height. By extension, removal of beachgrasses and shortening of foredunes non-linearly increased exposure to flooding and erosion hazards, creating an ecosystem service tradeoff between plover conservation and coastal protection. Nevertheless, because the magnitude of these tradeoffs depends upon nearshore morphology, targeted placement of foredune restoration areas can lessen tradeoff severity.

This dissertation provides insights into the determinants of invasion success and the impacts invaders can have on communities, ecosystem processes, and ecosystem services. At the outset of the invasion, *Ammophila* was intentionally introduced because of its superior performance in mobile-sand environments – traits that also made it a successful invader in aeolian environments. Further, the Pacific Northwest foredune system was highly invasible, in part because the endemic dune grass *Elymus mollis* facilitated the survival and growth of the introduced grasses. Thus, management of the ‘*Ammophila* problem’ must contend with both invasive non-native plants and invasible

endemic foredune communities. Nevertheless, the introduction of *Ammophila* provides some benefits to society, including erosion control and coastal protection via sediment stabilization and dune building. Although complete eradication of *Ammophila* spp. from the Pacific Northwest is infeasible, selective control may provide some conservation benefits, while maintaining the coastal protection and erosion control needs of communities. Even so, further work is needed to ensure that habitat restoration efforts holistically restore ecosystem function and broadly improve the performance of the endemic foredune community.

Future investigations into the two *Ammophila* invasions should examine the role of propagule pressure in the establishment and spread of these species. Invasion success is a result of propagule pressure, environmental filters, and biotic interactions. Over the past decade, numerous studies have characterized abiotic influences on *A. arenaria*, *A. breviligulata*, and *E. mollis* performance and species interactions (e.g., Zarnetske et al. 2013, David et al. 2015, 2016, Chapter 3-4). These species-specific differences in performance and interactions across sand supply gradients explain much of the present-day distributions and abundances of foredune grasses. However, the role of propagule supply for influencing the rate of spread of *Ammophila* within and between littoral cells remains unexplored. Multiple factors may influence how quickly these species locally propagate within barren and occupied backshore, and regionally within and among littoral cells via rhizome fragmentation. Because both local and regional spread, can be influenced by shoreline change rates (e.g., creation of new backshore habitat), sand burial (Chapter 3), storms (e.g., mortality, mode of dispersal), and coastal currents, prediction of the spread of *A. breviligulata* will require an interdisciplinary, collaborative approach that leverages a combination of observational work, experimentation, and modeling. Through this multidecadal research effort, scientists will be better able to predict the course of the *Ammophila* invasions and their impacts on ecosystem processes and services. Finally, communication of this compendium of scientific knowledge to policymakers and stakeholders will ensure that decision-makers are well-informed about the present and potential future state of the coast amidst species invasions and a changing climate.

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Appendices

Appendix A. Chapter 2 supplemental figures and tables

Appendix A, Table A1. The latitude and longitude of 80 transects at 20 sites used to determine beachgrass tiller density and foredune geomorphology along the Washington and Oregon coasts. In 2012, we placed three cross-shore replicate transects at each location at 10 m alongshore spacing. In 2014, we resurveyed geomorphology and vegetation along 70 of 80 transects. Together, 2012 and 2014 collected vegetation abundance measurements using 7,953 and 1,616 georeferenced quadrats, respectively between the vegetation line and the foredune heel. Hacker et al. (2012) previously surveyed 77 of these transects at 19 sites in 2006.

Littoral cell (sub-cell)	Site ID	Site name	Latitude	Longitude	Years Surveyed
Columbia River (Grayland)	GH82	Cohasset	46.854342	-124.113813	2012, 2014
	GH18	Cohasset	46.852397	-124.113092	2012, 2014
	GH17	Cohasset	46.849800	-124.112204	2012, 2014
	GH09	Cohasset	46.838119	-124.108116	2012, 2014
	GH06	Grayland	46.829527	-124.105597	2012, 2014
	GH05	Grayland	46.799260	-124.098925	2012, 2014
	GH13	Grayland	46.798100	-124.098230	2012, 2014
	GH01	Grayland	46.789635	-124.098302	2012, 2014
Columbia River (Long Beach)	LBP07	Leadbetter Point	46.613266	-124.068739	2012
	LBP08	Leadbetter Point	46.608715	-124.068301	2012
	LB08	Leadbetter Point	46.606149	-124.067809	2012, 2014
	LB11	Leadbetter Point	46.600934	-124.067103	2012, 2014
	LB1020	Long Beach	46.552850	-124.061358	2012, 2014
	LB06	Long Beach	46.537819	-124.059991	2012, 2014
	LB12	Long Beach	46.509853	-124.059061	2012, 2014
	LB05	Long Beach	46.485011	-124.058476	2012, 2014
	LB02	Long Beach	46.474637	-124.058541	2012, 2014
	LB03	Long Beach	46.452979	-124.058487	2012, 2014
	LB09	Long Beach	46.433571	-124.059150	2012, 2014
	LB07	Long Beach	46.392864	-124.060838	2012, 2014
	LB35	North Head	46.354998	-124.063646	2012, 2014
	LB36A	North Head	46.336592	-124.066240	2012, 2014
	LB37	North Head	46.321767	-124.068154	2012, 2014
Columbia River (Clatsop)	EASTJETTY	Clatsop Plains	46.221383	-124.008179	2012, 2014
	FS02	Clatsop Plains	46.205879	-123.997694	2012, 2014
	IREDALE43	Clatsop Plains	46.179087	-123.979933	2012, 2014
	KIM44	Clatsop Plains	46.149362	-123.963234	2012, 2014
	RILEA45	Clatsop Plains	46.113631	-123.946862	2012, 2014
	FS03	Clatsop Plains	46.101930	-123.942048	2012, 2014
	FS01	Clatsop Plains	46.052340	-123.930463	2012, 2014
	DELRAY46	Clatsop Plains	46.049610	-123.929892	2012, 2014
	DELRAY46A	Clatsop Plains	46.045820	-123.930317	2012, 2014
	SEASIDE	Clatsop Plains	46.002330	-123.928450	2012, 2014
Rockaway	NB04	Nehalem Bay	45.690590	-123.939212	2012, 2014
	NB03	Nehalem Bay	45.682545	-123.939313	2012, 2014

Appendix A, Table A1 (Continued)

Littoral cell (sub-cell)	Site ID	Site name	Latitude	Longitude	Years Surveyed
Netarts	CL03	Cape Lookout	45.427318	-123.959969	2012, 2014
	CL02	Cape Lookout	45.421804	-123.960675	2012, 2014
	CL01	Cape Lookout	45.380963	-123.966265	2012, 2014
Sand Lake	SL02	Sand Lake	45.285898	-123.963004	2012, 2014
	SL01	Sand Lake	45.282318	-123.962626	2012, 2014
Neskowin	PC03	Pacific City	45.194278	-123.968257	2012, 2014
	PC01	Pacific City	45.189876	-123.968376	2012, 2014
	PC02	Pacific City	45.174066	-123.970032	2012, 2014
Newport	SB02	South Beach	44.604539	-124.066645	2012, 2014
	SB01	South Beach	44.599673	-124.066734	2012, 2014
	GP01	Governor Patterson	44.414627	-124.084204	2012, 2014
	GP02	Governor Patterson	44.410389	-124.084868	2012, 2014
	GP03	Governor Patterson	44.407324	-124.085418	2012, 2014
Coos	SNJ02	Siuslaw Jetty	44.025873	-124.136642	2012, 2014
	SNJ03	Siuslaw Jetty	44.022043	-124.138176	2012, 2014
	SSJ01	Siuslaw Jetty	44.011707	-124.136557	2012, 2014
	SSJ02	Siuslaw Jetty	44.006122	-124.136528	2012, 2014
	SSJ03	Siuslaw Jetty	44.000514	-124.137052	2012, 2014
	SILT01	Siltcoose River	43.870088	-124.156612	2012, 2014
	SILT02	Siltcoose River	43.867568	-124.157311	2012, 2014
	SILT03	Siltcoose River	43.864305	-124.158051	2012, 2014
	DONR05	Dunes Overlook	43.847736	-124.160821	2012
	DONR06	Dunes Overlook	43.846130	-124.161340	2012
	DONR04	Dunes Overlook	43.835784	-124.163247	2012
	DO01	Dunes Overlook	43.835369	-124.163120	2012, 2014
	DO02	Dunes Overlook	43.825009	-124.165301	2012, 2014
	DO03	Dunes Overlook	43.821181	-124.166082	2012, 2014
	TKNR06	Tahkenitch Creek	43.815137	-124.167230	2012, 2014
	TKNR05	Tahkenitch Creek	43.810440	-124.168083	2012, 2014
	TKNR04	Tahkenitch Creek	43.806657	-124.168761	2012, 2014
	TMNR06	Tenmile Creek	43.646108	-124.210367	2012, 2014
	UD03	Umpqua Dunes	43.608418	-124.218174	2012, 2014
	TMNR05	Tenmile Creek	43.607529	-124.218368	2012, 2014
UD02	Umpqua Dunes	43.596967	-124.221297	2012, 2014	
UD01	Umpqua Dunes	43.593683	-124.222220	2012, 2014	
TMNR04	Tenmile Creek	43.582365	-124.225528	2012, 2014	
Bandon	BANNR04	Bandon SNA	43.067144	-124.437459	2012
	BANNR03	Bandon SNA	43.064603	-124.438067	2012, 2014
	BANNR05	Bandon SNA	43.061468	-124.438824	2012
	BANNR06	Bandon SNA	43.060354	-124.439157	2012, 2014
	BANNR07	Bandon SNA	43.059343	-124.439452	2012
	BANNR02	Bandon SNA	43.058359	-124.439645	2012, 2014
	BANNR08	Bandon SNA	43.056078	-124.440304	2012, 2014
	Elk	MCKNR04	Elk River	42.798966	-124.527959
MCKNR05		Elk River	42.798760	-124.527851	2012

Appendix A, Table A2. Foredune Morphology Gaussian Bayesian network variables (nodes), their definitions, and data transformations. Variables were transformed to ensure that each variable conformed to a Gaussian distribution.

Foredune Morphology-GBN _{combined}			Foredune Morphology-GBN _{species}		
Variable Name	Description	Transformation	Variable Name	Description	Transformation
Shoreline. Change Rate (SCR)	End point rate of shoreline change for Oregon (1967-2002) and Washington (1986-2002) (m/yr.) (Ruggiero et al. 2013)	$(SCR+2)^{0.05}$	Shoreline Change Rate (SCR)	End point rate of shoreline change for Oregon (1967-2002) and Washington (1986-2002) (m/yr.) (Ruggiero et al. 2013)	$(SCR+2)^{0.05}$
Shoreface Slope (β_{SF})	Slope between 15m and 10m below local mean sea level (LMSL)	$\log(\beta_{SF})$	Shoreface Slope (β_{SF})	Slope between 15m and 10m below local mean sea level (LMSL)	$\log(\beta_{SF})$
Backshore Slope (β_{BS})	Slope between mean high water (MHW) and the 4m contour above LMSL	$\log(\beta_{BS})$	Backshore Slope (β_{BS})	Slope between mean high water (MHW) and the 4m contour above LMSL	$\log(\beta_{BS})$
Mean Grain Size (D50)	Mean sediment grain size of surface sand samples collected at the vegetation line (mm)	$-\log_2(D50)$	Mean Grain Size	Mean sediment grain size of surface sand samples collected at the vegetation line (mm)	$-\log_2(D50)$
Beachgrass Density (BG Density)	Mean tiller density of <i>Ammophila</i> species among quadrats located on d_{face} (tillers/m ²)	$(BG\ Density)^{1/3}$	Dominant Beachgrass Species	Beachgrass species with >50% relative percent areal cover on the foredune face	0 = AMBR 1 = AMAR
			AMAR Density (AMAR Density)	Mean tiller density of <i>Ammophila arenaria</i> among quadrats located on d_{face} (tillers/m ²)	$(AMAR\ Density)^{1/3}$
			AMBR Density (AMBR Density)	Mean tiller density of <i>Ammophila breviligulata</i> among quadrats located on d_{face} (tillers/m ²)	$(AMBR\ Density)^{1/3}$
Dune Face Width (d_{face} width)	Horizontal distance between the 4m contour above LMSL and the foredune crest (m)	$\log(d_{face}\ width)$	Dune Face Width (d_{face} width)	Horizontal distance between the 4m contour above LMSL and the foredune crest (m)	$\log(d_{face}\ width)$
Dune Face Slope (d_{face} slope)	Slope between the 4m contour above LMSL and the foredune crest	$\log(d_{face}\ slope)$	Dune Face Slope (d_{face} slope)	Slope between the 4m contour above LMSL and the foredune crest	$\log(d_{face}\ slope)$
Dune Crest Elevation (d_c elevation)	Foredune crest elevation (m above LMSL)	$(d_c\ elevation)^{-3/2}$	Dune Crest Elevation (d_c elevation)	Foredune crest elevation (m above LMSL)	$(d_c\ elevation)^{-3/2}$
Dune Toe Elevation (d_t elevation)	Foredune toe elevation (m above LMSL)	$\log(d_t\ elevation)$	Dune Toe Elevation (d_t elevation)	Foredune toe elevation (m above LMSL)	$\log(d_t\ elevation)$

Appendix A, Table A3. Prohibited directional relationships (edges) for the Foredune Morphology Gaussian Bayesian networks (Foredune Morphology-GBNs). Based on the parent-child typology, child nodes are conditionally dependent on parent nodes.

Foredune Morphology GBN _{combined}		Foredune Morphology GBN _{species}	
Parent	Child	Parent	Child
Backshore Slope	SCR	AMBR Beachgrass Density	SCR
Backshore Slope	SCR	Backshore Slope	SCR
Beachgrass Density	SCR	Backshore Slope	SCR
d_c Elevation	SCR	d_c Elevation	SCR
d_c Elevation	SCR	d_c Elevation	SCR
d_t Elevation	SCR	Dominant Species	SCR
d_t Elevation	SCR	Dominant Species	SCR
Dune Face Slope	SCR	d_t Elevation	SCR
Dune Face Slope	SCR	d_t Elevation	SCR
Dune Face Width	SCR	Dune Face Slope	SCR
Dune Face Width	SCR	Dune Face Slope	SCR
Mean Sediment Diameter	SCR	Dune Face Width	SCR
Shoreface Slope	SCR	Dune Face Width	SCR
		AMAR Beachgrass Density	SCR
		Mean Sediment Diameter	SCR
		Shoreface Slope	SCR
Backshore Slope	Mean Sediment Diameter	AMBR Beachgrass Density	Mean Sediment Diameter
Backshore Slope	Mean Sediment Diameter	Backshore Slope	Mean Sediment Diameter
Beachgrass Density	Mean Sediment Diameter	Backshore Slope	Mean Sediment Diameter
d_c Elevation	Mean Sediment Diameter	d_c Elevation	Mean Sediment Diameter
d_c Elevation	Mean Sediment Diameter	d_c Elevation	Mean Sediment Diameter
d_t Elevation	Mean Sediment Diameter	Dominant Species	Mean Sediment Diameter
d_t Elevation	Mean Sediment Diameter	Dominant Species	Mean Sediment Diameter
Dune Face Slope	Mean Sediment Diameter	d_t Elevation	Mean Sediment Diameter
Dune Face Slope	Mean Sediment Diameter	d_t Elevation	Mean Sediment Diameter
Dune Face Width	Mean Sediment Diameter	Dune Face Slope	Mean Sediment Diameter
Dune Face Width	Mean Sediment Diameter	Dune Face Slope	Mean Sediment Diameter
		Dune Face Width	Mean Sediment Diameter
		Dune Face Width	Mean Sediment Diameter
		AMAR Beachgrass Density	Mean Sediment Diameter
Backshore Slope	Shoreface Slope	AMBR Beachgrass Density	Shoreface Slope
Backshore Slope	Shoreface Slope	Backshore Slope	Shoreface Slope
Beachgrass Density	Shoreface Slope	Backshore Slope	Shoreface Slope

Appendix A, Table A3 (Continued)

Morphology GBN _{combined}		Morphology GBN _{species}	
Parent	Child	Parent	Child
d_c Elevation	Shoreface Slope	d_c Elevation	Shoreface Slope
d_c Elevation	Shoreface Slope	d_c Elevation	Shoreface Slope
d_t Elevation	Shoreface Slope	Dominant Species	Shoreface Slope
d_t Elevation	Shoreface Slope	Dominant Species	Shoreface Slope
Dune Face Slope	Shoreface Slope	d_t Elevation	Shoreface Slope
Dune Face Slope	Shoreface Slope	d_t Elevation	Shoreface Slope
Dune Face Width	Shoreface Slope	Dune Face Slope	Shoreface Slope
Dune Face Width	Shoreface Slope	Dune Face Slope	Shoreface Slope
Mean Sediment Diameter	Shoreface Slope	Dune Face Width	Shoreface Slope
		Dune Face Width	Shoreface Slope
		AMAR Beachgrass Density	Shoreface Slope
		Mean Sediment Diameter	Shoreface Slope
d_c Elevation	Backshore Slope	d_c Elevation	Backshore Slope
d_t Elevation	Backshore Slope	Dominant Species	Backshore Slope
Dune Face Slope	Backshore Slope	d_t Elevation	Backshore Slope
Dune Face Width	Backshore Slope	Dune Face Slope	Backshore Slope
		Dune Face Width	Backshore Slope
d_c Elevation	Beachgrass Density	AMBR Beachgrass Density	Dominant Species
d_t Elevation	Beachgrass Density	Backshore Slope	Dominant Species
Dune Face Slope	Beachgrass Density	Backshore Slope	Dominant Species
Dune Face Width	Beachgrass Density	d_c Elevation	Dominant Species
		d_c Elevation	Dominant Species
		d_t Elevation	Dominant Species
		d_t Elevation	Dominant Species
		Dune Face Slope	Dominant Species
		Dune Face Slope	Dominant Species
		Dune Face Width	Dominant Species
		Dune Face Width	Dominant Species
		AMAR Beachgrass Density	Dominant Species
		Mean Sediment Diameter	Dominant Species
		Shoreface Slope	Dominant Species
		SCR	Dominant Species
		d_c Elevation	AMBR Beachgrass Density
		d_t Elevation	AMBR Beachgrass Density
		Dune Face Slope	AMBR Beachgrass Density

Appendix A, Table A3 (Continued)

Morphology GBN _{combined}		Morphology GBN _{species}	
Parent	Child	Parent	Child
		Dune Face Width	AMBR Beachgrass Density
		AMAR Beachgrass Density	AMBR Beachgrass Density
		AMBR Beachgrass Density	AMAR Beachgrass Density
		d_c Elevation	AMAR Beachgrass Density
		d_t Elevation	AMAR Beachgrass Density
		Dune Face Slope	AMAR Beachgrass Density
		Dune Face Width	AMAR Beachgrass Density
d_c Elevation	Dune Face Slope	d_c Elevation	Dune Face Slope
d_t Elevation	Dune Face Slope	Dominant Species	Dune Face Slope
		d_t Elevation	Dune Face Slope
d_c Elevation	Dune Face Width	d_c Elevation	Dune Face Width
d_t Elevation	Dune Face Width	Dominant Species	Dune Face Width
Dune Face Slope	Dune Face Width	d_t Elevation	Dune Face Width
		Dune Face Slope	Dune Face Width
d_t Elevation	d_c Elevation	Dominant Species	d_c Elevation
		d_t Elevation	d_c Elevation
Dune Face Slope	d_t Elevation	Dominant Species	d_t Elevation
		Dune Face Slope	d_t Elevation

Appendix A, Table A4. Sand accretion Gaussian Bayesian network variables (nodes), their definitions, and data transformations. Variables were transformed to ensure that each variable conformed to a Gaussian distribution.

Accretion-GBN _{combined}			Accretion-GBN _{species}		
Variable Name	Description	Transformation	Variable Name	Description	Transformation
Shoreline Change Rate (SCR)	End point rate of shoreline change for Oregon (1967-2002) and Washington (1986-2002) (m/yr.) (Ruggiero et al. 2013)	$(SCR+2)^{0.05}$	Shoreline Change Rate (SCR)	End point rate of shoreline change for Oregon (1967-2002) and Washington (1986-2002) (m/yr.) (Ruggiero et al. 2013)	$(SCR+2)^{0.05}$
Shoreface Slope (β_{SF})	Slope between 15m and 10m below local mean sea level (LMSL)	$\log(\beta_{SF})$	Shoreface Slope (β_{SF})	Slope between 15m and 10m below local mean sea level (LMSL)	$\log(\beta_{SF})$
Backshore Slope (β_{BS})	Slope between mean high water (MHW) and the 4m contour above LMSL	$\log(\beta_{BS})$	Backshore Slope (β_{BS})	Slope between mean high water (MHW) and the 4m contour above LMSL	$\log(\beta_{BS})$
Mean Grain Size (D50)	Mean sediment grain size of surface sand samples collected at the vegetation line (mm)	$-\log_2(D50)$	Mean Grain Size	Mean sediment grain size of surface sand samples collected at the vegetation line (mm)	$-\log_2(D50)$
Quadrat Elevation (zLMSL)	Elevation of quadrats (m) relative to LMSL in 2012	$\log(zLMSL)$	Quadrat Elevation (zLMSL)	Elevation of quadrats (m) relative to LMSL in 2012	$\log(zLMSL)$
			Dominant Beachgrass Species	Beachgrass species with >50% relative percent areal cover on the foredune face	0 = AMBR 1 = AMAR
Landward Beachgrass Density	Tiller density of <i>Ammophila</i> species in the quadrat located 5m directly landward of a particular quadrat in 2012 (tillers/m ²)	$\log(\text{Landward BG Density} + 1)$	Landward AMAR Density	Tiller density of <i>Ammophila arenaria</i> in the quadrat located 5m directly landward of a particular quadrat in 2012 (tillers/m ²)	$\log(\text{Landward AMAR Density} + 1)$
			Landward AMBR Density	Tiller density of <i>Ammophila breviligulata</i> in the quadrat located 5m directly landward of a particular quadrat in 2012 (tillers/m ²)	$\log(\text{Landward AMBR Density} + 1)$

Appendix A, Table A4 (Continued)

Accretion-GBN _{combined}			Accretion-GBN _{species}		
Variable Name	Description	Transformation	Variable Name	Description	Transformation
Beachgrass Density	Tiller density of <i>Ammophila</i> species in a particular quadrat in 2012 (tillers/m ²)	log(BG Density + 1)	AMAR Density	Tiller density of <i>Ammophila arenaria</i> in a particular quadrat in 2012 (tillers/m ²)	log(AMAR Density + 1)
			AMBR Density	Tiller density of <i>Ammophila breviligulata</i> in a particular quadrat in 2012 (tillers/m ²)	log(AMBR Density + 1)
Seaward Beachgrass Density	Tiller density of <i>Ammophila</i> species in the quadrat located 5m directly seaward of a particular quadrat in 2012 (tillers/m ²)	log(Seaward BG Density + 1)	Seaward AMAR Density	Tiller density of <i>Ammophila arenaria</i> in the quadrat located 5m directly seaward of a particular quadrat in 2012 (tillers/m ²)	log(Seaward AMAR Density + 1)
			Seaward AMBR Density	Tiller density of <i>Ammophila breviligulata</i> in the quadrat located 5m directly seaward of a particular quadrat in 2012 (tillers/m ²)	log(Seaward AMBR Density)
Δ Beachgrass Density	The log response ratio of <i>Ammophila</i> tiller density in a particular quadrat between 2012 and 2014	log(BG Density ₂₀₁₄ + 1) / (BG Density ₂₀₁₂ + 1)	Δ AMAR Density	The log response ratio of <i>Ammophila arenaria</i> density in a particular quadrat between 2012 and 2014	log(AMAR Density ₂₀₁₄ + 1) / (AMAR Density ₂₀₁₂ + 1)
			Δ AMBR Density	The log response ratio of <i>Ammophila breviligulata</i> density in a particular quadrat between 2012 and 2014	log(AMBR Density ₂₀₁₄ + 1) / (AMBR Density ₂₀₁₂ + 1)
Δ Elevation	The change in elevation (m) between 2012 and 2014 for a particular quadrat	zLMSL ₂₀₁₄ – zLMSL ₂₀₁₂	Δ Elevation	The change in elevation (m) between 2012 and 2014 for a particular quadrat	zLMSL ₂₀₁₄ – zLMSL ₂₀₁₂

Appendix A, Table A5. Prohibited directional relationships (edges) for the sand accretion Gaussian Bayesian networks (Accretion-GBNs). Based on the parent-child typology, child nodes are conditionally dependent on parent nodes.

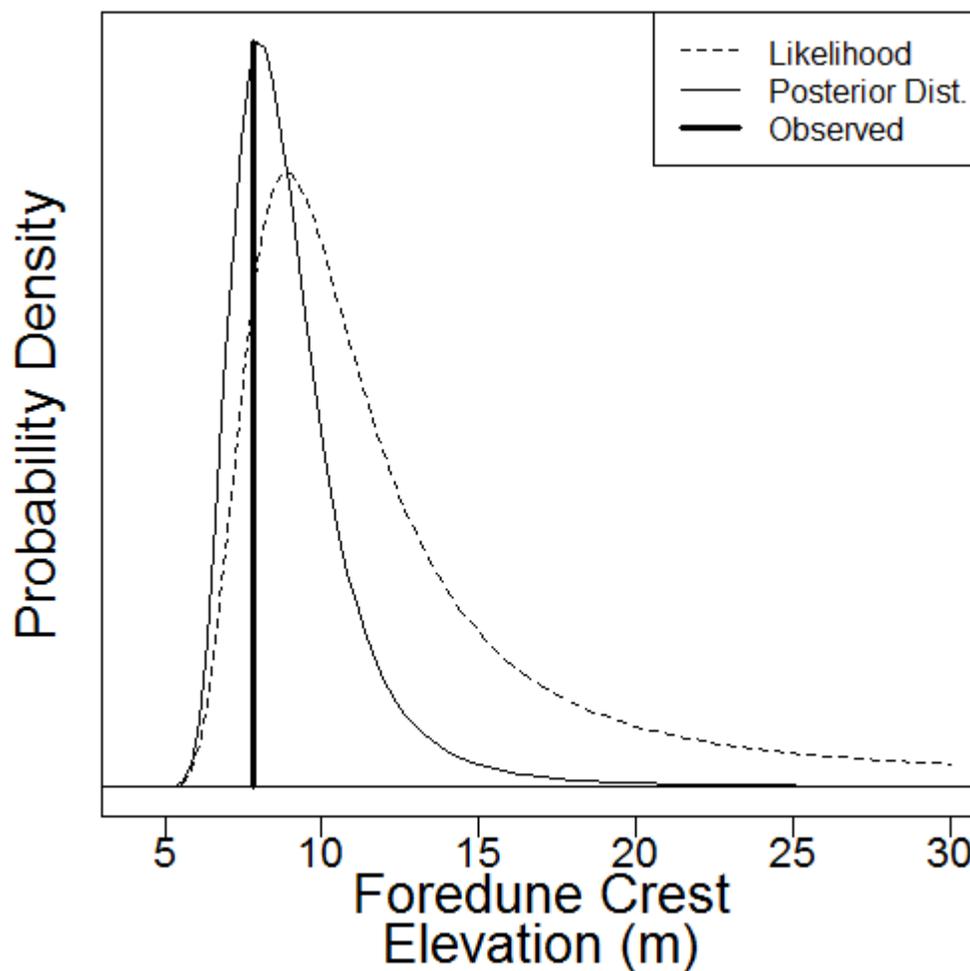
Accretion GBN _{combined}		Accretion GBN _{species}	
Parent	Child	Parent	Child
Backshore Slope	SCR	AMAR Beachgrass Density	SCR
Beachgrass Density	SCR	AMBR Beachgrass Density	SCR
Δ Beachgrass Density	SCR	Backshore Slope	SCR
Δ Elevation (2012-2014)	SCR	Δ AMAR Density	SCR
Landward Beachgrass Density	SCR	Δ AMBR Density	SCR
Mean Sediment Diameter	SCR	Δ Elevation (2012-2014)	SCR
Shoreface Slope	SCR	Landward AMAR Density	SCR
Quadrat Elevation	SCR	Landward AMBR Density	SCR
Seaward Beachgrass Density	SCR	Mean Sediment Diameter	SCR
		Shoreface Slope	SCR
		Quadrat Elevation	SCR
		Seaward AMAR Density	SCR
		Seaward AMBR Density	SCR
Backshore Slope	Shoreface Slope	AMAR Beachgrass Density	Shoreface Slope
Beachgrass Density	Shoreface Slope	AMBR Beachgrass Density	Shoreface Slope
Δ Beachgrass Density	Shoreface Slope	Backshore Slope	Shoreface Slope
Δ Elevation (2012-2014)	Shoreface Slope	Δ AMAR Density	Shoreface Slope
Landward Beachgrass Density	Shoreface Slope	Δ AMBR Density	Shoreface Slope
Mean Sediment Diameter	Shoreface Slope	Δ Elevation (2012-2014)	Shoreface Slope
Quadrat Elevation	Shoreface Slope	Landward AMAR Density	Shoreface Slope
Seaward Beachgrass Density	Shoreface Slope	Landward AMBR Density	Shoreface Slope
		Mean Sediment Diameter	Shoreface Slope
		Quadrat Elevation	Shoreface Slope
		Seaward AMAR Density	Shoreface Slope
		Seaward AMBR Density	Shoreface Slope
Backshore Slope	Mean Sediment Diameter	AMAR Beachgrass Density	Mean Sediment Diameter
Beachgrass Density	Mean Sediment Diameter	AMBR Beachgrass Density	Mean Sediment Diameter
Δ Beachgrass Density	Mean Sediment Diameter	Backshore Slope	Mean Sediment Diameter
Δ Elevation (2012-2014)	Mean Sediment Diameter	Δ AMAR Density	Mean Sediment Diameter
Landward Beachgrass Density	Mean Sediment Diameter	Δ AMBR Density	Mean Sediment Diameter
Quadrat Elevation	Mean Sediment Diameter	Δ Elevation (2012-2014)	Mean Sediment Diameter
Seaward Beachgrass Density	Mean Sediment Diameter	Landward AMAR Density	Mean Sediment Diameter
		Landward AMBR Density	Mean Sediment Diameter

Appendix A, Table A5 (Continued)

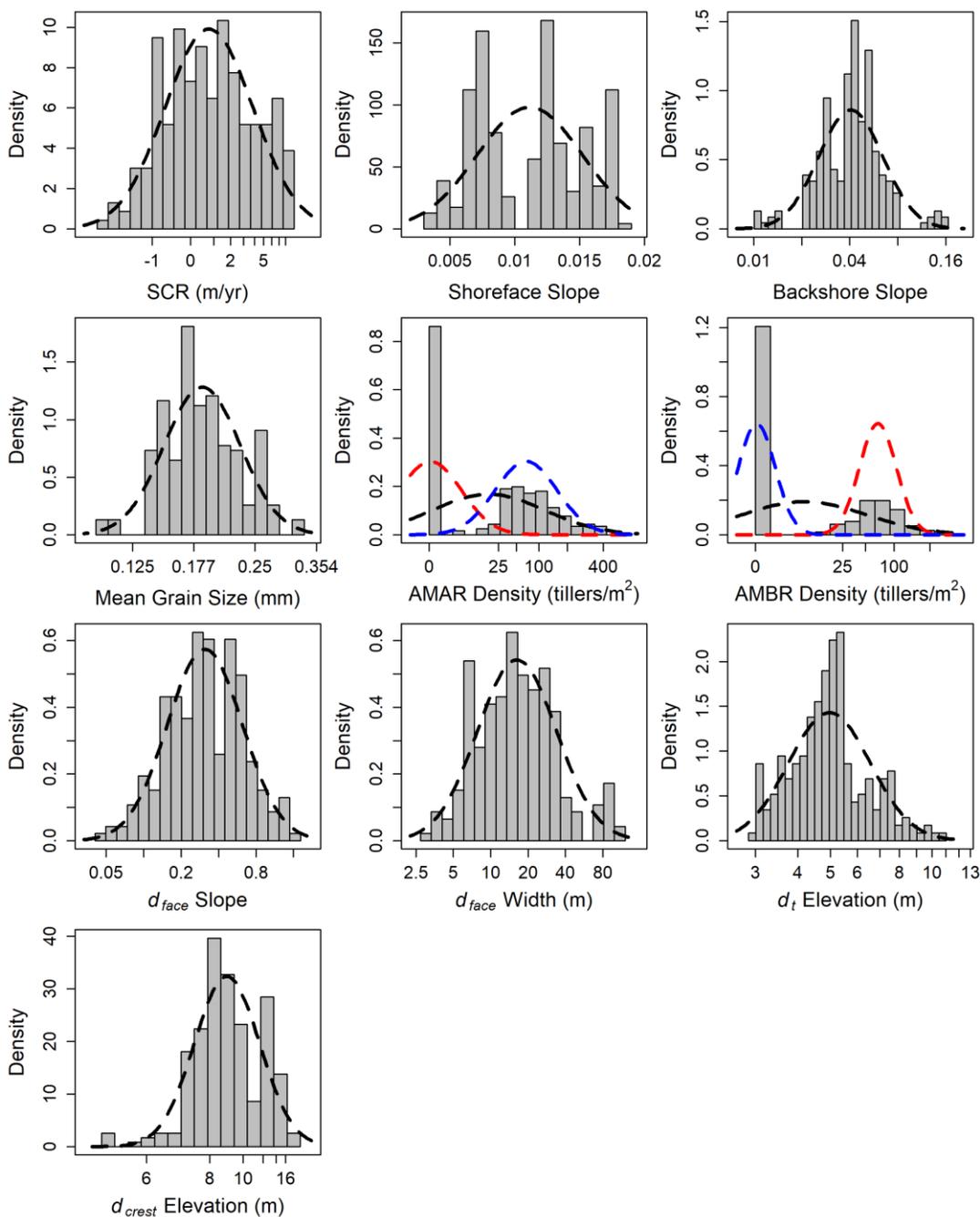
Accretion GBN _{combined}		Accretion GBN _{species}	
Parent	Child	Parent	Child
		Quadrat Elevation	Mean Sediment Diameter
		Seaward AMAR Density	Mean Sediment Diameter
		Seaward AMBR Density	Mean Sediment Diameter
Beachgrass Density	Backshore Slope	AMAR Beachgrass Density	Backshore Slope
Δ Beachgrass Density	Backshore Slope	AMBR Beachgrass Density	Backshore Slope
Δ Elevation (2012-2014)	Backshore Slope	Δ AMAR Density	Backshore Slope
Landward Beachgrass Density	Backshore Slope	Δ AMBR Density	Backshore Slope
Quadrat Elevation	Backshore Slope	Δ Elevation (2012-2014)	Backshore Slope
Seaward Beachgrass Density	Backshore Slope	Landward AMAR Density	Backshore Slope
		Landward AMBR Density	Backshore Slope
		Quadrat Elevation	Backshore Slope
		Seaward AMAR Density	Backshore Slope
		Seaward AMBR Density	Backshore Slope
Beachgrass Density	Quadrat Elevation	AMAR Beachgrass Density	Quadrat Elevation
Δ Beachgrass Density	Quadrat Elevation	AMBR Beachgrass Density	Quadrat Elevation
Δ Elevation (2012-2014)	Quadrat Elevation	Δ AMAR Density	Quadrat Elevation
Landward Beachgrass Density	Quadrat Elevation	Δ AMBR Density	Quadrat Elevation
Seaward Beachgrass Density	Quadrat Elevation	Δ Elevation (2012-2014)	Quadrat Elevation
		Landward AMAR Density	Quadrat Elevation
		Landward AMBR Density	Quadrat Elevation
		Seaward AMAR Density	Quadrat Elevation
		Seaward AMBR Density	Quadrat Elevation
		AMAR Beachgrass Density	Dominant Species
		AMBR Beachgrass Density	Dominant Species
		Backshore Slope	Dominant Species
		Δ AMAR Density	Dominant Species
		Δ AMBR Density	Dominant Species
		Δ Elevation (2012-2014)	Dominant Species
		Landward AMAR Density	Dominant Species
		Landward AMBR Density	Dominant Species
		Mean Sediment Diameter	Dominant Species
		Shoreface Slope	Dominant Species
		Quadrat Elevation	Dominant Species
		SCR	Dominant Species
		Seaward AMAR Density	Dominant Species
		Seaward AMBR Density	Dominant Species

Appendix A, Table A5 (Continued)

Accretion GBN _{combined}		Accretion GBN _{species}	
Parent	Child	Parent	Child
Beachgrass Density	Landward Beachgrass Density	AMAR Beachgrass Density	Landward AMAR Density
Δ Beachgrass Density	Landward Beachgrass Density	AMBR Beachgrass Density	Landward AMAR Density
Δ Elevation (2012-2014)	Landward Beachgrass Density	Δ AMAR Density	Landward AMAR Density
Seaward Beachgrass Density	Landward Beachgrass Density	Δ AMBR Density	Landward AMAR Density
		Δ Elevation (2012-2014)	Landward AMAR Density
		Seaward AMAR Density	Landward AMAR Density
		Seaward AMBR Density	Landward AMAR Density
		AMAR Beachgrass Density	Landward AMBR Density
		AMBR Beachgrass Density	Landward AMBR Density
		Δ AMAR Density	Landward AMBR Density
		Δ AMBR Density	Landward AMBR Density
		Δ Elevation (2012-2014)	Landward AMBR Density
		Landward AMAR Density	Landward AMBR Density
		Seaward AMAR Density	Landward AMBR Density
		Seaward AMBR Density	Landward AMBR Density
Δ Beachgrass Density	Beachgrass Density	Δ AMAR Density	AMAR Beachgrass Density
Δ Elevation (2012-2014)	Beachgrass Density	Δ AMBR Density	AMAR Beachgrass Density
Seaward Beachgrass Density	Beachgrass Density	Δ Elevation (2012-2014)	AMAR Beachgrass Density
		Seaward AMAR Density	AMAR Beachgrass Density
		Seaward AMBR Density	AMAR Beachgrass Density
		AMAR Beachgrass Density	AMBR Beachgrass Density
		Δ AMAR Density	AMBR Beachgrass Density
		Δ AMBR Density	AMBR Beachgrass Density
		Δ Elevation (2012-2014)	AMBR Beachgrass Density
		Seaward AMAR Density	AMBR Beachgrass Density
		Seaward AMBR Density	AMBR Beachgrass Density
Δ Beachgrass Density	Seaward Beachgrass Density	Δ AMAR Density	Seaward AMAR Density
Δ Elevation (2012-2014)	Seaward Beachgrass Density	Δ AMBR Density	Seaward AMAR Density
		Δ Elevation (2012-2014)	Seaward AMAR Density
		Δ AMAR Density	Seaward AMBR Density
		Δ AMBR Density	Seaward AMBR Density
		Δ Elevation (2012-2014)	Seaward AMBR Density
		Seaward AMAR Density	Seaward AMBR Density
Δ Elevation (2012-2014)	Δ Beachgrass Density	Δ Elevation (2012-2014)	Δ AMAR Density
		Δ AMAR Density	Δ AMBR Density
		Δ Elevation (2012-2014)	Δ AMBR Density

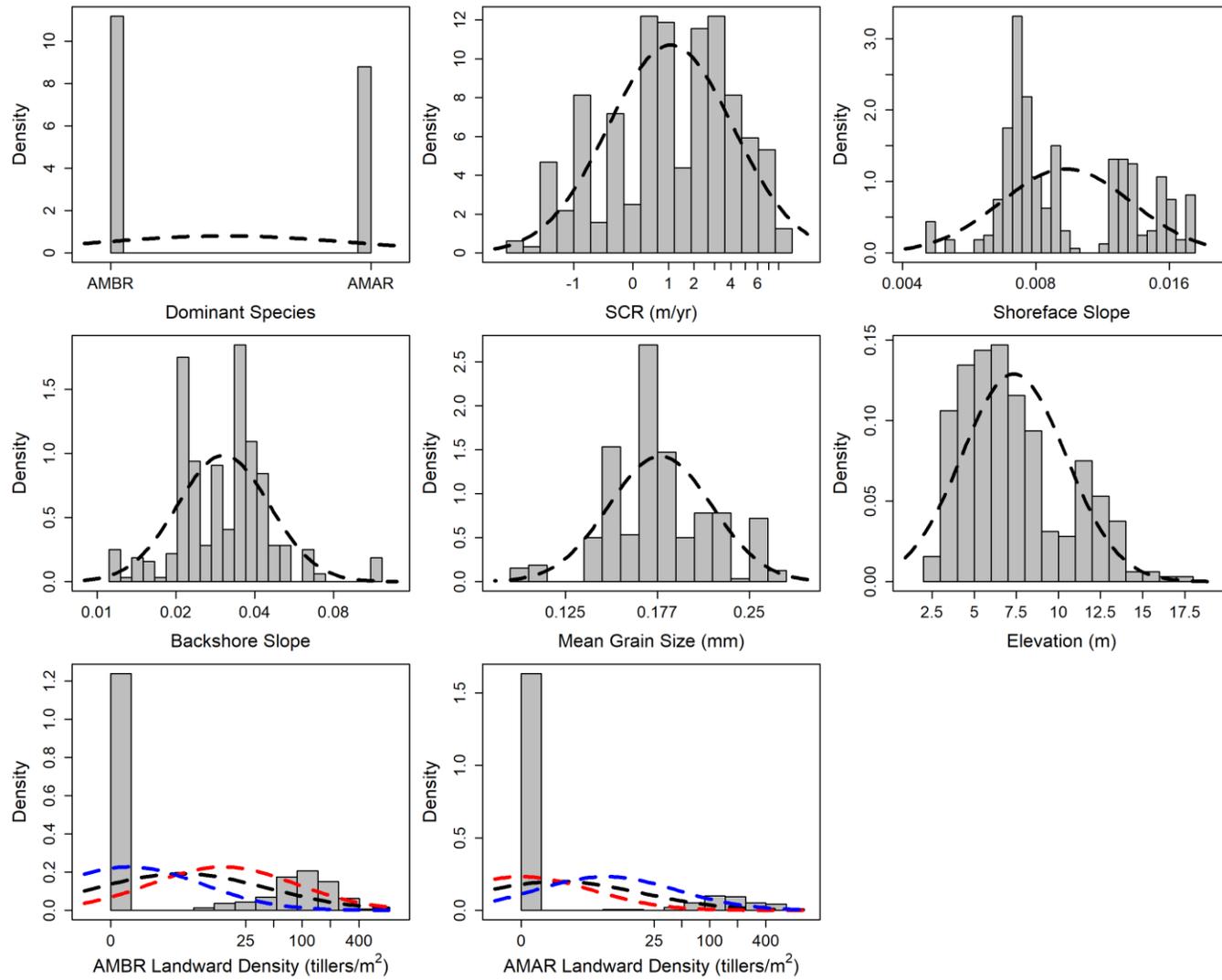


Appendix A, Figure A1. Back-transformed probability density function (pdf) plot of the likelihood function for foredune crest (d_c) elevation (dashed) and the posterior distribution for d_c elevation when incorporating prior knowledge (solid) for a single foredune profile. The observed d_c elevation is represented by the bolded vertical line. Narrowing of the posterior distribution and the leftward shift of the maximum a posteriori estimate (mode of the posterior distribution) towards the observed value indicates that prior knowledge improved the precision and accuracy of the predicted d_c elevation, respectively, for this specific transect.

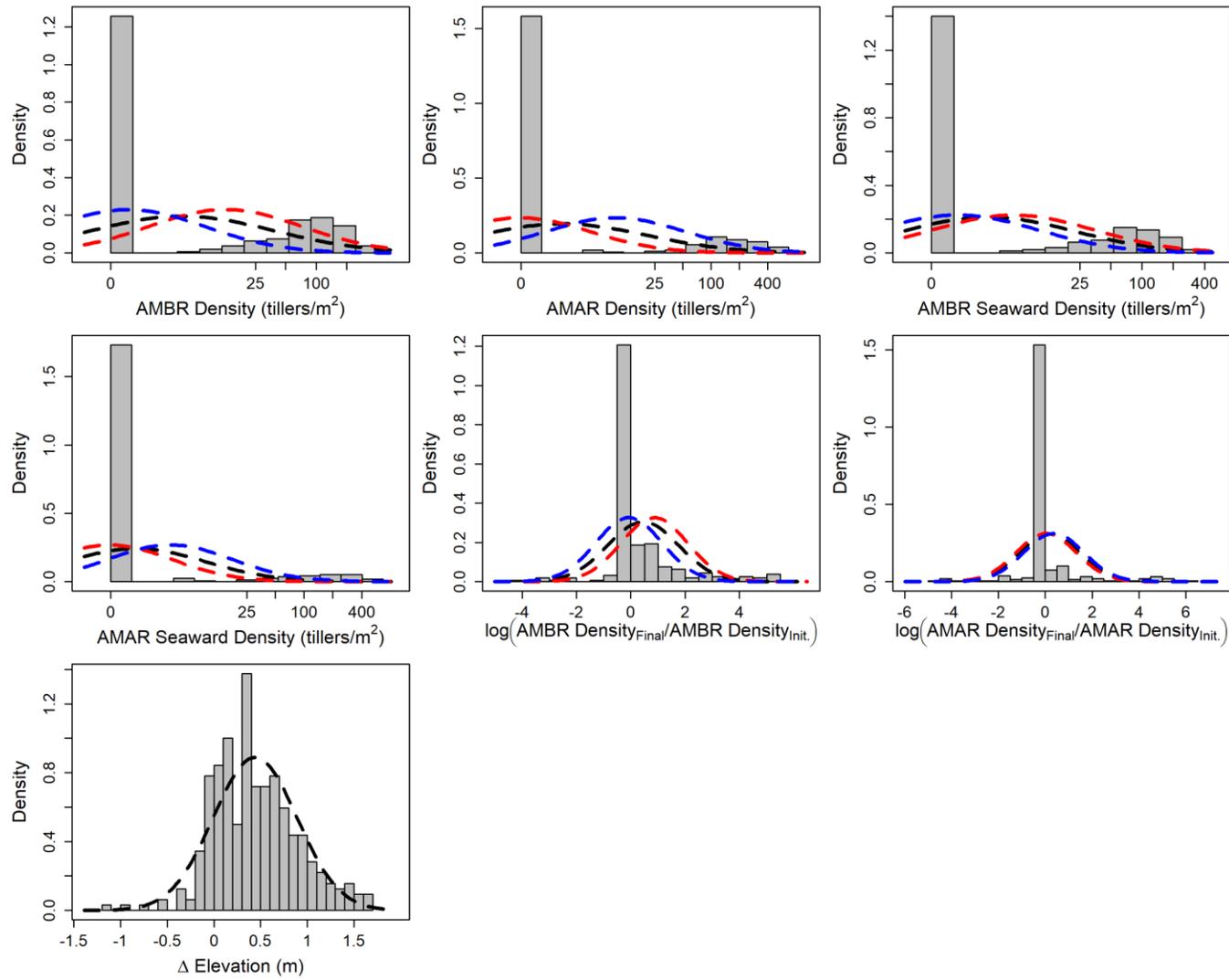


Appendix A, Figure A2. Likelihood function for the foredune morphology Gaussian Bayesian network, with vegetation variables separated by species (Morphology-GBN_{species}; Figure 2.3B). Histograms show the distribution of the underlying dataset, with data transformations described in Appendix A, Table A2. Black dashed lines show the likelihood function for each node. For vegetation variable nodes, colored dashed lines show the likelihood functions when the dominant species is known (Blue = *Ammophila arenaria* (AMAR) is dominant, Red = *A. breviligulata* (AMBR) is dominant).

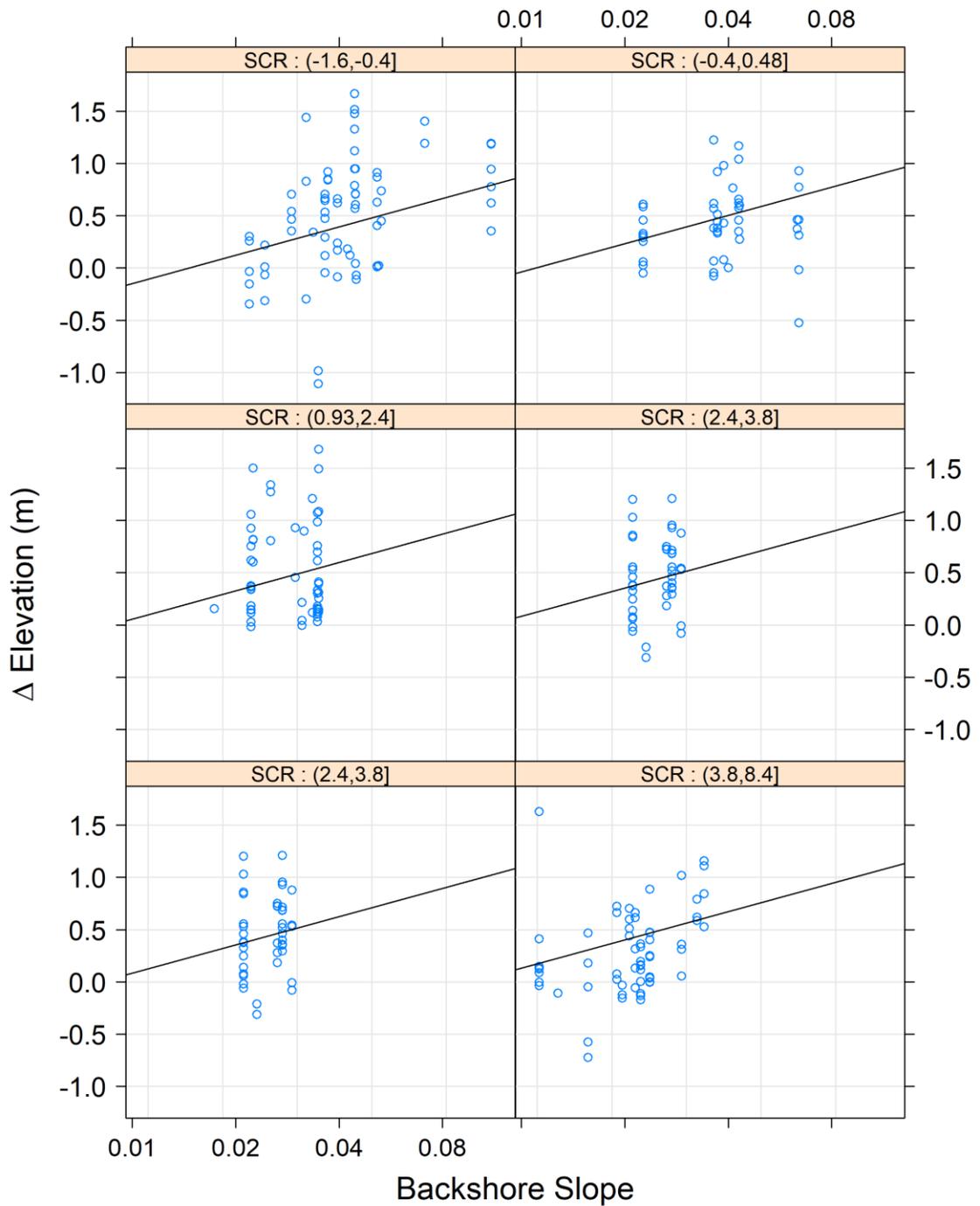
Appendix A, Figure A3. Likelihood function for the sand accretion Gaussian Bayesian network, with vegetation variables separated by species (Accretion-GBN_{species}; Figure 2.4Figure 2.3B). Histograms show the distribution of the underlying dataset, with data transformations described in Appendix A, Table A4. Black dashed lines show the likelihood function for each node. For vegetation variable nodes, colored dashed lines show the likelihood functions when dominant species is known (Blue = *Ammophila arenaria* (AMAR) is dominant, Red = *A. breviligulata* (AMBR) is dominant).



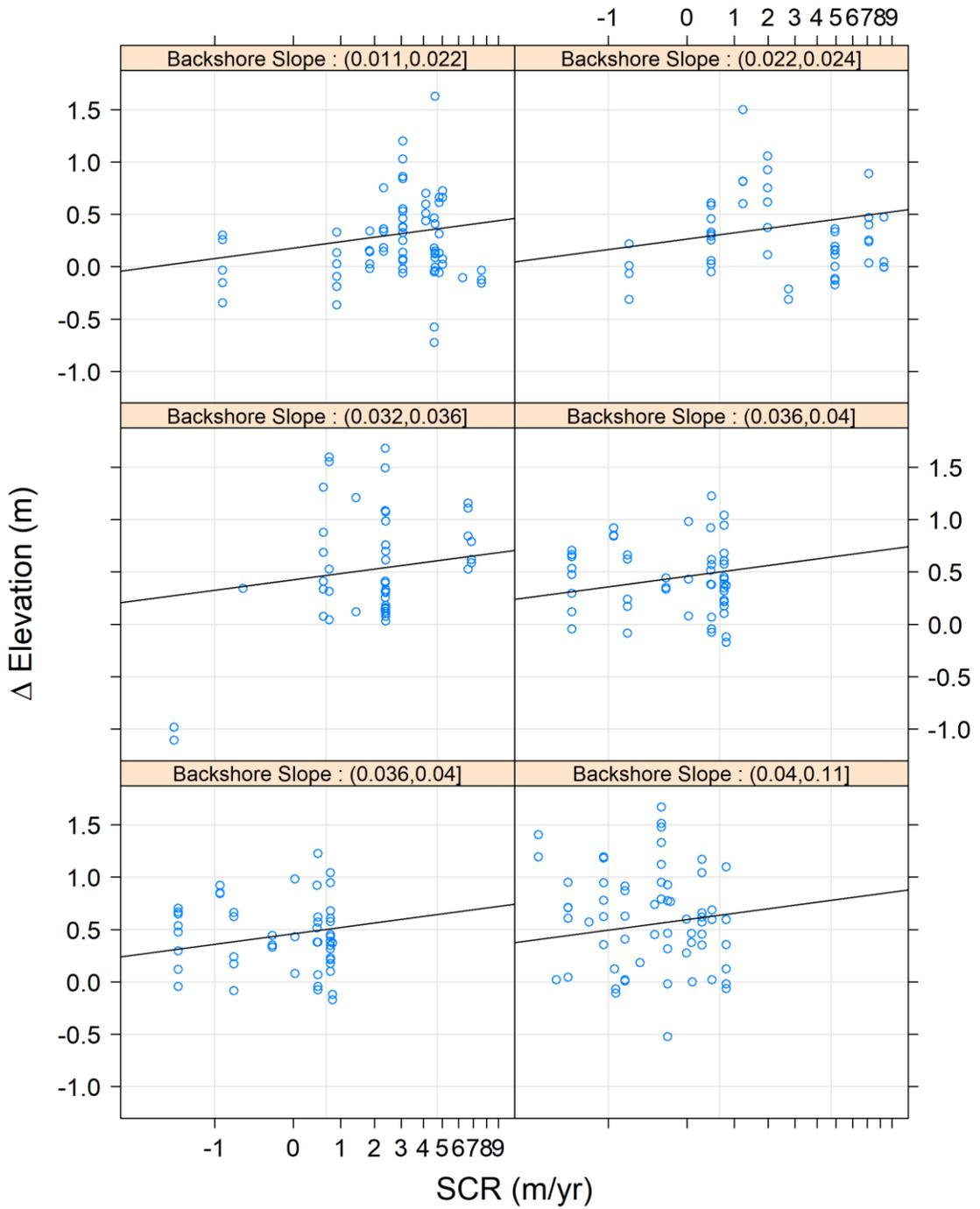
Appendix A, Figure A3



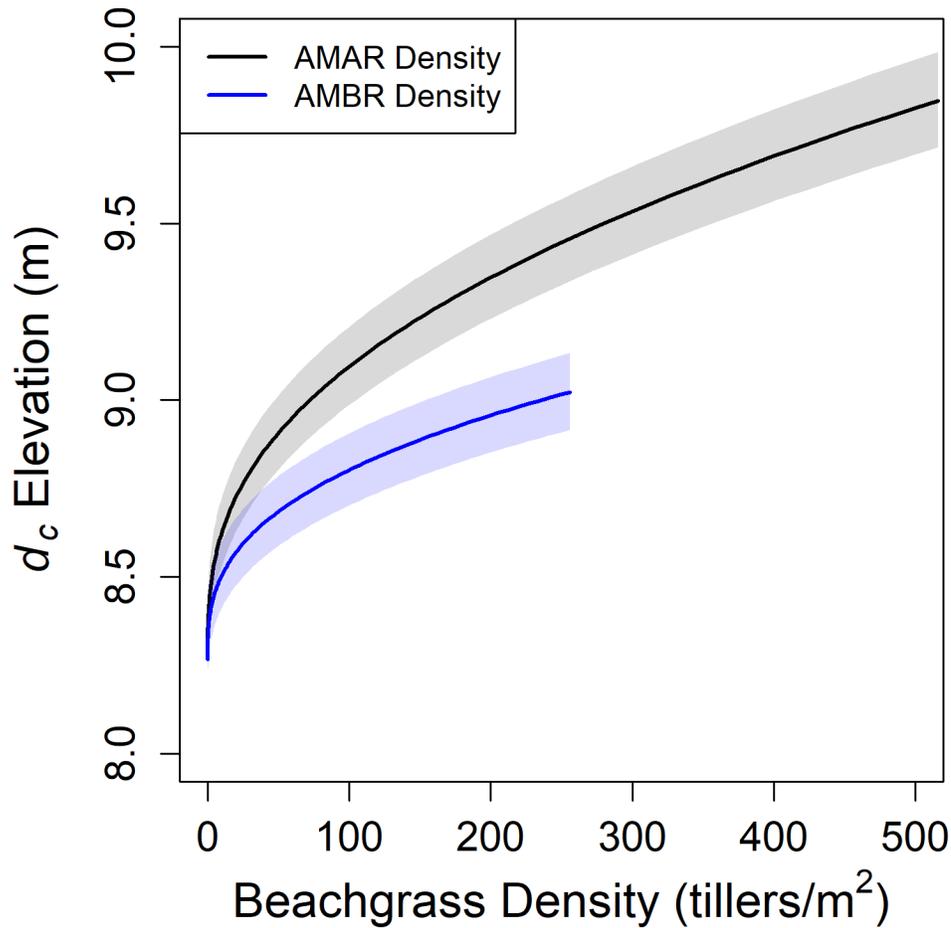
Appendix A, Figure A3 (Continued)



Appendix A, Figure A4. Relationship between backshore slope and elevation change (Δ Elevation, m) between 2012 and 2014, across a gradient of shoreline change rates (SCR, m/yr.). Data (blue circles) and fitted regression line (black line) are shown for each SCR bin.



Appendix A, Figure A5. Relationship between shoreline change rate (SCR, m/yr.) and elevation change (Δ Elevation, m) between 2012 and 2014, across a gradient of backshore slopes. Data (blue circles) and fitted regression line (black line) are shown for each backshore slope bin.



Appendix A, Figure A6. Relationship between foredune crest (d_c) elevation (m) and the density of *Ammophila arenaria* (AMAR) and *A. breviligulata* (AMBR) tillers on the foredune face. Lines and bands indicate the d_c elevation expected value and standard error across a range of beachgrass densities. d_c elevation was predicted using the species-specific foredune morphology Gaussian Bayesian network (Morphology-GBN_{species}; Figure 2.3B), with non-foredune morphology and vegetation nodes held constant.

Appendix B. Chapter 3 supplemental figures and tables

Appendix B, Table B1. List of site and plot information for all experimental plots: community type, indicating the dominant foredune grass species; plot easting and northing coordinates (WGS84 UTM 10N); short-term shoreline change rate (ST_SCR); long-term shoreline change rate (LT_SCR, (Ruggiero et al. 2013)); date of planting; date of excavation (destructive sampling of plots); and mean annual rate of sand deposition. ABANDONED indicated that the plot was abandoned prior to completion of the experiment.

Site	Plot	Community Type	Easting (UTM 10N) (m)	Northing (UTM 10N) (m)	ST_SCR (m/yr.)	LT_SCR (m/yr.)	Date Planted	Date Excavated	Sand Deposition Rate (cm/yr.)
Grayland	GRAY-1	ELMO	415840	5185932	3.0	-0.3	5/19/2010	10/22/2012	28.2
Grayland	GRAY-2	AMBR	415841	5185908	3.0	-0.3	5/19/2010	10/22/2012	16.9
Grayland	GRAY-3	AMAR	415835	5185873	2.9	-0.3	5/19/2010	10/22/2012	46.0
Heather	HEATH-1	ELMO	415892	5179223	31.8	5.7	5/18/2010	10/22/2012	28.0
Heather	HEATH-2	AMBR	415899	5179208	31.4	5.8	5/18/2010	10/22/2012	26.0
Leadbetter Point	LBP-2	ELMO	418218	5161895	8.3	-1.3	5/13/2010	ABANDONED*	NA
Leadbetter Point	LBP-1	AMBR	418225	5161877	8.3	-1.3	5/12/2010	10/23/2012	35.7
Leadbetter Point	LBP-3	ELMO	N.D.	5160134	0.8	2.9	12/29/2010	10/23/2012	23.3
Long Beach	LB-1	ELMO	418735	5151115	2.5	1.9	5/12/2010	10/11/2012	50.4
Long Beach	LB-2	AMBR	418739	5151085	2.6	1.9	5/12/2010	10/11/2012	27.5
Long Beach	LB-3	AMBR	417597	5129361	0.8	2.9	5/12/2010	10/10/2012	22.5
Long Beach	LB-4	AMBR	N.D.	5129352	5.6	-1.0	12/28/2010	10/11/2012	6.4
Iredale	IRE-1	AMAR	424672	5113567	0.8	4.5	5/8/2010	ABANDONED*	NA
Iredale	IRE-2	AMBR	425504	5111288	1.1	4.5	5/8/2010	10/10/2012	28.6
Iredale	IRE-3	ELMO	425500	5111258	1.1	4.5	5/9/2010	10/10/2012	40.2
Clatsop Plains	CP-4	ELMO	427541	5103583	3.9	4.0	7/6/2010	10/10/2012	56.2
Clatsop Plains	CP-5	AMBR	427556	5103578	3.9	4.0	7/6/2010	10/9/2012	36.0
Clatsop Plains	CP-6	AMAR	427543	5103574	3.9	4.0	7/6/2010	10/9/2012	51.9
Clatsop Plains	CP-1	AMAR	427788	5101818	3.0	3.8	5/8/2010	ABANDONED*	NA

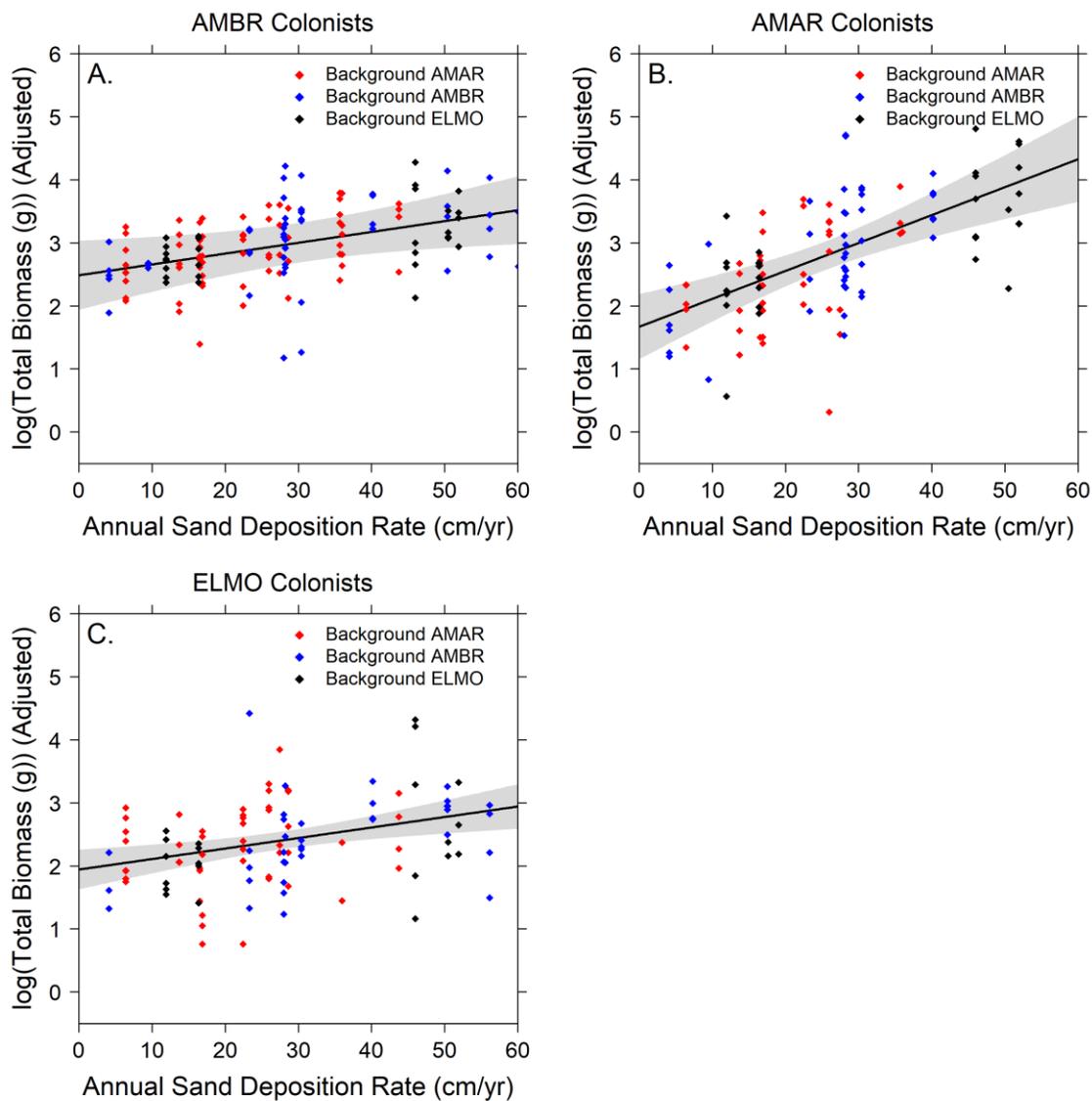
Appendix B, Table B1 (Continued)

Site	Plot	Community Type	Easting (UTM 10N) (m)	Northing (UTM 10N) (m)	ST_SCR (m/yr.)	LT_SCR (m/yr.)	Date Planted	Date Excavated	Sand Deposition Rate (cm/yr.)
Clatsop Plains	CP-2	AMBR	427795	5101801	3.0	3.8	5/8/2010	ABANDONED*	NA
Clatsop Plains	CP-3	ELMO	427789	5101775	3.0	3.8	5/4/2010	ABANDONED*	NA
Seaside	SEA-5	ELMO	428125	5094843	0.7	1.5	7/7/2010	9/27/2012	30.4
Seaside	SEA-1	AMBR	428113	5094759	0.9	1.4	5/9/2010	9/27/2012	16.5
Seaside	SEA-3	AMAR	428108	5094740	0.9	1.4	5/9/2010	ABANDONED*	NA
Seaside	SEA-4	ELMO	428094	5094724	1.0	1.4	7/1/2010	9/27/2012	41.0
Seaside	SEA-2	ELMO	428088	5094708	1.0	1.4	5/9/2010	ABANDONED*	NA
Cape Lookout	CL-1	AMAR	424913	5030951	-1.5	-1.0	4/25/2010	9/26/2012	50.5
Cape Lookout	CL-2	AMBR	424900	5030848	-1.5	-1.0	4/25/2010	ABANDONED*	NA
Cape Lookout	CL-3	ELMO	424225	5024959	-1.4	-0.9	5/8/2010	9/26/2012	4.1
Sand Lake	SL-1	ELMO	424396	5013734	-0.5	0.9	4/23/2010	9/25/2012	9.5
Sand Lake	SL-2	AMAR	424364	5013532	-0.4	-0.1	4/23/2010	9/25/2012	16.4
Sand Lake	SL-3	AMBR	424344	5013445	-0.5	-0.2	4/23/2010	9/25/2012	13.7
Pacific City	PC-1	AMBR	423950	5005964	0.3	0.1	4/24/2010	9/24/2012	43.8
Pacific City	PC-2	AMAR	423923	5004490	0.0	-0.2	4/23/2010	9/24/2012	12.0
Pacific City	PC-4	ELMO	423898	5004488	0.0	-0.2	6/24/2010	9/25/2012	60.1
Pacific City	PC-3	ELMO	423895	5004483	0.1	-0.2	4/24/2010	ABANDONED*	NA

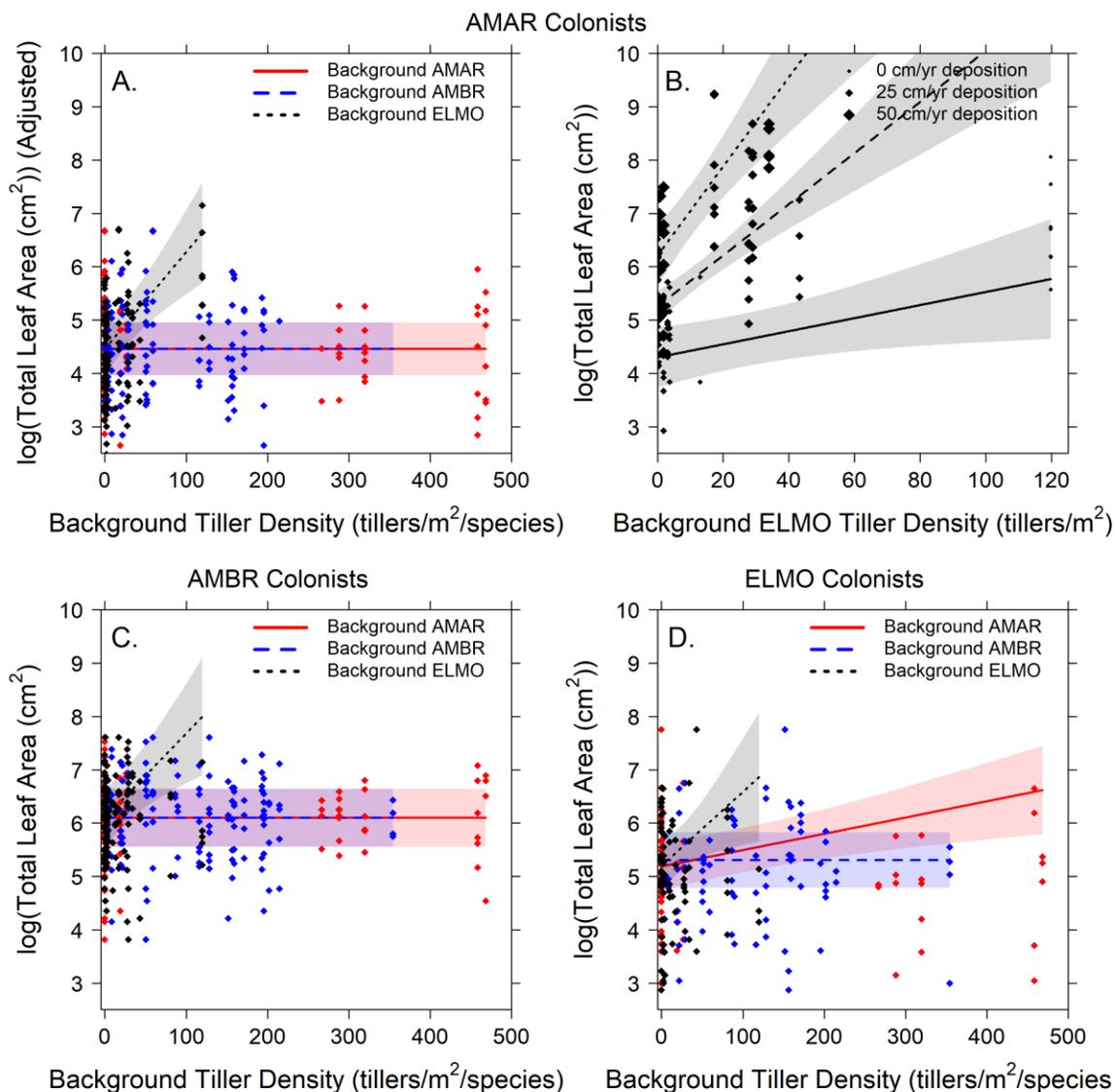
*Plants in plot suffered high mortality, often due to excessive sand burial or other disturbance.

Appendix B, Table B2. Summary statistics for the number of *A. breviligulata* (AMBR), *A. arenaria* (AMAR), and *Elymus mollis* (ELMO) tillers within each community type, presented as mean (minimum, maximum).

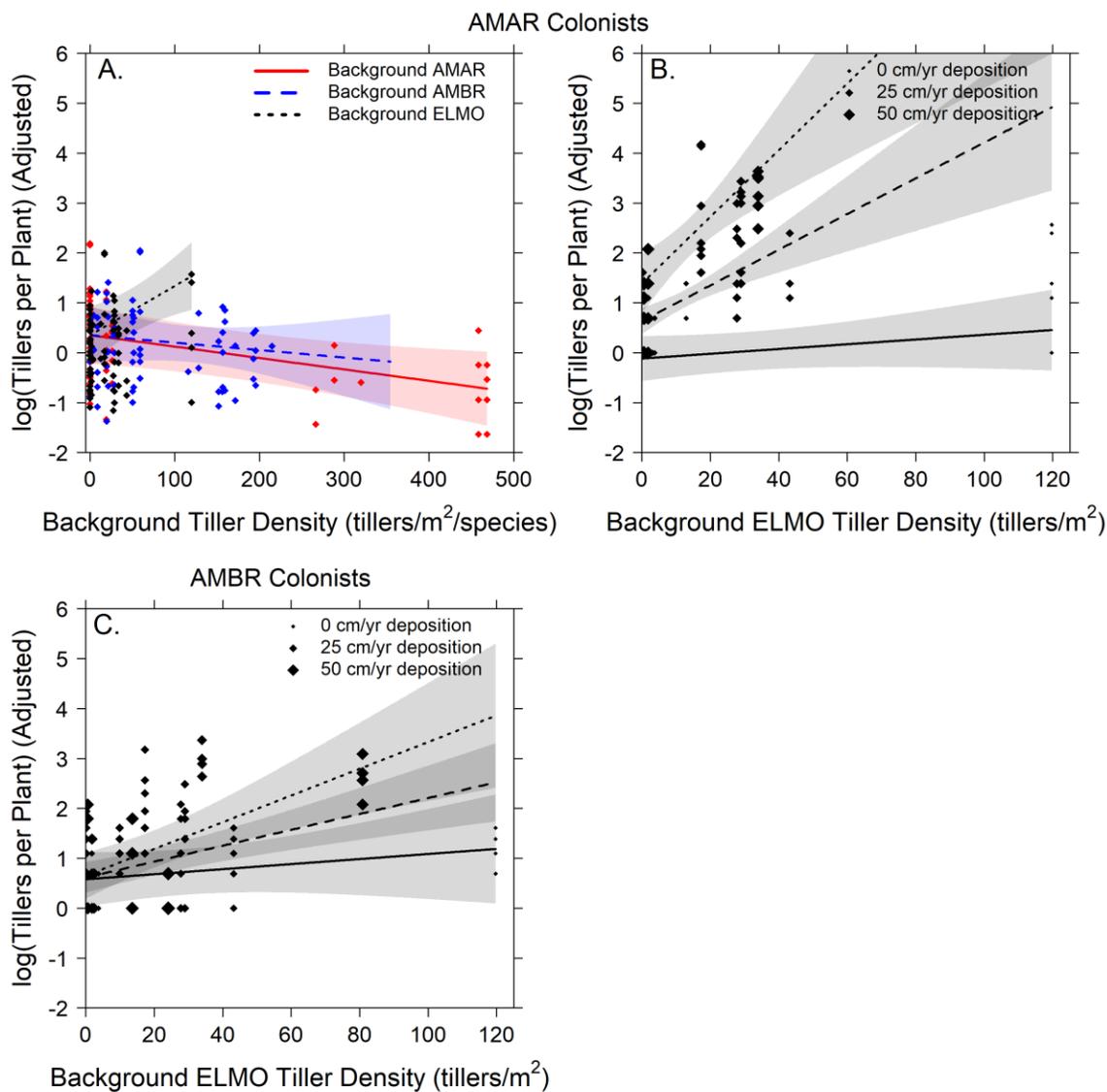
Community Type	Background AMBR Tiller Density (tillers/m ²)	Background AMAR Tiller Density (tillers/m ²)	Background ELMO Tiller Density (tillers/m ²)
AMBR	173.6 (116, 354.3)	2.5 (0, 19.1)	1.3 (0, 9.9)
AMAR	16.1 (0, 51.9)	366.6 (266.7, 468.5)	2.3 (0, 3.7)
ELMO	51.3 (1.2, 151.9)	5 (0, 26.5)	41.4 (13, 119.8)



Appendix B, Figure B1. Partial residual plot illustrating relationships between colonist log(total dry biomass) and the annual sand deposition rate within invaded communities (A) for *A. breviligulata* (AMBR) colonists, (B) for *Ammophila arenaria* (AMAR) colonists, (C) for *E. mollis* (ELMO) colonists. Points show the effects of background tiller density of AMAR (red), AMBR (blue), and ELMO (black) within each plot (1 point per species per plot = 3 points per plot). Lines and bands show the fitted relationships and 95% confidence intervals, after accounting for initial biomass.



Appendix B, Figure B2. Partial residual plot illustrating relationships between colonist log(total leaf area) and species-specific tiller densities of invaded communities (A-B) for *A. arenaria* (AMAR) colonists, (C) for *Ammophila breviligulata* (AMBR) colonists, (D) for *E. mollis* (ELMO) colonists. Points show the effects of background tiller density of AMAR (red), AMBR (blue), and ELMO (black) within each plot (1 point per species per plot = 3 points per plot). Lines and bands show the fitted relationships and 95% confidence intervals, after accounting for initial biomass.



Appendix B, Figure B3. Partial residual plot illustrating relationships between colonist $\log(\text{tillers per plant})$ and species-specific tiller densities of invaded communities (A-B) for *A. arenaria* (AMAR) colonists and (C) for *Ammophila breviligulata* (AMBR) colonists. Points show the effects of background tiller density of AMAR (red), AMBR (blue), and ELMO (black) within each plot (1 point per species per plot = 3 points per plot). Lines and bands show the fitted relationships and 95% confidence intervals, after accounting for initial biomass.

Appendix C. Chapter 4 supplemental figures and tables

Appendix C, Table C1. Mean daily maximum air temperature (°C) at coastal meteorological observation stations in Westport, WA (NOAA Station WPTW1), Newport, OR (NOAA Station NWPO3), San Francisco, CA (NOAA Station FTPC1), and Santa Monica, CA (NOAA Station ICAC1). Date range: 2010-2016.

Month	Westport, WA	Newport, OR	San Francisco, CA	Santa Monica, CA
January	9.4	11.0	13.7	18.4
February	10.1	10.7	14.6	17.3
March	11.2	11.0	14.9	16.8
April	12.2	11.3	15.0	17.1
May	13.9	12.5	14.9	17.6
June	15.6	13.6	15.5	18.3
July	16.5	14.2	15.7	19.7
August	17.5	14.3	16.4	20.3
September	17.8	15.6	17.8	21.3
October	15.2	14.5	18.3	21.1
November	11.3	12.4	16.1	20.0
December	8.5	9.8	13.6	17.6

Appendix C, Table C2. Mean daily maximum air and soil temperatures (°C) around or within planters at Hatfield Marine Science Center (HMSC), Newport, OR between April 2014 and September 2015. Heat and sand burial treatments were applied between July 1, 2014 and September 9, 2015. Air temperature measurements were obtained from the HMSC meteorological tower. Soil temperature measurements were recorded using a HOBO temperature data logger placed 4 cm below the soil surface, near the center of each sand-filled planter. * - prior to initiation of heat treatment.

Year	Month	Air Temperature	Soil Temperature (Unheated)	Soil Temperature (Heated)	Soil Temperature Difference (Heated-Unheated)
2014	May*	18.5	24.6	25.4	0.8
	June*	18.0	23.6	24.5	0.9
	July	19.8	27.0	29.7	2.6
	August	19.9	25.5	29.3	3.8
	September	21.1	23.7	25.7	2.0
	October	18.2	18.6	21.7	3.1
	November	19.2	12.4	14.5	2.1
	December	12.0	11.2	13.5	2.3
2015	January	14.6	12.1	14.4	2.3
	February	15.1	14.5	16.5	2.0
	March	15.2	15.8	18.1	2.4
	April	14.6	16.9	19.1	2.2
	May	15.7	20.0	22.4	2.3
	June	17.8	23.4	24.8	1.4
	July	21.1	27.2	28.7	1.5
	August	20.6	24.5	26.6	2.0

Appendix C, Table C3. Restricted maximum likelihood (REML) parameter estimates and 95% confident intervals for the best supported model (based on AIC_c model comparison) of log-response ratios for total biomass, aboveground (AG) biomass, and belowground (BG) biomass for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) using the factors *A. arenaria* (N_{AMAR}) or *A. breviligulata* (N_{AMBR}) initial tiller density, heat, and sand burial treatments.

Response Variable Species	Fixed Predictor	REML Estimates	95% confidence interval	
			Lower	Upper
$\log\left(\frac{\text{Total Biomass}}{\text{Initial Total Biomass}}\right)$				
AMAR	Intercept	0.420	0.249	0.589
	N _{AMBR}	-0.020	-0.032	-0.009
AMBR	Intercept	1.392	1.143	1.617
	N _{AMAR}	-0.011	-0.018	-0.004
	Sand Burial	-0.168	-0.363	0.001
$\log\left(\frac{\text{AG Biomass}}{\text{Initial AG Biomass}}\right)$				
AMAR	Intercept	0.239	0.055	0.421
	N _{AMBR}	-0.021	-0.035	-0.009
AMBR	Intercept	1.203	0.969	1.407
	N _{AMAR}	-0.008	-0.016	-0.001
	Sand Burial	-0.213	-0.413	-0.024
$\log\left(\frac{\text{BG Biomass}}{\text{Initial BG Biomass}}\right)$				
AMAR	Intercept	0.702	0.428	0.954
	N _{AMBR}	-0.023	-0.035	-0.010
	Heat	0.189	-0.141	0.553
	Sand Burial	0.515	0.154	0.848
	Heat:Sand Burial	-0.606	-1.081	-0.087
AMBR	Intercept	2.205	1.945	2.471
	N _{AMBR}	-0.018	-0.026	-0.010
	Heat	-0.444	-0.811	-0.070

Appendix C, Table C4. Substantially supported models (based on AIC_c model comparison) of log-response ratios for total biomass, aboveground biomass, and belowground biomass for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) using the predictors *A. arenaria* (N_{AMAR}) or *A. breviligulata* (N_{AMBR}) initial tiller density, heat, and sand burial treatments.

Response Var. Species	Fixed Predictors	df	L	AIC _c	Δ _i	W _i
$\log\left(\frac{\text{Total Biomass}}{\text{Initial Total Biomass}}\right)$						
AMAR	N _{AMBR}	5	-225.3	460.9	0.0	0.348
AMBR	N _{AMAR} + Sand	6	-165.9	344.3	0.0	0.214
	N _{AMAR} + Sand + Heat	7	-165.3	345.2	0.9	0.135
	N _{AMAR}	5	-167.4	345.2	1.0	0.133
$\log\left(\frac{\text{AG Biomass}}{\text{Initial AG Biomass}}\right)$						
AMAR	N _{AMBR}	5	-237.0	484.4	0.0	0.230
	N _{AMBR} + Heat + Sand + Heat:Sand	8	-234.2	485.2	0.9	0.149
	N _{AMBR} + Sand	6	-236.5	485.5	1.1	0.130
AMBR	N _{AMAR} + Sand	6	-166.8	346.1	0.0	0.263
	N _{AMAR} + Heat + Sand	7	-166.6	347.8	1.8	0.109
	N _{AMAR} + Sand + N _{AMAR} :Sand	7	-166.6	347.9	1.8	0.105
$\log\left(\frac{\text{BG Biomass}}{\text{Initial BG Biomass}}\right)$						
AMAR	N _{AMBR} + Sand + Heat + Sand:Heat	8	-223.9	464.5	0.0	0.230
	N _{AMBR} + Sand + Heat + Sand:Heat + Sand:N _{AMBR}	9	-223.2	465.3	0.8	0.153
	N _{AMBR} + Sand + Heat + Sand:Heat + Heat:N _{AMBR}	9	-223.6	466.2	1.7	0.097
AMBR	N _{AMAR} + Heat	6	-190.8	394.1	0.0	0.254
	N _{AMAR} + Heat + Heat:N _{AMAR}	7	-190.5	395.7	1.5	0.119
	N _{AMAR} + Sand + Heat	7	-190.6	395.8	1.7	0.111

Appendix C, Table C5. Restricted maximum likelihood (REML) parameter estimates and 95% confident intervals for the best supported model (based on AIC_c model comparison) of log-response ratios of tiller density (tillers/quadrant) for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) using the factors *A. arenaria* (N_{AMAR}) or *A. breviligulata* (N_{AMBR}) initial tiller density, sand burial, and heat treatments.

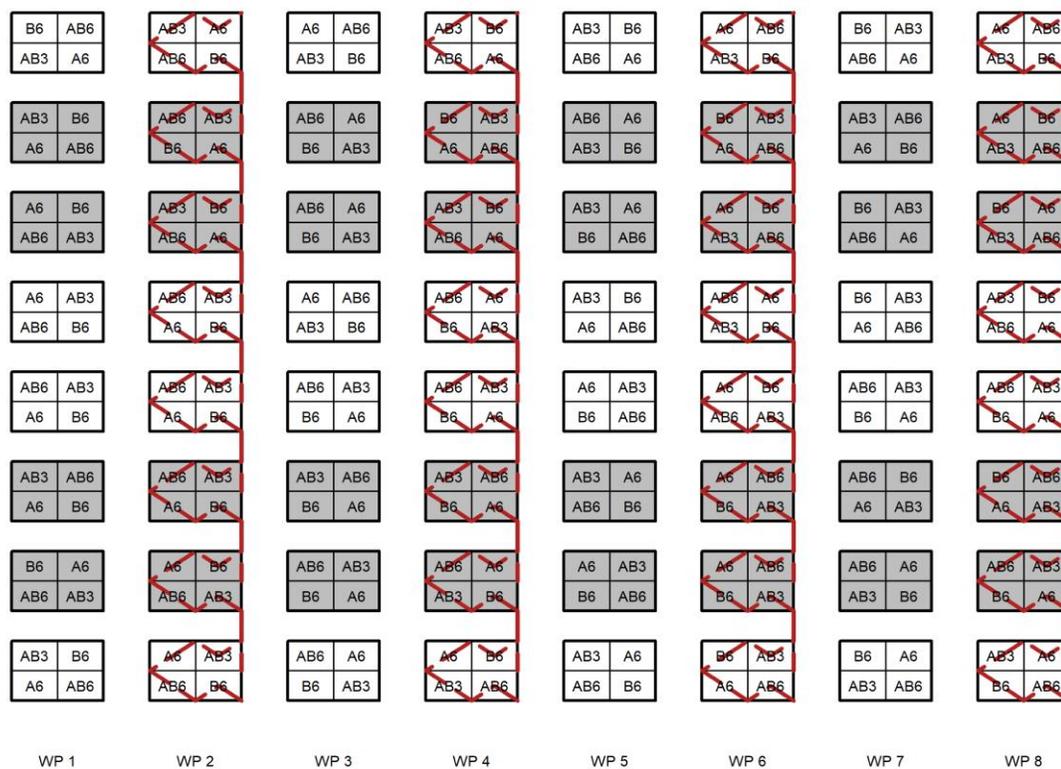
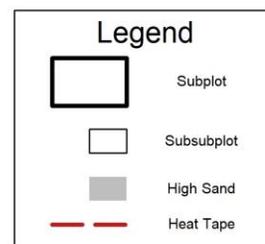
Response Variable	Fixed Predictor	REML Estimates	95% confidence interval	
			Lower	Upper
Log(N _{AMAR,Final} / N _{AMAR,Init.})	Intercept	0.268	-0.015	0.546
	N _{AMAR}	-0.017	-0.027	-0.007
	N _{AMBR}	-0.012	-0.021	-0.003
Log(N _{AMBR,Final} / N _{AMBR,Init.})	Intercept	1.869	1.303	2.439
	N _{AMAR}	-0.010	-0.021	0.000
	N _{AMBR}	-0.065	-0.093	-0.037
	Sand	-0.919	-1.535	-0.324
	Heat	0.031	0.001	0.064
	Sand:N _{AMBR}	1.869	1.303	2.439

Appendix C, Table C6. Substantially supported models (based on AIC_c model comparison) of log-response ratios for tiller length, leaf width, and total leaf area for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) using the factors *A. arenaria* (N_{AMAR}) or *A. breviligulata* (N_{AMBR}) initial tiller density, sand burial, and heat treatments.

Response	Fixed Predictors	df	L	AIC _c	Δ _i	W _i
Tiller Length						
AMAR	N _{AMAR} + N _{AMBR} + Heat + N _{AMBR} :Heat	9	611.5	-1204.8	0.0	0.195
	N _{AMAR} + N _{AMBR} + Heat	8	609.8	-1203.4	1.4	0.098
	N _{AMAR} + N _{AMBR} + Heat + N _{AMBR} :Heat	9	610.8	-1203.3	1.5	0.093
AMBR	N _{AMBR} + Sand	7	613.2	-1212.3	0.0	0.222
	N _{AMBR} + Sand + N _{AMAR} + Sand: N _{AMAR}	9	614.6	-1211.0	1.3	0.116
	N _{AMBR} + Sand + N _{AMBR} :Sand	8	613.3	-1210.5	1.7	0.093
Leaf Width						
AMAR	Sand + N _{AMAR} + Sand: N _{AMAR}	8	288.8	-561.5	0.0	0.346
	Sand	6	285.9	-559.7	1.8	0.139
	Heat + Sand + N _{AMAR} + Sand: N _{AMAR}	9	288.9	-559.5	2.0	0.127
AMBR	N _{AMBR} + Sand + Heat + N _{AMBR} :Heat	9	74.1	-130.0	0.0	0.242
	N _{AMBR} + Sand + N _{AMBR} :Sand	8	73.1	-130.0	0.1	0.235
	N _{AMBR} + Sand + Heat + N _{AMBR} :Heat + Sand:Heat	10	74.2	-128.2	1.8	0.097
Total. Leaf Area						
AMAR	Sand	6	-413.6	839.2	0.0	0.215
	Sand + N _{AMAR} + Sand:N _{AMAR}	8	-411.8	839.7	0.5	0.166
	Heat + Sand	7	-413.2	840.6	1.4	0.109
AMBR	N _{AMBR} + Sand + N _{AMBR} :Sand	8	-646.3	1308.8	0.0	0.184
	---	5	-649.7	1309.5	0.7	0.127
	N _{AMBR} + Sand	7	-647.9	1310.0	1.1	0.104

Appendix C, Table C7. Restricted maximum likelihood (REML) parameter estimates and 95% confident intervals for the best supported model (based on AIC_c model comparison) of log-response ratios for tiller length, leaf width, and total leaf area for *A. arenaria* (AMAR) and *A. breviligulata* (AMBR) using the factors *A. arenaria* (N_{AMAR}) or *A. breviligulata* (N_{AMBR}) initial tiller density, heat, and sand burial treatments.

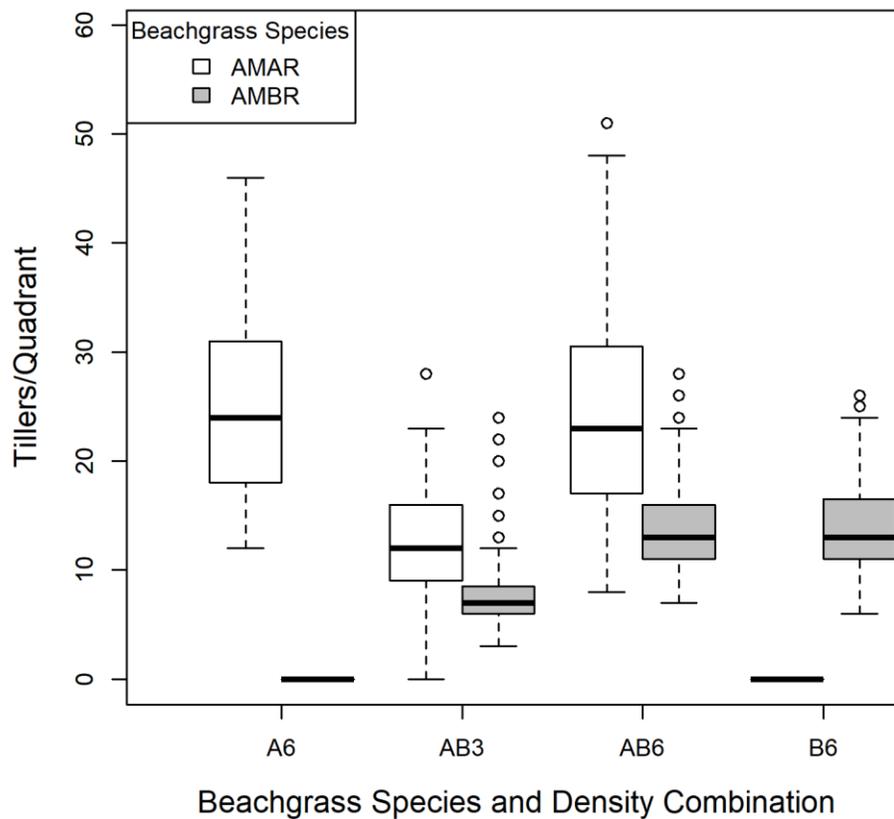
Response Variable		Fixed Predictor	REML Estimates	95% confidence interval	
Species	Lower			Upper	
Tiller Length					
AMAR	Intercept		4.320	4.264	4.377
	N _{AMAR}		0.002	0.000	0.003
	N _{AMBR}		0.002	0.000	0.004
	Heat		0.076	0.008	0.144
	N _{AMBR} :Heat		-0.002	-0.005	0.000
AMBR	Intercept		4.427	4.380	4.474
	N _{AMBR}		0.004	0.002	0.006
	Sand		-0.033	-0.059	-0.006
Leaf Width					
AMAR	Intercept		1.391	1.329	1.453
	Sand		0.204	0.118	0.289
	N _{AMAR}		0.002	-0.001	0.004
	Sand: N _{AMAR}		-0.004	-0.008	-0.001
AMBR	Intercept		2.005	1.914	2.098
	N _{AMBR}		-0.002	-0.006	0.002
	Sand		0.125	0.077	0.173
	Heat		-0.134	-0.258	-0.010
	N _{AMBR} :Heat		2.005	1.914	2.098
Total Leaf Area					
AMAR	Intercept		4.086	3.981	4.190
	Sand		0.131	0.036	0.225
AMBR	Intercept		4.891	4.615	5.169
	N _{AMBR}		-0.003	-0.016	0.010
	Sand		-0.156	-0.476	0.162
	N _{AMBR} :Sand		0.015	-0.002	0.032



Appendix C, Figure C1. Study experimental design of beachgrass species interaction experiment at Hatfield Marine Science Center, Newport, OR. Study design consisted of 8 whole plots (columns), 64 subplots (bags), and 256 sub-subplots (quadrants). Heat treatments (heat tape in red) were applied to whole plots, such that all bags within a single whole plot are connected via a single heat tape circuit. Sand additions (grey boxes) were applied to individual bags, and grass species combinations were applied within quadrants. Text inside quadrants indicates initial beachgrass planting combinations: A6 = 6 *Ammophila arenaria* plants; B6 = 6 *A. breviligulata* plants; AB3 = 3 *A. arenaria* and 3 *A. breviligulata* plants; and AB6 indicates 6 *A. arenaria* and 6 *A. breviligulata* plants. Photo by R. Biel.



Appendix C, Figure C2. Photographs depicting geotextile bag construction and experimental treatments. (Top-left) Geotextile bag subdivided into four quadrants using greenhouse film. (Top-right) Bags receiving high sand burial treatment with different combinations of *Ammophila* within each quadrant. (Bottom-left) Heat tape woven through wire mesh, just prior to sand addition. Heat tape and wire mesh were buried beneath 4 cm of sand. (Bottom-right) Photograph of heat and sand burial treatments. All heat treatments within a single whole plot (column of bags) are connected via a single electrical circuit of heat tape (black wire). Sand burial treatment levels are evident from the differing geotextile bag heights. Photo by R. Biel.



Appendix C, Figure C3. Initial *A. arenaria* (AMAR; white) and *A. breviligulata* (AMBR; gray) tiller densities per quadrant for each beachgrass plant density treatment combination. A6 = 6 *Ammophila arenaria* plants; B6 = 6 *A. breviligulata* plants; AB3 = 3 *A. arenaria* and 3 *A. breviligulata* plants; and AB6 indicates 6 *A. arenaria* and 6 *A. breviligulata* plants.

Appendix D. Chapter 5 supplemental figures and tables

Appendix D, Table D1. Site names, transect coordinates, and beachgrass removal status for Oregon and Washington, USA, coast dunes.

HRA	HRA Name	Site Name	Treatment	UTM Easting	UTM Northing	Longitude	Latitude
1	Leadbetter Point	LBP01†	Beachgrass Removal	418032.2	5166110.4	-124.0711	46.6435
1	Leadbetter Point	LBP02†	Beachgrass Removal	418011.6	5165452.9	-124.0712	46.6376
1	Leadbetter Point	LBP03†	Beachgrass Removal	417995.7	5164924.2	-124.0713	46.6329
1	Leadbetter Point	LBP04†	Beachgrass Removal	418021.8	5164413.0	-124.0709	46.6283
1	Leadbetter Point	LBP06†	Beachgrass Removal	418044.8	5163832.0	-124.0705	46.6230
1	Leadbetter Point	LBP05†	Beachgrass Removal	418059.9	5163505.5	-124.0702	46.6201
1	Leadbetter Point	LBP07†	Reference	418113.1	5162740.4	-124.0694	46.6132
1	Leadbetter Point	LBP08†	Reference	418160.0	5162235.5	-124.0687	46.6087
1	Leadbetter Point	LB08	Reference	418175.5	5161949.4	-124.0685	46.6061
1	Leadbetter Point	LB11	Reference	418226.5	5161369.1	-124.0677	46.6009
1	Leadbetter Point	LB1020	Reference	418579.9	5156020.8	-124.0621	46.5528
1	Leadbetter Point	LB06	Reference	418644.2	5154363.7	-124.0610	46.5379
2	Dunes Overlook North	DONR05†	Reference	406647.3	4855623.7	-124.1614	43.8478
2	Dunes Overlook North	DONR06†	Reference	406630.8	4855441.1	-124.1616	43.8462
2	Dunes Overlook North	DOR03†	Beachgrass Removal	406582.2	4855113.2	-124.1621	43.8432
2	Dunes Overlook North	DOR02†	Beachgrass Removal	406553.7	4854888.1	-124.1624	43.8412
2	Dunes Overlook North	DOR01†	Beachgrass Removal	406532.5	4854724.1	-124.1627	43.8397
2	Dunes Overlook North	DONR04†	Reference	406460.9	4854294.5	-124.1635	43.8358
3	Dunes Overlook South	DO01	Reference	406451.3	4854250.9	-124.1636	43.8354
3	Dunes Overlook South	DOR04†	Beachgrass Removal	406423.6	4853998.3	-124.1639	43.8331
3	Dunes Overlook South	DOR05†	Beachgrass Removal	406384.4	4853745.1	-124.1643	43.8309
3	Dunes Overlook South	DOR06†	Beachgrass Removal	406349.3	4853455.9	-124.1647	43.8282
3	Dunes Overlook South	DO02	Reference	406276.3	4853100.5	-124.1656	43.8250

Appendix D, Table D1 (Continued)

HRA	HRA Name	Site Name	Treatment	UTM Easting	UTM Northing	Longitude	Latitude
3	Dunes Overlook South	DO03	Reference	406203.0	4852676.6	-124.1664	43.8212
4	Tahkenitch Creek	TKNR06†	Reference	406096.5	4852007.8	-124.1676	43.8152
4	Tahkenitch Creek	TKNR05†	Reference	406014.0	4851490.3	-124.1686	43.8105
4	Tahkenitch Creek	TKNR04†	Reference	405948.9	4851069.8	-124.1693	43.8067
4	Tahkenitch Creek	TKR03†	Beachgrass Removal	405937.7	4850892.8	-124.1694	43.8051
4	Tahkenitch Creek	TKR02†	Beachgrass Removal	405892.4	4850559.1	-124.1699	43.8021
4	Tahkenitch Creek	TKR01†	Beachgrass Removal	405827.2	4850135.2	-124.1706	43.7983
5	Ten-Mile Creek	UD02	Reference	401392.9	4827840.8	-124.2217	43.5970
5	Ten-Mile Creek	UD01	Reference	401303.6	4827481.1	-124.2227	43.5938
5	Ten-Mile Creek	TMNR04†	Reference	401029.6	4826223.7	-124.2259	43.5824
5	Ten-Mile Creek	TMR03†	Beachgrass Removal	400844.8	4825390.7	-124.2280	43.5749
5	Ten-Mile Creek	TMR02†	Beachgrass Removal	400828.6	4825237.4	-124.2282	43.5735
5	Ten-Mile Creek	TMR01†	Beachgrass Removal	400818.2	4825172.5	-124.2283	43.5729
6	Bandon SPMA	BANR01†	Beachgrass Removal	382952.7	4769370.4	-124.4376	43.0680
6	Bandon SPMA	BANNR04	Reference	382932.0	4769279.0	-124.4378	43.0672
6	Bandon SPMA	BANR02	Beachgrass Removal	382907.2	4769169.9	-124.4381	43.0662
6	Bandon SPMA	BANNR03†	Reference	382875.3	4768998.5	-124.4385	43.0647
6	Bandon SPMA	BANR03	Beachgrass Removal	382823.4	4768745.3	-124.4390	43.0624
6	Bandon SPMA	BANNR05	Reference	382809.5	4768650.7	-124.4392	43.0615
6	Bandon SPMA	BANNR06	Reference	382781.0	4768528.7	-124.4395	43.0604
6	Bandon SPMA	BANNR07	Reference	382755.9	4768416.0	-124.4398	43.0594
6	Bandon SPMA	BANNR02†	Reference	382733.0	4768308.2	-124.4401	43.0584
6	Bandon SPMA	BANR07	Beachgrass Removal	382701.1	4768180.0	-124.4404	43.0573
6	Bandon SPMA	BANNR08	Reference	382682.2	4768054.5	-124.4406	43.0561
6	Bandon SPMA	BANR06†	Beachgrass Removal	382661.2	4767914.9	-124.4409	43.0549
6	Bandon SPMA	BANR05†	Beachgrass Removal	382650.8	4767802.8	-124.4410	43.0539
6	Bandon SPMA	BANR04†	Beachgrass Removal	382639.4	4767708.5	-124.4411	43.0530

Appendix D, Table D1 (Continued)

HRA	HRA Name	Site Name	Treatment	UTM Easting	UTM Northing	Longitude	Latitude
7	Elk River	MCKNR01†	Beachgrass Removal	374836.5	4740198.9	-124.5307	42.8041
7	Elk River	MCKNR02†	Beachgrass Removal	374977.3	4739801.2	-124.5289	42.8006
7	Elk River	MCKNR04	Reference	375030.7	4739616.8	-124.5282	42.7989
7	Elk River	MCKNR05	Reference	375043.7	4739594.4	-124.5281	42.7987
7	Elk River	MCKNR03A	Beachgrass Removal	375045.8	4739532.6	-124.5280	42.7982
7	Elk River	MCKR01†	Beachgrass Removal	375135.0	4739292.8	-124.5269	42.7960
7	Elk River	MCKR02†	Beachgrass Removal	375213.8	4739005.9	-124.5258	42.7934
7	Elk River	MCKR03†	Beachgrass Removal	375318.6	4738510.8	-124.5245	42.7890

† Site established by Zarnetske et al. (2010)

Appendix D, Table D2. Beachgrass removal management actions performed at each HRA (see Table S1) between Winter 2006 and Winter 2013. H=Herbicide; HP = Hand-pull; B = Bulldoze; D = Disc; P = Plowed; R = Rototill; M = Unspecified mechanical maintenance; -- = No action; NA = No Information (Lauten et al. 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, Pearson et al. 2007, 2008, 2008, 2009a, 2009b, 2010, 2012, 2013).

	Leadbetter Point	Dunes Overlook North	Dunes Overlook South	Tahkenitch Creek	Ten-Mile Creek	Bandon SPMA	Elk River
2013	H, B, D	M	M	M	M	H, B	NA
2012	R, H	H, HP	H	H, HP	HP	--	B
2011	B, H	D	B	B	B	B	NA
2010	B, H	B	B	B	B	--	NA
2009	M, D, H	HP, B	B	B	B	P	NA
2008	M, H	B	B	B	M	M	B
2007	M	B	B	--	D	B	B
2006	H, HP, B, D	--	--	--	D	B, D	B

Appendix D, Table D3. Plant species classification as endemic foredune species, exotic foredune species, native backdune plant, and exotic backdune at the HRA study sites (see Table S1).

Species	Abbreviation	Habitat	Status
<i>Elymus mollis</i>	ELMO	Beach and Foredune	Endemic
<i>Abronia latifolia</i>	ABLA	Beach and Foredune	Endemic
<i>Abronia umbellata ssp. breviflora</i>	ABUM	Beach and Foredune	Endemic
<i>Ambrosia chamissonis</i>	AMCH	Beach and Foredune	Endemic
<i>Calystegia soldanella</i>	CASO	Beach and Foredune	Endemic
<i>Ammophila arenaria</i>	AMAR	Beach and Foredune	Exotic
<i>Ammophila breviligulata</i>	AMBR	Beach and Foredune	Exotic
<i>Cakile edentula</i>	CAED	Beach and Foredune	Exotic
<i>Cakile maritima</i>	CAMA	Beach and Foredune	Exotic
<i>Achillea millefolium</i>	ACMI	Backdune	Native
<i>Anaphalis margaritacea</i>	ANMA	Backdune	Native
<i>Arctostaphylos uva-ursi</i>	ARUV	Backdune	Native
<i>Aster subspicatus</i>	ASSU	Backdune	Native
<i>Equisetum arvense</i>	EQAR	Backdune	Native
<i>Fragaria chiloensis</i>	FRCH	Backdune	Native
<i>Galium aparine</i>	GAAP	Backdune	Native
<i>Gaultheria shallon</i>	GASH	Backdune	Native
<i>Gnaphalium purpureum</i>	GNPU	Backdune	Native
<i>Lathyrus japonicus</i>	LAJA	Backdune	Native
<i>Lathyrus littoralis</i>	LALI	Backdune	Native
<i>Lupinus littoralis</i>	LULI	Backdune	Native
<i>Pinus contorta</i>	PICO	Backdune	Native
<i>Rumex occidentalis</i>	RUOC	Backdune	Native
<i>Solidago simplex</i>	SOSI	Backdune	Native
<i>Tanacetum bipinnatum</i>	TABI	Backdune	Native
<i>Vaccinium ovatum</i>	VAOV	Backdune	Native
<i>Aira caryophylla</i>	AICA	Backdune	Exotic
<i>Aira praecox</i>	AIPR	Backdune	Exotic
<i>Cytisus scoparius</i>	CYSC	Backdune	Exotic
<i>Erechtites minima</i>	ERMI	Backdune	Exotic
<i>Hypochaeris radicata</i>	HYRA	Backdune	Exotic
<i>Rumex acetosella</i>	RUAC	Backdune	Exotic
<i>Senecio sylvaticus</i>	SESY	Backdune	Exotic
<i>Sonchus asper</i>	SOAS	Backdune	Exotic
<i>Ulex europaeus</i>	ULEU	Backdune	Exotic

Appendix D, Table D4. Linear mixed model test statistics for comparison of nearshore slope, foreshore slope, backshore slope, log(foedune toe elevation), and foedune crest elevation among the seven HRA-sites (Fig. 1, Table S1). For nearshore, foreshore, and backshore slope, HRA-site were used as fixed effects. For log(foedune toe elevation) and foedune crest elevation, fixed effects were HRA-site and beachgrass treatment nested within HRA-site. (**bold**: significant at $p < 0.05$).

Response Variable	Predictor	df	F	p
Nearshore Slope	HRA	6, 51	914.2	< 0.0001
Foreshore Slope	HRA	6, 51	44.7	< 0.0001
Backshore Slope	HRA	6, 51	34.1	< 0.0001
Foredune Toe Elevation (m)	HRA	6, 44	11.8	< 0.0001
	HRA x Beachgrass Removal	7, 44	11.0	< 0.0001
Foredune Crest Elevation (m)	HRA	6, 44	1.4	0.23
	HRA x Beachgrass Removal	7, 44	15.0	< 0.0001

Appendix D, Table D5. Post-hoc pairwise comparisons of nearshore and beach morphometrics among HRA-sites (Appendix D, Table D4). Groupings indicate significant differences among HRA-sites, after correcting for multiple comparisons using a Bonferroni correction.

HRA-Site	Post-Hoc Groupings		
	Nearshore Slope	Foreshore Slope	Backshore Slope
Leadbetter Point	1	1	1
Dunes Overlook North	2	2 3	1 2
Dunes Overlook South	2	2 4	3
Tahkenitch Creek	3	2 3	1 2
Ten-Mile Creek	4	2	2 3
Bandon SPMA	5	4	2
Elk River	6	3 4	4

Appendix D, Table D6. Post-hoc pairwise comparisons for differences in foredune morphometrics within each HRA site (Appendix D, Table D4). P-value indicates significant differences between removal and reference locations within each HRA-site, after correcting for multiple comparisons using a Bonferroni correction

HRA-Site	Log Foredune Toe Elevation [log(m)]			Foredune Crest Elevation (m)		
	(Removal – Reference) ± SE	t-value	p-value	(Removal – Reference) ± SE	t-value	p-value
Leadbetter Point	- 0.06 ± 0.06	t ₄₄ = -0.97	0.34	- 1.35 ± 0.48	t ₄₄ = - 2.80	0.0075
Dunes Overlook North	- 0.02 ± 0.15	t ₄₄ = -0.16	0.87	- 1.48 ± 0.68	t ₄₄ = - 2.17	0.036
Dunes Overlook South	- 0.26 ± 0.15	t ₄₄ = -1.81	0.08	- 1.69 ± 0.68	t ₄₄ = - 2.47	0.017
Tahkenitch Creek	- 0.72 ± 0.15	t ₄₄ = -4.91	< 0.0001	- 3.50 ± 0.68	t ₄₄ = - 5.12	< 0.0001
Ten-Mile Creek	- 0.36 ± 0.17	t ₄₄ = -2.16	0.037	- 3.34 ± 0.68	t ₄₄ = - 4.89	< 0.0001
Bandon SPMA	- 0.51 ± 0.09	t ₄₄ = -5.45	< 0.0001	- 0.13 ± 0.45	t ₄₄ = - 0.28	0.78
Elk River	- 0.49 ± 0.13	t ₄₄ = -3.78	0.0005	- 4.08 ± 0.68	t ₄₄ = - 6.03	< 0.0001

Appendix D, Table D7. Bayesian hypothesis testing of the effects of beachgrass removal on the dune plant community. Hypotheses are structured to reflect management goals. Higher probabilities indicate a higher chance that restoration improved management targets. Bolded probabilities indicate a high degree of support for the hypothesis ($\alpha = 0.05$).

Species	One Sided Hypotheses	HRA Site						
<i>Ammophila</i> spp.	Prob [pct. cover _{rmvl} < pct. cover _{ref}]	0.999	0.988	0.999	1.000	0.999	0.775	1.000
<i>Elymus mollis</i>	Prob [pct. cover _{rmvl} > pct. cover _{ref}]	0.949	1.000	0.983	1.000	0.161	0.407	0.684
<i>Abronia umbellata</i>	Prob [odds of incidence _{rmvl} > odds of incidence _{ref}]	0.990	0.995	0.994	0.352	0.335	0.874	0.085 [†]
<i>Abronia latifolia</i>	Prob [odds of incidence _{rmvl} > odds of incidence _{ref}]	0.092	0.925	0.338	0.730	0.742	0.822	0.037
<i>Ambrosia chamissonis</i>	Prob [odds of incidence _{rmvl} > odds of incidence _{ref}]	0.241	0.332	0.332	0.345	0.317	0.377	0.084
<i>Calystegia soldanella</i>	Prob [odds of incidence _{rmvl} > odds of incidence _{ref}]	0.372	0.321	0.337	0.335	0.344	0.324	0.280

[†] *A. Umbellata* seeds germinated in a control area near the banks of Elk River. As a result, it was present in both removal and control transects. *A. Umbellata* was not observed in control areas at any other HRA sites.

Appendix E. Demand for coastal dune ecosystem services.

Although this study examined ecosystem service (ES) supply, determination of ES demand is also important for efficient allocation of resources. For western snowy plover conservation, the plover is federally listed as threatened, with recovery priority 3C, indicating that plovers have high threat level, a high potential for recovery, and are therefore a high priority for restoration at an estimated cost in excess of \$150 million USD (USFWS 2007). For endemic plant conservation, pink sand verbena (*Abronia umbellata* var. *breviflora*) is federally listed as a species of concern by the US Fish and Wildlife Service, is considered endangered by the states of Oregon and Washington, and is also a target of conservation efforts (Giles-Johnson and Kaye 2014).

Although most Pacific Northwest HRAs are located on secluded federal, state, or private lands, some HRAs still utilize coastal protection and sand stabilization services from invasive beachgrasses. Numerous historical and proposed western snowy plover critical habitat areas are located on barrier spits that protect inland harbors, estuaries, and wetlands from wave attack (USFWS 2007, 2012). However, beachgrass removal may compromise barrier spit stability and exacerbating erosion and overwash (BLM 2006). Consequently, some HRAs maintain foredunes with *Ammophila* spp. to protect essential infrastructure (e.g., Coos Bay North Spit HRA (USACE 2016)). Beachgrasses may also facilitate other sought-after ESs within coastal dunes and adjacent wetlands and forests. Foredunes have facilitated the formation or expansion of coastal wetlands and forests (Wiedemann and Pickart 2008) that provide wildlife habitat, water filtration, and carbon fixation. For example, at the New River plover HRA, beachgrass removal increased plovers nesting, but also remobilized sand, causing foredune shortening, infilling of New River, and eutrophication (BLM 2008). This degradation in water quality threatened critical fish habitat for Oregon Coast Coho salmon (federal threatened) and Oregon Coast steelhead (sensitive). In response, HRA managers reconstructed and revegetated the foredune with European beachgrass to protect riverine habitat, but also maintained suboptimal plover nesting habitat in the backdune portion of New River spit (BLM 2008). Although beachgrass are non-native to the Pacific Northwest, they sometimes

provide necessary coastal protection and sand stabilization services at HRAs to support both human infrastructure and ESs in adjacent systems.

