AN ABSTRACT OF THE DISSERTATION OF

Phoebe Lehmann Zarnetske for the degree of Doctor of Philosophy in Zoology presented on September 9, 2011.

Title: The Influence of Biophysical Feedbacks and Species Interactions on Grass Invasions and Coastal Dune Morphology in the Pacific Northwest, USA

Abstract approved:

Sally D. Hacker Eric W. Seabloom

Biological invasions provide a unique opportunity to study the mechanisms that regulate community composition and ecosystem function. Invasive species that are also ecosystem engineers can substantially alter physical features in an environment, and this can lead to cascading effects on the biological community. Aquatic-terrestrial interface ecosystems are excellent systems to study the interactions among invasive ecosystem engineers, physical features, and biological communities, because interactions among vegetation, sediment, and fluids within biophysical feedbacks create and modify distinct physical features. Further, these systems provide important ecosystem services including coastal protection afforded by their natural features. In this dissertation, I investigate the interactions and feedbacks among sand-binding beach grass species (a native, *Elymus mollis* (Trin.), and two non-natives, *Ammophila arenaria* (L.) Link and *A. breviligulata* Fernald), sediment supply, and dune shape along the U.S. Pacific Northwest coast. Dunes dominated by *A. arenaria* tend to be taller and narrower compared to the shorter, wider dunes dominated by *A. breviligulata*. These patterns suggest an ecological control on dune shape, and thus, coastal vulnerability to overtopping waves. I investigate the causes and consequences of these patterns with experiments, field observations, and modeling. Specifically, I investigate the relative roles of vegetation and sediment supply in shaping coastal dunes over inter-annual and multi-decadal time scales (Chapter 2), characterize a

biophysical feedback between beach grass species growth habit and sediment supply (Chapter 3), uncover the mechanisms leading to beach grass coexistence and whether *A. breviligulata* can invade and dominate new sections of coastline (Chapter 4), and examine the non-target effects resulting from management actions that remove *Ammophila* for the recovery of the threatened Western Snowy plover (*Charadrius alexandrinus nivosus*) (Chapter 5).

I found that vegetation and sediment supply play important roles in dune shape changes across inter-annual and multi-decadal time scales (Chapter 2). I determined that a biophysical feedback between the beach grass growth habits and sediment supply results in species-specific differences in sand capture ability, and thus, is a likely explanation for differences in dune shape (Chapter 3). I found that all three beach grass species can coexist across different sediment deposition rates, and that this coexistence is largely mediated by positive direct and indirect species interactions. I further determined that *A. breviligulata* is capable of invading and dominating the beach grass community in regions where it is currently absent (Chapter 4). Combined, these findings indicate that *A. breviligulata* is an inferior dune building species as compared to *A. arenaria*, and suggest that in combination with sediment supply gradients, these species differences ultimately lead to differences in dune shape. Potential further invasions of *A. breviligulata* into southern regions of the Pacific Northwest may diminish the coastal protection ability of dunes currently dominated by *A. arenaria*, but this effect could be moderated by the predicted near co-dominance of *A. arenaria* in these lower sediment supply conditions. Finally, I found that the techniques used to remove *Ammophila* for plover recovery have unintended consequences for the native and endemic dune plant communities, and disrupt the natural disturbance regime of shifting sand. A whole-ecosystem restoration focus would be an improvement over the target-species approach, as it would promote the return of the natural disturbance regime, which in turn, would help recover the native biological community. The findings from this dissertation research provide a robust knowledge base that can guide further investigations of biological and physical

changes to the coastal dunes, can help improve the management of dune ecosystem services and the restoration of native communities, and can help anticipate the impacts of future beach grass invasions and climate change induced changes to the coast.

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The Influence of Biophysical Feedbacks and Species Interactions on Grass Invasions and Coastal Dune Morphology in the Pacific Northwest, USA

by
Phoebe Lehmann Zarnetske

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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.

Phoebe Lehmann Zarnetske, Author

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CONTRIBUTION OF AUTHORS

Chapter 2: Dr. Peter Ruggiero provided critical assistance with the concept of this chapter, input on the writing, and generating the sediment rates data. Jeremy Mull developed geomorphic data extraction methods, and generated much of that data.

Chapter 3: Dr. Peter Ruggiero provided critical methodological insight on the experiments, and input on the writing. Dr. Timothy Maddux and Jason Killian both provided key insight on the methodology and design of the wind tunnel experiment, as well as input on the writing. Jason Killian designed the wind tunnel. Dr. Daniel Cox provided insight on the wind tunnel experiment and input on the writing.

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

Page

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF APPENDICES

LIST OF APPENDIX TABLES

LIST OF APPENDIX FIGURES

DEDICATION

This dissertation is dedicated to my parents, Scott and Becky Lehmann.

The Influence of Biophysical Feedbacks and Species Interactions on Grass Invasions and Coastal Dune Morphology in the Pacific Northwest, USA

1 – General Introduction

Biological invasions often change the community composition and the abiotic template of an ecosystem over relatively short time scales. For this reason, invasions provide a unique opportunity to investigate how systems respond to changing biological and physical conditions. By uncovering the mechanisms behind these changes, we can develop more robust predictions concerning how biological communities and their environment will respond to perturbations. In turn, this greater understanding contributes to the fields of community and restoration ecology, but also to the growing fields of ecosystem services and ecological impacts from climate change. In particular, invasions provide insights into the mechanisms influencing species coexistence (Shea and Chesson 2002), the ways in which species modify habitats and natural disturbance regimes (Cuddington and Hastings 2004, Hastings et al. 2007), and how we can improve restoration and conservation of ecological communities given the legacy effects of invaders (Hacker and Dethier 2006, Zarnetske et al. 2010).

Species that modify the physical environment have large impacts on the biological community and disturbance regime (Jones et al. 1994, Jones et al. 2010). When these species are non-native and "engineer" their environment, their influence can be substantial (Cuddington and Hastings 2004). Ecosystems at the aquatic-terrestrial interface such as coastal dunes, mangrove forests, and salt marshes, are ideal systems to study how both native and non-native ecosystem engineers modify the biological and physical components within an ecosystem. In these systems, interactions among vegetation, sediment, and fluids within biophysical feedbacks create distinct physical features that are constantly modified by their interacting components (Murray et al. 2008b, Barbier et al. 2011). These environments also provide important ecosystem services including coastal protection from large storm waves and tsunamis (Sallenger 2000, Liu et al. 2005, Barbier et al. 2011). The ecosystem services provided by these natural coastal barriers are becoming

increasingly important (Barbier et al. 2008, Barbier et al. 2011) to the over one-third of the world's population living in coastal areas (Millennium Ecosystem Assessment 2005, UN Environment Programme 2006), especially given increasing wave heights (Ruggiero et al. 2010, Young et al. 2011) and climate change predictions of sea level rise and intensified storms (Bindoff 2007).

Here I investigate how two non-native beach grass species (*Ammophila arenaria* and *A. breviligulata*) and a native beach grass species (*Elymus mollis*) modify the biological community and physical features of the coastal dune ecosystem in the Pacific Northwest of the United States. Prior to the introductions of *A. arenaria* and *A. breviligulata* for sand stabilization, the coastal dunes of the Pacific Northwest were largely shaped by wind owing to their sparse endemic vegetation (Cooper 1958). The *Ammophila* introductions and subsequent invasions led to densely vegetated and large continuous foredune ridges (Cooper 1958, Seabloom and Wiedemann 1994, Wiedemann and Pickart 1996) that provide superior coastal protection from wave overtopping (Sallenger 2000). However, the invasions also led to declines in native species, including the Western Snowy plover (*Charadrius alexandrinus nivosus*) which was placed on the Endangered Species List (USFWS 2007).

Much of this dissertation research was prompted by historical and current observations about the distributions of dominant beach grass species and dune shapes along the Pacific Northwest coast. Specifically, coastal dunes dominated by *A. arenaria* are generally taller and narrower as compared to the shorter and wider dunes dominated by *A. breviligulata* (Seabloom and Wiedemann 1994, Hacker et al. 2011). These observations suggest a beach grass species-specific control on foredune shape. However, a spatial gradient in sediment supply rates to the beaches and dunes correlates with the current day distributions of these two species, and thus also the foredune shape (Hacker et al. 2011, Ruggiero et al. 2011). The northern portions of the study area receive more sediment supply where *A. breviligulata* dominates and where dunes are lower and wider, while the southern portions of the study area receive less

sediment supply where *A. arenaria* dominates and where dunes are taller and narrower. Thus, it is important to determine the underlying mechanisms controlling dune shape, including the relative contributions of biological and physical factors.

In Chapter 2, I investigate whether the changes in foredune shape across multi-decadal and inter-annual time scales are due to changes in biological or physical variables, or a combination of the two. I used regression models to determine whether the change in vegetation or sediment supply rates explained more of the variation in foredune shape change within the Columbia River Littoral Cell (Fig. 2.1). The change in vegetation was more important for the increase in dune width at multi-decadal scales, while sediment supply rates associated with more of the small increase in dune crest elevation across multi-decadal and inter-annual time scales. However, within a narrow range of sediment supply, vegetation associated with more of the dune crest and width change. Overall, most models contained a combination of biological and physical variables that were sometimes interactive, suggesting that vegetation and sediment are highly coupled within a biophysical feedback. This feedback is explored and described in Chapter 3.

In Chapter 3, I uncover the biophysical mechanisms responsible for differences in foredune shape along the Pacific Northwest coast. I conducted two experiments that either controlled for sediment supply or for vegetation. A wind tunnel experiment controlled for sediment supply and investigated how sand capture ability differs across the three beach grass species and different tiller densities. Each species had higher sand capture efficiency as tiller density increased, and at natural field densities, the sand capture efficiency of *A. arenaria* was higher than *A. breviligulata*, which was higher than *E. mollis*. A mesocosm experiment controlled for beach grass species composition, and investigated how different sand deposition rates influence the growth of the three species in mixtures or monocultures. Sand deposition promoted different growth habits among beach grass species such that *A. arenaria* produced dense vertical growth while *A. breviligulata* and *E. mollis* produced horizontal spreading

growth. Combined, these experiments provide evidence for a species-specific control on dune shape that is mediated by sand supply rates. Specifically, the biophysical feedback between sediment supply and species-specific growth habit results in shorter, wider dunes where *A. breviligulata* is dominant, and taller, narrower dunes where *A. arenaria* is dominant.

Today, *A. breviligulata* remains largely absent from foredunes receiving lower sediment supply rates (in the southern Oregon coast where *A. arenaria* is dominant) but it has been unclear whether this is a consequence of dispersal limitation, species interactions, physiological tolerance of sand supply, or some combination of these factors (Hacker et al. 2011). In Chapter 4, I investigate the long term equilibrium abundances of each beach grass species across a sand supply gradient with 3-species Lotka-Volterra models parameterized with the short term mesocosm experiment and long term field abundances. With this model, I investigated whether the patterns in beach grass species distributions equate to species coexistence, whether sand supply rate mediates coexistence, and which species interaction mechanisms lead to coexistence. I found that across all sand supply rates, two communities are possible – all three species can coexist or the two invaders can exclude the native. Under all scenarios, *A. breviligulata* is consistently the dominant species. Therefore, following initial establishment, *A. breviligulata* can invade and dominate the foredune communities in the more southern, lower sediment supply regions. I found that positive direct and indirect interactions among species were largely responsible for coexistence, and that the strength of facilitation and indirect effects increased with sand supply rate. Therefore, the environmental context of sand supply rate is responsible for mediating the interactions that ultimately lead to coexistence.

In Chapter 5, I investigate the non-target effects of invasive species management when various methods of *Ammophila* removal are employed to promote the recovery of a single species. The *Ammophila* invasions throughout the Pacific Northwest reduced the bare ground required for the nesting of the federally threatened

Western Snowy plover (*Charadrius alexandrinus nivosus*) (USFWS 2007). Restoring the plover requires *Ammophila* removal, but I found that most of the removal methods result in unintended negative effects on the native and endemic dune plant community within the removal areas (i.e., reducing diversity). My research suggests that lower intensity hand pulling and targeted herbicide are preferable *Ammophila* removal techniques because they allow the recovery of endemic plant communities and the natural disturbance regime of shifting sand. These methods are preferable to the more common, frequent, and intensive mechanical techniques that negatively impact the endemic ecosystem natural disturbance regime. Further, these lower intensity methods will allow the foredune shape to remain more intact, thus preserving its coastal protection capability where wave overwash is a concern. Management plans typically target individual threatened species for recovery or individual invasive species for removal. This case study serves as an important example to promote whole-ecosystem restoration rather than targeted-species management.

My dissertation research integrates pattern and process investigations and thus provides a robust knowledge base from which to better predict responses of the coastal dune ecosystem to biological and physical changes. Among these changes are potential further invasions by *A. breviligulata*, continued species-specific modifications to dune shape, increasing coastal vulnerability from higher wave heights and sea level, and finally, new or expanded restoration and conservation areas. With this knowledge base, scientists and managers may better anticipate how these changes will impact coastal dune ecological communities and ecosystem services, and thus, will be in a better position to inform policy and management.

2 – Coastal foredune evolution: evidence for biotic control

Phoebe L. Zarnetske, Peter Ruggiero, Eric W. Seabloom, Sally D. Hacker

ABSTRACT

Interactions and feedbacks among biotic and abiotic factors (biophysical feedbacks) create and modify physical features and biological communities within an environment. It is often difficult to tease apart the relative roles of biotic and abiotic factors in modifying a system, especially because these factors often change simultaneously. However, understanding their relative roles is necessary to make predictions about how an environment changes. Across 21 years (1988-2009) and 100 kilometers of coastline, we investigate the relative contributions of biological and physical processes in shaping coastal foredunes along the Columbia River Littoral Cell (CRLC) in the U.S. Pacific Northwest (PNW). This system is particularly well suited to investigate this interplay because it contains significant gradients in the physical forces (e.g., sediment supply) and biological forces (e.g., grass species and densities) that dominate foredune evolution. Here we use a correlative modeling approach to assess the relative contributions of biological versus physical variables associated with foredune shape change across inter-annual to multi-decadal scales. We then use insight gained from fine scale, short term mechanistic experiments to explore the underlying causes of changes in foredune shape, and to determine when and how biological and physical variables influence this change. At the multi-decadal time scales, we found evidence in support of biological variables strongly influencing foredune width change across the region, and influencing foredune crest change more strongly than physical variables in regions with sediment supply rates of ± 2m/yr. Physical variables associated more strongly with the changes in foredune shape across inter-annual scales. These results demonstrate that vegetation and sediment interact over multiple time scales to influence foredune shape. Foredune shape significantly impacts coastal vulnerability to wave overwash and inundation, thus this assessment is pertinent to coastal management and dune restoration considerations especially in light of documented increases in storm-induced wave heights and predictions of climate change induced sea level rise.

2.1 INTRODUCTION

Biological and physical factors interact across a range of temporal and spatial scales to shape distinct landscape features such as marshes, rivers, and coastal dunes (Fisher et al. 2007, Murray et al. 2008, Gutierrez et al. 2011). Such features result from a few dominant interacting ingredients – fluid media, sediment, and vegetation – and often arise at the interface between aquatic and terrestrial environments. The relative contribution from biological and physical factors in shaping landscape features can change as the vegetation or the type or supply of sediment changes (Murray et al. 2008). Further, the relative influence of the factors may vary across spatial and temporal scales (Levin 1992). Therefore, investigating changes across scales (Turner 1989, Wiens 1989, Levin 1992) is necessary to more fully understand how the processes of interacting vegetation and sediment influence different landscape patterns. Assigning the relative contributions of biological and physical factors across broad spatial and temporal scales can be achieved through investigating broad patterns with a correlative approach. However, to more fully understand these broad patterns, it is necessary to connect them with their underlying biological and physical processes – e.g., with insight gained from mechanistic experiments, long term datasets, and models. We can gain further understanding about the role of biological and physical factors in shaping landscape features by integrating experiments and observational data across the fields of ecology and geomorphology (Murray et al. 2008). Employing this interdisciplinary approach will deepen understanding in both fields, but also will provide a more complete framework for guiding decisions concerning ecosystem services, resource management, and conservation in these interface environments.

Here we investigate the relative influence of biological and physical forces in shaping coastal foredunes along the U.S. Pacific Northwest (PNW) coast. This system is particularly well suited for this investigation as it contains spatial gradients in foredune shape, sediment supply rates, and dominant vegetation variables (Seabloom and Wiedemann 1994, Ruggiero et al. 2005, Hacker et al. 2011, Zarnetske et al. in

review). Further, these variables have been measured at seasonal to multi-decadal time scales across a large section of this region, the Columbia River Littoral Cell (CRLC) (Fig. 2.1), beginning in 1988 (Seabloom and Wiedemann 1994, Ruggiero et al. 2005, Hacker et al. 2011, Mull 2011). Oceanographic and climatic forces in the PNW produce strong winds and an intense wave climate that move large amounts of sediment on and offshore (Allan and Komar 2006, Ruggiero et al. 2010). Therefore, sediment supply potentially has more control over changes in foredune shape as compared to biological forces on this coastline.

Over the last century, two non-native ecosystem engineering grasses – *Ammophila arenaria*, and *A. breviligulata* – were introduced to stabilize sand near developed coastal areas in the late 1800's (*A. arenaria*) and 1935 (*A. breviligulata*). The introductions led to subsequent invasions across the entire dune-backed beach system, changing the system from a mobile sand environment with patchy native vegetation (including the native grass, *Elymus mollis*) to large, vegetated and stabilized foredune ridges aligned parallel to the shoreline (Cooper 1958, Wiedemann and Pickart 1996) – in turn, this led to a cascade of biological effects on native species, but also improved coastal protection for coastal communities (Wiedemann and Pickart 1996, Zarnetske et al. 2010, Hacker et al. 2011).

The beach grass species have been, and continue to be the dominant biological influence in the foredune system. Across the PNW, dune shape varies by dominant *Ammophila* species – those dominated by *A. arenaria* tend to be taller and narrower while those dominated by *A. breviligulata* tend to be lower and wider (Seabloom and Wiedemann 1994, Hacker et al. 2011). In the last several decades, *A. breviligulata* continued to spread and overtake *A. arenaria* as the dominant foredune grass in the northern section of the PNW – coincident with this invasion, we documented a decline in the foredune crest height of some foredunes in the CRLC from 1988 to 2006 (Hacker et al. 2011). With wind tunnel and mesocosm experiments, we determined that the grasses differ in their ability to capture sand through differences in growth

habit and density (where *A. arenaria* > *A. breviligulata* > *E. mollis* for sand capture efficiency), and that a biophysical feedback involving sediment supply and species-specific growth response is a likely explanation for differences in dune shape (Zarnetske et al. in review).

Although these findings from fine scale and short term studies suggest that biological factors potentially play a large role in shaping, and perhaps changing, foredune morphology, we have yet to determine the relative influence of biological versus physical forces over different time scales across the region. For instance, the biological signature may not be as strong over multi-decadal and inter-annual time scales, given that coastal dune evolution in the CRLC, PNW, and around the globe is strongly influenced by physical forces – especially the supply of ocean-derived sediment via aeolian transport (Hesp 1989, Psuty 1992). Additionally, spatial gradients in sand supply may interact with the vegetation to mediate their effects such that regions with lower sand supply rates may experience more influence from biological factors. Here we investigate whether inter-annual and multi-decadal changes in foredune shape are due in large part to gradients of biological or physical variables, or some combination of the two. We investigate support for the following hypotheses concerning changes in foredune shape: H_1: Physical variables will associate with the change in foredune shape across both time scales, and H_2: Biological variables will more strongly associate with the change in foredune shape for a restricted range of low sediment supply rates, across both time scales.

2.2 METHODS

To investigate the relative roles of invasive grass ecosystem engineers and sediment supply in shaping coastal foredunes over the past two decades in the CRLC, we combined biological and geomorphological field data in a regression model framework. Below we describe where and how these data were collected, and the statistical methods used for analysis.

2.2.1. Study area

The CRLC contains four concave, prograded barrier plain littoral sub-cells separated by estuaries; here, we focus on the southernmost three sub-cells (Fig. 2.1). The region is characterized by wide and shallow sloped dissipative beaches (Wright and Short 1984) primarily backed by dune fields with a median mid-beach sand grain size of 0.20 mm (Ruggiero et al. 2005). Winter near-shore ocean conditions can be severe with open-ocean significant wave heights annually reaching 10 m and occasionally 14 to 15 m (Ruggiero et al. 2010). Since the 1970's, the five highest storm induced wave heights per year have steadily increased in height by 0.071 m/yr (Allan and Komar 2002, Ruggiero et al. 2010). Despite multicentury-scale coseismic subsidence events along the Cascadia subduction zone, the CRLC barriers experienced net progradation (~0.5 m/yr) over the past few thousand years due to interseismic rebound, a large supply of fine sand delivered by the Columbia River, and a relatively intense wave climate able to mobilize this sand (Kaminsky et al. 2010). Over the last century, the sediment supply rates to the beaches and dunes were highly influenced by the construction of jetties at the mouths of the Columbia River (1885–1917) and Grays Harbor (1898–1916) (Kaminsky et al. 2010). In the decades following jetty construction, winter waves and ocean currents redistributed sediment away from the ebb-tidal deltas in a net northward direction along the shoreline, while summer currents transported sediment onshore at high rates (Kaminsky et al. 2010). These processes doubled the rate of shoreline advancement, as compared to pre-jetty rates; the net shoreline advancement has been upwards of 1 km, especially in regions near the jetties (Kaminsky et al. 2010). In recent decades, sediment supply to the regions adjacent to the jetties declined, evidenced by high erosion rates, but the majority of the dune fields and beaches in the CRLC continued to accumulate sand.

2.2.2. Data collection

Vegetation and foredune shape data

In 1988, 2006, and 2009, we measured biological variables (plant community composition, tiller density, and relative percent cover by species, cover type) within 20 x 50 cm quadrats placed every 5 m along foredune transects across the region (1988 and 2009 had 26 transects in common, and 2006 and 2009 had 33 transects in common; tiller density was not measured in 2006; see Seabloom and Wiedemann 1994, Zarnetske et al. 2010, Hacker et al. 2011, Zarnetske et al. in review, for further details on transect methods). For the same years and transects, and at the same spatial resolution, we measured foredune elevations once per transect during summer months with a survey rod and hand level – from these data we generated response variables for foredune morphometrics (foredune crest elevation (m) relative to MLLW, and one-half foredune width (m) – maximum horizontal distance from foredune toe to foredune crest). Due to relatively high sediment supply and progradation rates, foredunes measured in 1988 and 2009 are not necessarily the same distinct morphological feature, while foredunes measured in 2006 and 2009 typically are the same feature. Hence, the 1988 to 2009 timeframe represents multi-decadal changes in the shape of the potentially different foredunes, while 2006 to 2009 represents the inter-annual evolution of a particular foredune feature.

Sediment supply rate data

For each transect location, we used nearby or overlapping geomorphic data to generate sediment supply and accumulation rate proxies in the system, over inter-annual to multi-decadal timeframes. The rates that were calculated at nearby beach profile locations were then interpolated to the nearest vegetation transect location. The proximity of vegetation transects to beach profiles ranged from 0 to 1950 m, with a median distance of 566 m.

In calculating these sediment supply rates, we first extracted quantitative morphometric parameters describing the foredune shape (e.g., foredune toe) from topographic beach profile surveys and lidar data, and extracted shoreline position from lidar data and aerial photo sets. We used data from the topographic beach profile surveys obtained by the CRLC Beach Morphology Monitoring Program begun in 1997 (Ruggiero et al. 2005). These surveys collected beach and foredune elevations with Real Time Kinematic Differential Global Positioning System (RTK DGPS) surveying techniques, taken quarterly, from 1997 to 2009, spaced approximately every 3 to 4 km along this section of coastline (Ruggiero et al. 2005). The lidar data were collected in the summer of 2002 and represent continuous coverage of the beach and foredune (Mull 2011). We developed automated techniques to extract the morphometric parameters from the lidar data modified from Elko et al. (2002), Stockdon et al. 2009. Finally, the ortho-rectified aerial photos of the beach and dunes date from the 1950's for Washington, and from 1967 for Oregon (Kaminsky et al. 2010).

Sediment supply rates

We derived several sediment supply rate proxies that attempt to integrate the main physical forces of ocean currents, sediment distribution, and wind important to foredune geomorphology (Hesp 1989, Psuty 1992). Shoreline change rate (SCR, m/yr) is the rate at which the shoreline position extends (progrades) seaward (positive rate), erodes landward (negative rate), or maintains position (zero rate), and is taken here as a proxy for sediment supply rate to the beach. The multi-decadal SCR (SCR50) was calculated from two shoreline position endpoints at the vegetation transect locations: [1] proxy-based shorelines from aerial photo sets and [2] datum-based shoreline positions representing the mean high water (MHW) line extracted from 2002 lidar data. We applied the methodology of Ruggiero and List (2009) to account for the bias between proxy-based and datum-based shorelines before computing change rates. The

decadal and inter-annual SCRs were calculated using linear regression through the summer shoreline positions, during each time period, and interpolated to vegetation transect locations.

We generated a decadal scale, time-varying foredune sediment supply rate (DSR, $m^3/m/yr$) – to reflect the volumetric sediment supply rate directly to the foredunes. This metric is a direct measurement of the accumulated sediment deposition on the foredune, in other words, the rate of foredune volume growth over time. Decadal-scale DSR was calculated from the cross-shore location of the foredune heel (topographic low landward of foredune crest) in 1999, and the subsequent locations of the 5m contour (NAVD88), from RTK DGPS topographic beach profiles (Ruggiero et al. 2005). Inter-annual scale DSR was calculated the same way, but starting from the foredune heel in 2006. We used the 5 m contour rather than the foredune toe as the seaward limit of our volume calculation because there is less error associated with deriving its position. Finally, we generated foredune vertical growth rate (VGR, m/yr) – the rate at which the present foredune increased (positive rate) or decreased (negative rate) in elevation, computed at the horizontal location of the end year crest location. Decadal and inter-annual VGR were calculated from topographic beach profiles, and then interpolated to the vegetation transect location. For decadal VGR, we took the average yearly change in profile elevation from 1999 to 2009. Inter-annual VGR was calculated the same way, but starting with 2006.

The sediment supply rates represent time scales relevant to the foredune shape and vegetation changes. The multi-decadal shoreline change rate was calculated from shoreline positions from aerial photo sets (1950's for Washington and 1967 for Oregon) and from 2002 lidar data to reflect bulk rates across the last half century. Decadal rates were calculated from 1999 to 2009, and approximate the rates during the 1988 to 2009 transects; although the period 1988 to 2009 is multi-decadal, the period 1999 to 2009 is an appropriate timeframe for calculating the sediment supply and accumulation rates because a major El Niño/La Niña event in 1997/1998 had a large

effect on sediment supply (Kaminsky et al. 1998, Allan and Komar 2002, Ruggiero et al. 2005). Inter-annual rates were calculated from 2006 to 2009, and reflect the same time period of transect data.

2.2.3. Statistical methods

We quantified the change in foredune shape from 1998 to 2009 and from 2006 to 2009. We then investigated whether the change in foredune shape was associated with biological or physical variables (or both). In this assessment, we used regression techniques and converted all response and explanatory variables to absolute change metrics (i.e., 2009 – 1988, 2009 – 2006) and relative change metrics (i.e., (2009 - 1988)/1988), (2009 - 2006)/ 2006)). We removed locations near the mouths of estuaries and streams that are highly influenced by physical forcing other than open ocean sandy beach processes. These areas typically had excessive values of SCR50 and we only used data within the following range: -11 m/yr < SCR50 > 11 m/yr. We then subset this dataset further to assess the influence of vegetation change metrics under more similar physical conditions (i.e., controlled for SCR50 by restricting the data to SCR50±2m/yr). With each of these four datasets (1988 to 2009, and 2006 to 2009 both with and without the control for physical conditions), we ran a hierarchical partitioning analysis (with R package hier.part and R^2 as the goodness-of-fit metric) to determine the overall relative influence of biological vs. physical variables on foredune shape change. We also ran a suite of normal generalized linear models (GLMs) and associated ANOVAs, and used extra-sums of squares F-tests and AIC to select top models for each response metric (Burnham and Anderson 2002). To conform to the assumptions of linear regression, natural-log (ln) transformations were assigned to variables based on residual and normal quantile plot investigations for the glm analysis. We also used two-sided t-tests to determine whether the regional changes in biological variables and foredune shape differed from zero, and whether they were positive or negative changes (these tests incorporated a Bonferroni

adjustment for multiple comparisons). All statistics were run in R 2.13.1 (R Development Core Team 2010).

2.3 RESULTS

2.3.1. Trends in foredune evolution and vegetation change

Across the CRLC, changes in foredune shape were more variable within the inter-annual time scale than across the multi-decadal time scale (Fig. 2.2, Appendix A). Over multi-decadal scales (1988 to 2009), the foredunes in the CRLC increased in width by an average of 27.062 m and also increased in crest elevation by an average of 1.385 m (Fig. 2.2a, Appendix A). From 1988 to 2006, the change in foredune crest was slightly positive (for transects within SCR50 ± 11 m/yr, mean change: 0.594 m, one-sample t-test t=2.47, df=30, p=0.019). Between 1997 and 2009, dune fields prograded at an average rate of 7 m^3/m/yr, largely in response to the high rates of sediment supply to the beaches seaward of the foredunes (prograding up to 5 m/yr). Over this timeframe, the 40-km stretch of the Long Beach sub-cell (Fig. 2.1) received the largest sediment supply – 300,000 m^3/yr (4 million cubic m of new dune volume).

From 1988 to 2009, *A. breviligulata* increased in abundance by an average of 21%, overall proportion of vegetation cover increased by an average of 31% and beach grass tiller density increased by an average of 34% over 1988 levels (although the absolute average change in tiller number – 12 more tillers/m^2 – was not significant) (Appendix A). Over inter-annual scales (2006 to 2009), foredunes increased in crest elevation by an average of 0.603 m, but variously changed in their width – from gaining 44 m to losing 60 m – resulting in an average relative increase of 0.190 m (Fig. 2.2b, Appendix A). Vegetation subtly changed between 2006 and 2009 – the overall proportion of vegetation cover decreased by an average of 14.5 % (with a 21.8% relative decrease compared to 2006), and *A. breviligulata* varied in its change

in abundance on foredune fronts – from a 34 % decline to a 56 % increase, which resulted in an insignificant regional average increase in abundance (Appendix A).

Foredunes within ± 2 m/yr of long term shoreline change rates (i.e., SCR50) changed shape and vegetation composition across both time scales, but consistent changes across the CRLC region only occurred across the multi-decadal time scale (Appendix A). Over the multi-decadal scale, the crest elevation of the foredune increased by an average of 1.122 m, the width of the foredune increased by an average of 39.271 m, and the overall proportion of vegetation cover increased by 43 % (Appendix A). Changes in *A. breviligulata* and tiller density were more varied – *A. breviligulata* ranged from a 35% decrease to a 94% increase, and tiller density ranged from a 76 tillers/m^2 decrease to a 123 tillers/m^2 increase (Appendix A). In contrast, the inter-annual scale changes in foredune shape and vegetation composition were inconsistent across the CRLC. The foredune crests ranged from a 1.230 m decrease to a 1.650 m increase and the foredune widths ranged from a 34.900 m decrease to a 15.040 m increase (Appendix A). The proportion of vegetation cover ranged from a 40% decrease to a 57% increase, while the abundance of *A. breviligulata* ranged from a 28% decrease to a 17% increase (Appendix A).

2.3.2. Model results for changes in foredune shape

We found strong evidence for both biological and physical factors being associated with foredune evolution across the CRLC at inter-annual and multi-decadal scales (Figs. 2.3-2.5). While both variable types were important, we found that foredune crest change across the region was largely associated with physical variables at multi-decadal (85%) and inter-annual (70%) time scales, as compared to biological variables (15% at multi-decadal, 30% at inter-annual) (Table 2.1). Foredune width change at multi-decadal scales was equally associated with physical variables (51-52% of the total R^2) and biological variables (48-49%) (Table 2.1). At inter-annual scales, the absolute foredune width change was highly associated with physical variables

(79%) as compared to biological variables (21%), but the relative change in foredune width was equally associated with physical and biological variables (49% and 51%, respectively) (Table 2.1). Across the entire range, there was more support for changes in biological variables being associated with foredune width evolution over the multi-decadal scale, while changes in physical variables were strongly associated with both scales of foredune crest change, and to a lesser extent, width change (Table 2.1).

However, within a restricted range of sediment supply (SCR50 ± 2m/yr), biological variables had more relative association with foredune crest change (63%) than physical variables (37%) and also a large relative association with foredune width over this time scale (37-58%) (Table 2.2). Within this restricted sediment supply range, physical variables had more relative association with foredune crest and width change (75-86%) than biological variables (Table 2.2). Within the limited sediment supply range, biological variables were strongly associated with the change in foredune crest while physical variables were strongly associated with the change in foredune width (Table 2.2)

Across the range, most top models contained both biological and physical variables, and some included interactions between both (Fig. 2.3). At the multi-decadal scale, we found that an absolute increase in crest elevation was largely associated with more positive long term shoreline change rate (SCR50) (Fig. 2.3, 2.5), but that the relative increase was also associated with a higher relative increase in vegetation cover and a negative interaction between vegetation cover and long term SCR50 (Table 2.3). The absolute or relative increase in foredune width was largely associated with biological factors including: an increase in the proportion of *A. breviligulata*, a loss in tiller density, and an increase in vegetation cover (Fig. 2.4, Table 2.3). Over this timeframe, increased foredune width was also associated with lower long term SCR50 (which interacted with an increase in the proportion of *A. breviligulata*), and to a lesser degree, lower decadal foredune supply rates (which interacted positively with relative change in tiller density) (Fig. 2.3, 2.5, Table 2.3). At

the inter-annual scale (2006 to 2009), we found that the increase in foredune crest was mostly associated with a positive long term SCR50, and to a lesser extent, increased vegetation cover (Figs. 2.3, 2.4, Table 2.3). An increase in absolute and relative foredune width was most associated with lower long term SCR50, and an absolute or relative increase in *A. breviligulata* (Figs. 2.3, 2.5, Table 2.3). Higher inter-annual DSR was also associated with some of the increase in foredune width (Fig. 2.3, 2.5, Table 2.3).

Within the restricted range of ±2 m/yr of long term shoreline change rates, the variety of changes in foredune shape were also associated with changes in both biological and physical factors (Table 2.4). At the multi-decadal scale, an increase in foredune crest was associated with higher vegetation cover and to a lesser extent, with higher decadal VGR and higher decadal SCR, although there was a negative interaction between vegetation cover and decadal SCR (Table 2.3). An increase in foredune width during this timeframe was most associated with a decline in tiller density and a negative interaction between decadal SCR and the change in tiller density (Table 2.4). Over the inter-annual timeframe, an increase in foredune crest was only associated with more positive long term SCR50, while an increase in foredune width was mostly associated with an increase in vegetation cover and a more negative inter-annual SCR (Table 2.4).

2.4 DISCUSSION

At both time scales, and across datasets, physical variables were strongly associated with the change in foredune shape. Therefore, we found strong evidence in support of our first hypothesis that physical variables consistently associate with foredune shape change across time scales. We also found that over the multi-decadal scale, biological variables strongly associated with the change in foredune width across the region, and strongly associated with the change in foredune crest in regions with sediment supply rates ±2 m/yr. Consequently, we also found some support for

our second hypothesis that biological variables play an important role within a restricted range of sediment supply rates. However, most top models contained both physical and biological variables, sometimes as interacting variables. It is clear from this assessment that both physical and biological forces are associated with the changes in foredune shapes across both time scales, which suggests that their influence is highly coupled.

Our experimental work suggests that this coupling is evidence of a biophysical feedback between sand supply and species-specific growth habit which may explain why *A. breviligulata* foredunes tend to be lower and wider while *A. arenaria* foredunes tend to be taller and narrower across the Pacific Northwest (Zarnetske et al. in review). Specifically, we have shown that the growth habit of *A. breviligulata* is distinctly horizontal and spreading, regardless of sand supply rate (Zarnetske et al. in review). This growth habit results in lower tiller density, and thus an inferior ability to capture sand and build tall dunes, especially compared with the dense vertical growth of *A. arenaria* tillers (Hacker et al. 2011, Zarnetske et al. in review). In turn, this lower sand capture ability translates to lower wider dunes in regions of high positive shoreline change rate as large amounts of sand supplied to the beach and foredune encounter lower density vegetation with less efficient capture ability (Bagnold 1941, Lancaster and Baas 1998). The high sediment supply then promotes a positive feedback with *A. breviligulata* to send out more horizontal growth, which reinforces its lower tiller density and lower sand capture efficiency (Baye 1990, Hacker et al. 2011, Zarnetske et al. in review).

The species-specific sand capture ability suggests that the increase in *A. breviligulata* in the CRLC over the last two decades has helped maintain lower, wider foredunes, as compared to the taller, steeper *A. arenaria* foredunes south of the CRLC. However, we know from experimental and species interaction modeling work that *A. breviligulata* is capable of dominating the beach grass community on foredune fronts across a wide range of sand supply rates (Zarnetske et al. in prep). If *A. breviligulata*

continues to invade sections of coastline where it is currently absent (e.g., south of the CRLC), then its dominance in these regions may have consequences for foredune shape (Zarnetske et al. in prep). The horizontal growth habit of *A. breviligulata* and its lower ability to capture sand may translate to lower, wider foredunes in some sections of coastline, and thus, may contribute to a decline in the coastal protective ecosystem services provided by taller foredunes currently existing in this region. We expect that a dominant shift toward lower, wider foredunes will be mediated by the superior foredune builder, *A. arenaria*, which is predicted to be a near-co-dominant in these low sand supply regions following invasion by *A. breviligulata* (Zarnetske et al. in prep, Zarnetske et al. in review).

In the CRLC, the crest on foredunes within SCR50 ± 11 m/yr has subtly increased across all year combinations (Appendix A). However, across all spatial and temporal scales, the changes in CRLC foredune crest elevations and width are variable, especially over the inter-annual scale (Fig. 2.4, 2.5, Appendix A). A likely explanation for the differences in foredune shape across time is the timing of field measurement in relation to the stage of foredune evolution. The majority of the coastline within the CRLC has been prograding over the last two decades, such that new foredune features have developed seaward of the historical foredune. In fact, we found that between 1997 and 2009, the high onshore sediment supply rates north of the Columbia River led to as many as 2 to 3 new foredunes with up to 3 to 4 m of vertical growth. In 1988, 2006, and 2009, the foredunes were in various stages of growth such that comparisons across years show both positive and negative changes. Mechanistic knowledge from our experiments and results from this correlative assessment lead us to the conclusion that *A. breviligulata* plays a significant role in changing foredune shape, especially in regions with highly positive sediment supply in the CRLC. Between 1988 and 2009, *A. breviligulata* increased in relative abundance on the foredune front while *A. arenaria* and *E. mollis* both declined (Fig. 2.4c). This overall increase in *A. breviligulata* combined with the highly positive shoreline change

rates are most likely responsible for the widening of foredunes across the region, but also maintaining the lower foredune crest elevations as compared to lower sediment supply and *A. arenaria* dominance in regions south of the CRLC. Lower foredune crests are typical of *A. breviligulata* foredunes (Hacker et al. 2011); across all the time periods investigated here, foredune crest elevation change did not exceed 3.25 m (a foredune on Long Beach increasing from 6.1 m in 1988 to 9.4 m in 2009), providing further support for *A. breviligulata* maintaining lower foredunes.

Across the Pacific Northwest, foredunes continuously change shape through biophysical feedbacks – this variation in shape is apparent from the high degree of inter-annual variability in foredune crest and width change in the CRLC (Fig. 2.4, 2.5, Appendix A). The specific shape of a foredune at the time of a large winter storm wave (or potentially a tsunami) becomes an important factor in determining its coastal protective capacity. Winter storm wave heights have steadily increased over the last 30 years (Ruggiero et al. 2010). Thus, foredunes will have to keep pace with increasing total water levels to prevent an increase in coastal flooding associated with larger waves. However, in high sediment supply regions, the rapid foredune turnover does not allow tall foredunes to develop. This rapid turnover is partially due to large amounts of onshore sediment supply, but also due to the low density growth habit of *A. breviligulata*. Our results indicate that as *A. breviligulata* becomes the dominant species, vegetation cover and tiller density generally decline – these results combined with other work (Zarnetske et al. in review) suggest that if *A. breviligulata* also becomes the dominant species in other lower sediment supply areas, the foredunes in these areas will also be unable to reach higher elevations (Fig. 2.4, 2.5) (Zarnetske et al. in review).

We have investigated the relative contributions of biological and physical forces shaping foredunes throughout the CRLC, over multi-decadal and inter-annual time scales. Our findings indicate that *A. breviligulata* and high sediment supply play important roles in shaping foredunes across both timeframes, and that vegetation is a

driver, rather than a passenger of this foredune evolution. This study and our finer-scale mechanistic experiments and models demonstrate that physical and biological forces are strongly coupled in a biophysical feedback that controls foredune shape over hours to decades. The patterns investigated here combined with the process level understanding gained from experimental and modeling work provide a robust knowledge base that can inform coastal conservation and management decisions concerned with future invasions by *A. breviligulata* (Zarnetske et al. in prep), dune restoration (Zarnetske et al. 2010), increasing wave heights (Ruggiero et al. 2010), and climate change impacts including sea level rise (Bindoff 2007).

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Table 2.1 Results from hierarchical partitioning analysis on the full set of CRLC field observational data. R^2 values represent the independent contribution of each explanatory variable, which is the proportion of the variation in the response variable that each explanatory variable explains on its own. Models were run separately for the timeframes 1988 to 2009 (n=26) and 2006 to 2009 (n=33). Absolute change models contained absolute change in foredune shape and vegetation variables while relative change models contained relative change in foredune shape and vegetation variables (see Notes below). All outlier transects were removed prior to running the models (we only used data within the range: -11 m/yr < SCR50 > 11 m/yr). The statistical significance (alpha=0.05) of the independent contribution of each explanatory variable was determined by using Monte Carlo randomization based on 1,000 permutations. The total R^2 is the R^2 from a full additive model of all the explanatory variables. The percent contribution of biological (Biol.) vs. physical (Phys.) variables reflects the percentage of the total variation in the response metric explained by the total independent contribution of all explanatory biological vs. physical variables.

	Explanatory Variable Individual R^2									
Response Metric	**AMBR**	**Cov**	**Till**	**SCR50**	**SCR**	**VGR**	**DSR**	**Total R^2**	**Total % Biol.**	**Total % Phys.**
1988 to 2009										
CrestChg	0.006	0.020	0.032	0.206*	0.061	0.035	0.017	0.378	15.45	84.55
CrestRelChg	0.031	0.005	0.021	0.220*	0.055	0.296	0.007	0.369	15.72	84.28
WidthChg	0.075	0.085	0.182*	0.259*	0.023	0.064	0.026	0.715	47.89	52.11
WidthRelChg	0.090	0.069	0.188*	0.176*	0.070	0.068	0.049	0.709	48.79	51.21
2006-2009										
CrestChg	0.032	0.097		0.199*	0.013	0.065	0.019	0.426	30.31	69.69
CrestRelChg	0.049	0.091		0.147*	0.012	0.065	0.016	0.380	36.70	63.30
WidthChg	0.062	0.027		0.077*	0.221*	0.026	0.015	0.429	20.78	79.22
WidthRelChg	0.156*	0.035		0.034	0.123*	0.023	0.007	0.379	50.56	49.44

Notes: Abbreviations are as follows:

CrestChg = change in foredune crest elevation over the model time period

CrestRelChg = change in foredune crest elevation over the model time period, relative to the first year elevation

WidthChg = change in horizontal foredune width from toe to crest over the model time period

WidthRelChg = change in horizontal foredune width from toe to crest over the model time period, relative to the first year width

Till = Tillers/m^2 (TillChg used in CrestChg, WidthChg models, TillRelChg used in CrestRelChg, WidthRelChg models)
TillChg = change in the number of tillers/m^2 of the three beach grass species, over the model time period
TillRelChg = change in the number of tillers/m^2 of the three beach grass species, over the model time period, relative to the first year density
Cov = Vegetation proportional cover (CovChg used in CrestChg, WidthChg models, CovRelChg used in CrestRelChg, WidthRelChg models)
CovChg = change in proportional vegetation cover (relative to bare ground) over the model time period
CovRelChg = change in proportional vegetation cover (relative to bare ground) over the model time period, relative to the first year cover
AMBR = *Ammophila breviligulata* proportional cover (AMBRChg used in CrestChg, WidthChg models, AMBRRelChg used in CrestRelChg, WidthRelChg models)
AMBRChg = change in proportional cover of *A. breviligulata* (relative to *A. arenaria* and *E. mollis*) over the model time period
AMBRRelChg = change in proportional cover of *A. breviligulata* (relative to *A. arenaria* and *E. mollis*) over the model time period, relative to the first year proportional cover of *A. breviligulata*
SCR50 = multi-decadal shoreline change rate (m/yr), over last half century
SCR = shoreline change rate (m/yr) over the model time period
DSR = foredune supply rate (m/yr) over the time model period
VGR = foredune vertical growth rate (m/yr) over the model time period

Table 2.2 Results from hierarchical partitioning analysis on the restricted set of CRLC field observational data (i.e., ± 2m/yr SCR50). R^2 values represent the independent contribution of each explanatory variable, which is the proportion of the variation in the response variable that each explanatory variable explains on its own. Models were run separately for the timeframes 1988 to 2009 (n=9) and 2006 to 2009 (n=11). Absolute change models contained absolute change in foredune shape and vegetation variables while relative change models contained relative change in foredune shape and vegetation variables (see Notes below). The statistical significance (alpha=0.05) of the independent contribution of each explanatory variable was determined by using Monte Carlo randomization based on 1,000 permutations. The total R^2 is the R^2 from a full additive model of all the explanatory variables. The percent contribution of biological (Biol.) vs. physical (Phys.) variables reflects the percentage of the total variation in the response metric explained by the total independent contribution of all explanatory biological vs. physical variables. See Table 2.1 Notes for abbreviations.

	Explanatory Variable Individual R^2									
Response Metric	**AMBR**	**Cov**	**Till**	**SCR50**	**SCR**	**VGR**	**DSR**	**Total R^2**	**Total % Biol.**	**Total % Phys.**
1988 to 2009										
CrestChg	0.077	0.463*	0.082	0.056	0.047	0.192	0.071	0.989	62.93	37.07
CrestRelChg	0.059	0.513*	0.050	0.065	0.061	0.125	0.117	0.994	62.98	37.02
WidthChg	0.151	0.048	0.172	0.076	0.068	0.310*	0.166	0.990	37.44	62.56
WidthRelChg	0.033	0.219	0.239	0.079	0.048	0.181	0.045	0.844	58.19	41.81
2006-2009										
CrestChg	0.006	0.091		0.212	0.184	0.094	0.080	0.668	14.45	85.55
CrestRelChg	0.004	0.093		0.201	0.181	0.122	0.082	0.683	14.24	85.76
WidthChg	0.008	0.162		0.202	0.465*	0.094	0.021	0.951	17.88	82.12
WidthRelChg	0.003	0.191		0.166	0.204	0.135	0.079	0.778	24.90	75.10

Table 2.3 Top generalized linear models (GLM) from the full set of CRLC field observational data. Models were run separately for the timeframes 1988 to 2009 and 2006 to 2009. All outlier transects were removed prior to running the models (we only used data within the range: -11 m/yr < SCR50 > 11 m/yr). Natural log response and explanatory transformations were applied based on residual investigations (residual vs. fitted plots, normal quantile plots). Models contain only uncorrelated explanatory variables (i.e., Pearson correlation coefficient <|±0.60|). For top model selection we used extra-sums of squares F-tests, and AIC. The dataset for 1988 to 2009 contains 26 transects, while the dataset for 2006 to 2009 contains 33 transects. Top competing models per response metric are included here. Explanatory variable significance is indicated by: * (P<0.05), ** (P<0.01), *** (P<0.001). See Table 2.1 Notes for abbreviations.

Response Metric	Linear Model	Model Results	ANOVA F-stat, p-value
1988 to 2009			
Change in foredune crest (m)	CrestChg = 0.508+0.315 [SCR50]*	df =24 AIC=72.046 ΔAIC=0 R^2=0.227	SCR50: F=7.061 (1,24), p=0.014
Relative change in foredune crest	CrestRelChg = -0.119+0.097 [SCR50]*** +0.182[CovRelChg]* -0.053[SCR50 x CovRelChg]*	df =22 AIC=-24.118 ΔAIC=0 R^2=0.415	SCR50: F=10.025 (1,22), p=0.004 CovRelChg: F=0.531 (1,22), p=0.474 SCR50 x CovRelChg: F=5.065 (1,22), p=0.035
	CrestRelChg = 0.052***+0.057 [SCR50]**	df =24 AIC=-22.226 ΔAIC=1.892 R^2=0.267	SCR50: F=8.719 (1,24), p=0.007
Change in foredune width (m)	WidthChg = 37.272***+72.072[AMBRChg]** -5.058[SCR50]*-17.585[AMBRChg x SCR50]*	df =22 AIC=223.61 ΔAIC=0 R^2=0.525	AMBRChg: F=5.874 (1,22), p=0.024 SCR50: F=12.903 (1,22), p=0.007 AMBRChg x SCR50: F=5.488 (1,22), p=0.029

	WidthChg = 47.950***-0.115[TillChg]** -6.972[SCR50]**	df =23 AIC=223.97 ΔAIC=0.36 R^2=0.479	TillChg: F=10.761 (1,23), p=0.003 SCR50: F=10.404 (1,23), p=0.004
	WidthChg = 7.884 +22.785[AMBRChg] +51.202[CovChg]*-0.115[TillChg]**	df =22 AIC=225.6 ΔAIC=1.99 R^2=0.487	AMBRChg: F=5.440 (1,22), p=0.029 CovChg: F=5.593 (1,22), p=0.027 TillChg: F=9.813 (1,22), p=0.005
Relative change in foredune width	WidthRelChg = 1.805*** -0.651[ln(TillRelChg+1)]**-0.271[SCR50]**	df =23 AIC=60.436 ΔAIC=0 R^2=0.425	TillRelChg: F=8.520 (1,23), p=0.008 SCR50: F=8.477 (1,23), p=0.008
	WidthRelChg = 2.373*** -2.249[ln(TillRelChg+1)]** -0.132[DSR]* +0.162[ln(TillRelChg+1) x DSR]*	df =22 AIC=62.093 ΔAIC=1.657 R^2=0.433	ln(TillRelChg+1): F=8.258 (1,22), p=0.009 DSR: F=3.506 (1,22), p=0.074 ln(TillRelChg+1) x DSR: F=5.003 (1,22), p=0.036
2006-2009			
Change in foredune crest (m)	CrestChg = -0.146 +1.753[CovChg]**+0.350[SCR50]***	df =30 AIC=75.712 ΔAIC=0 R^2=0.376	CovChg: F=2.023 (1,30), p=0.165 SCR50: F=16.043 (1,30), p<0.001
Relative change in foredune crest	CrestRelChg = -0.011 +0.111[ln(CovRelChg+1)]**+0.049[SCR50]***	df =30 AIC=-52.127 ΔAIC=0 R^2=0.354	ln(CovRelChg+1): F=2.022 (1,30), p=0.165 SCR50: F=14.412 (1,30), p<0.001

Change in foredune width (m)	WidthChg = -11.677 -2.725[SCR]**+1.856[DSR]	df =30 AIC=302.07 ΔAIC=0 R^2=0.244	SCR: F=5.676 (1,30), p=0.024 DSR: F=4.019 (1,30), p=0.055
	WidthChg = 0.717 +32.301[AMBRChg] -1.683[SCR]*	df =30 AIC=303.8 ΔAIC=1.73 R^2=0.204	AMBRChg: F=2.520 (1,30), p=0.123 SCR: F=5.150 (1,30), p=0.031
Relative change in foredune width	WidthRelChg = 0.175 +0.807[ln(AMBRRelChg+1)]*-0.028[SCR]	df =30 AIC=53.767 ΔAIC=0 R^2=0.209	ln(AMBRRelChg+1): F=5.221 (1,30), p=0.030 SCR: F=2.709 (1,30), p=0.110)
	WidthRelChg = 0.157 +0.796[ln(AMBRRelChg+1)]*	df =31 AIC=54.62 ΔAIC=0.853 R^2=0.138	ln(AMBRRelChg+1): F=4.948 (1,31), p=0.034

Table 2.4 Top generalized linear models (GLM) from the restricted set of CRLC field observational data. Models were run separately for the timeframes 1988 to 2009 and 2006 to 2009. To control for physical conditions, these data were restricted from the full dataset, to include transects that fall within the SCR50 range of ±2 m/yr. Natural log response and explanatory transformations were applied based on residual investigations (residual vs. fitted plots, normal quantile plots). Models contain only uncorrelated explanatory variables (i.e., Pearson correlation coefficient <|±0.60|). For top model selection we used extra-sums of squares F-tests, and AICc. The dataset for 1988 to 2009 contains 9 transects, while the dataset for 2006 to 2009 contains 11 transects. Top competing models per response metric are included here. Explanatory variable significance is indicated by: * (P<0.05), ** (P<0.01), *** (P<0.001). See Table 2.1 Notes for abbreviations.

Response Metric	Linear Model	Model Results	ANOVA F-stat, p-value
1988 to 2009			
Change in foredune crest (m)	CrestChg = -0.619+2.517[CovChg]*+3.842[VGR]	df =6 AICc=27.266 ΔAICc=0 R^2=0.678	CovChg: F=7.808 (1,6), p=0.031 VGR: F=4.797 (1,6), p=0.071
Relative change in foredune crest	CrestRelChg = -0.219 +0.203[SCR50]+0.419[ln(CovRelChg)]* -0.251[SCR50 x ln(CovRelChg)]*	df =6 AICc=5.049 ΔAICc=0 R^2=0.733	SCR50: F=0.287 (1,6), p=0.615 ln(CovRelChg): F=4.929 (1,6), p=0.077 SCR50 x ln(CovRelChg): F=8.517, p=0.033
Change in foredune width (m)	WidthChg = 5.967-2.111[SCR]+209.524[VGR]***	df =6 AICc=80.699 ΔAICc=0 R^2=0.884	SCR: F=8.363 (1,6), p=0.028 VGR: F=37.499 (1,6), p=0.001
	WidthChg = 5.351+12.548[AMBRChg] +184.915[VGR]*	df =6 AICc=84.311 ΔAICc=3.613 R^2=0.827	AMBRChg: F=18.959 (1,6), p=0.005 VGR: F=9.756 (1,6), p=0.020

Relative change in foredune width	WidthRelChg = 1.980*** -0.459[ln(TillRelChg+1)] -0.178[SCR]+[ln(TillRelChg+1) x SCR]**	df =5 AICc=34.870 ΔAICc=0 R^2=0.870	ln(TillRelChg+1): F=12.769(1,5), p=0.016 SCR: F=1.452 (1,5), p=0.282 ln(TillRelChg+1) x SCR: F=19.216 (1,5), p=0.007
	WidthRelChg = 0.248+0.981[ln(CovRelChg)]* -1.698[ln(TillRelChg+1)]**	df =6 AICc=27.871 ΔAICc=6.999 R^2=0.773	ln(CovRelChg): F=1.327 (1,6), p=0.293 ln(TillRelChg+1): F=19.134 (1,6), p=0.005
2006 to 2009			
Change in foredune crest (m)	CrestChg = 0.824 +0.812[SCR50]*	df =9 AICc=31.194 ΔAICc=0 R^2=0.370	SCR50: F=5.290 (1,9), p=0.047
Relative change in foredune crest	CrestRelChg = -0.099 +0.107[SCR50]	df =9 AICc=-12.189 ΔAICc=0 R^2=0.345	SCR50: F=4.731 (1,9), p=0.058
Change in foredune width (m)	WidthChg = -14.587** +23.196[CovChg]* -2.663[SCR]***	df =8 AICc=86.889 ΔAICc=0 R^2=0.865	CovChg: F=21.359 (1,8), p=0.002 SCR: F=29.927 (1,8), p<0.001
Relative change in foredune width	WidthRelChg = 0.157 +0.472[ln(CovRelChg+1)]	df =9 AICc=18.829 ΔAICc=0 R^2=0.344	ln(CovRelChg+1): F=4.715 (1,9), p=0.058

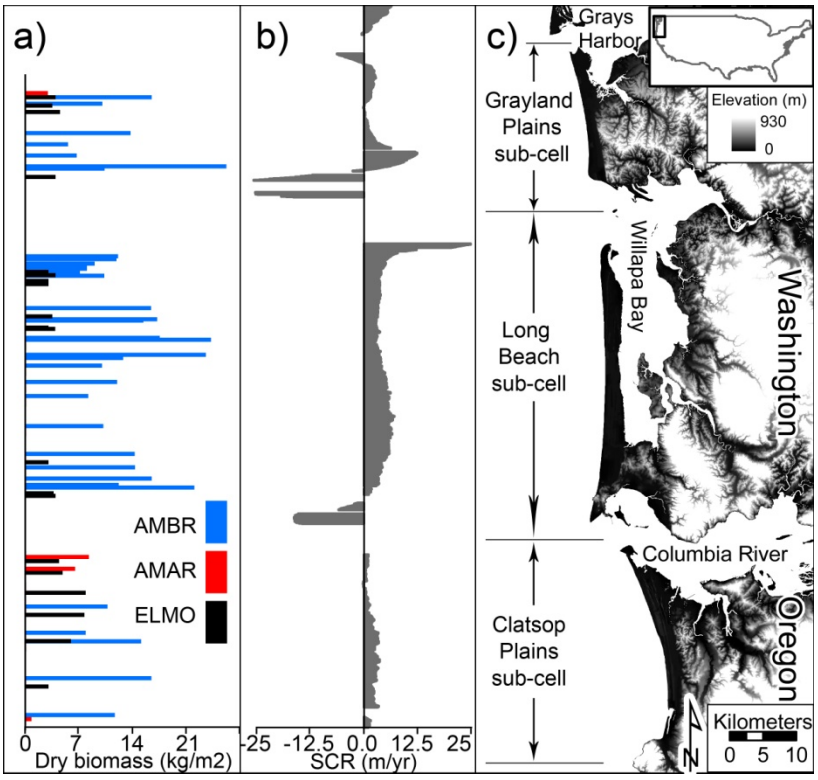
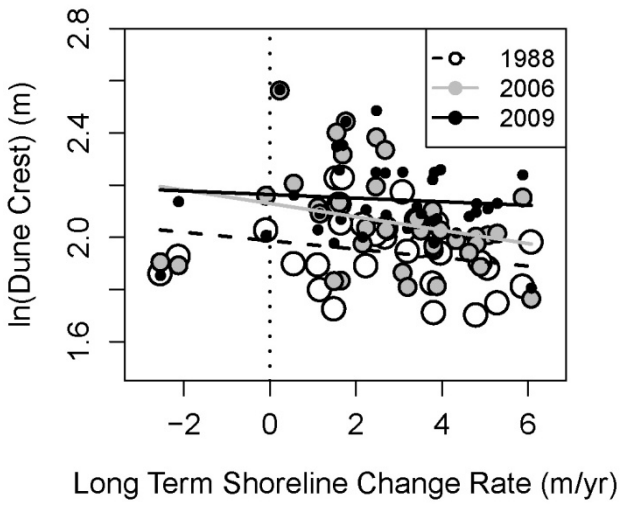


Figure 2.1 Representative biological and physical variables across the Columbia River Littoral Cell (CRLC). (a) Beach grass species abundance in 2009 (expressed as dry biomass (kg/m^2)), where AMBR is *A. breviligulata*, AMAR is *A. arenaria*, and ELMO is *E. mollis*, (b) long term shoreline change rate (m/yr) from the 1950's/60's to 2002, and (c) the CRLC with three of its sub-cells. The North Beach sub-cell is not shown but is located above the Grayland Plains sub-cell.

a)



b)

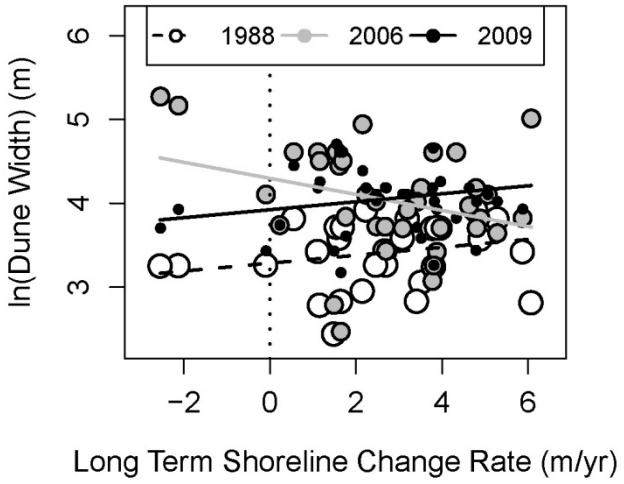


Figure 2.2. For a given year, the relationship between long term shoreline change rate (SCR50) and (a) ln(foredune crest) or (b) ln(foredune width).

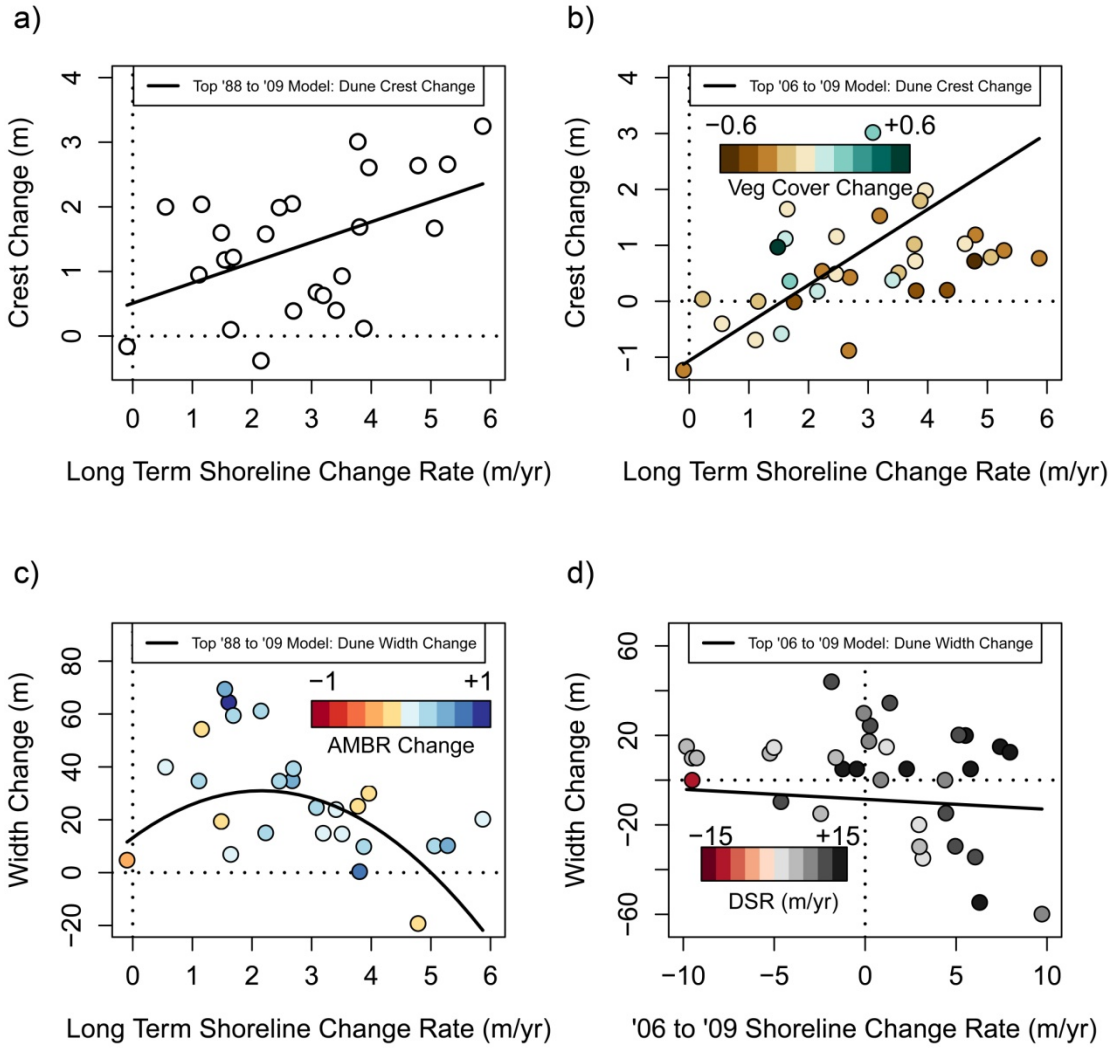


Figure 2.3. Top model results by foredune shape metric and time scale: (a) the change foredune crest elevation from 1988 to 2009, (b) the change in foredune crest elevation from 2006 to 2009, (c) the change in foredune width from 1988 to 2009, and (d) the change in foredune width from 2006 to 2009.

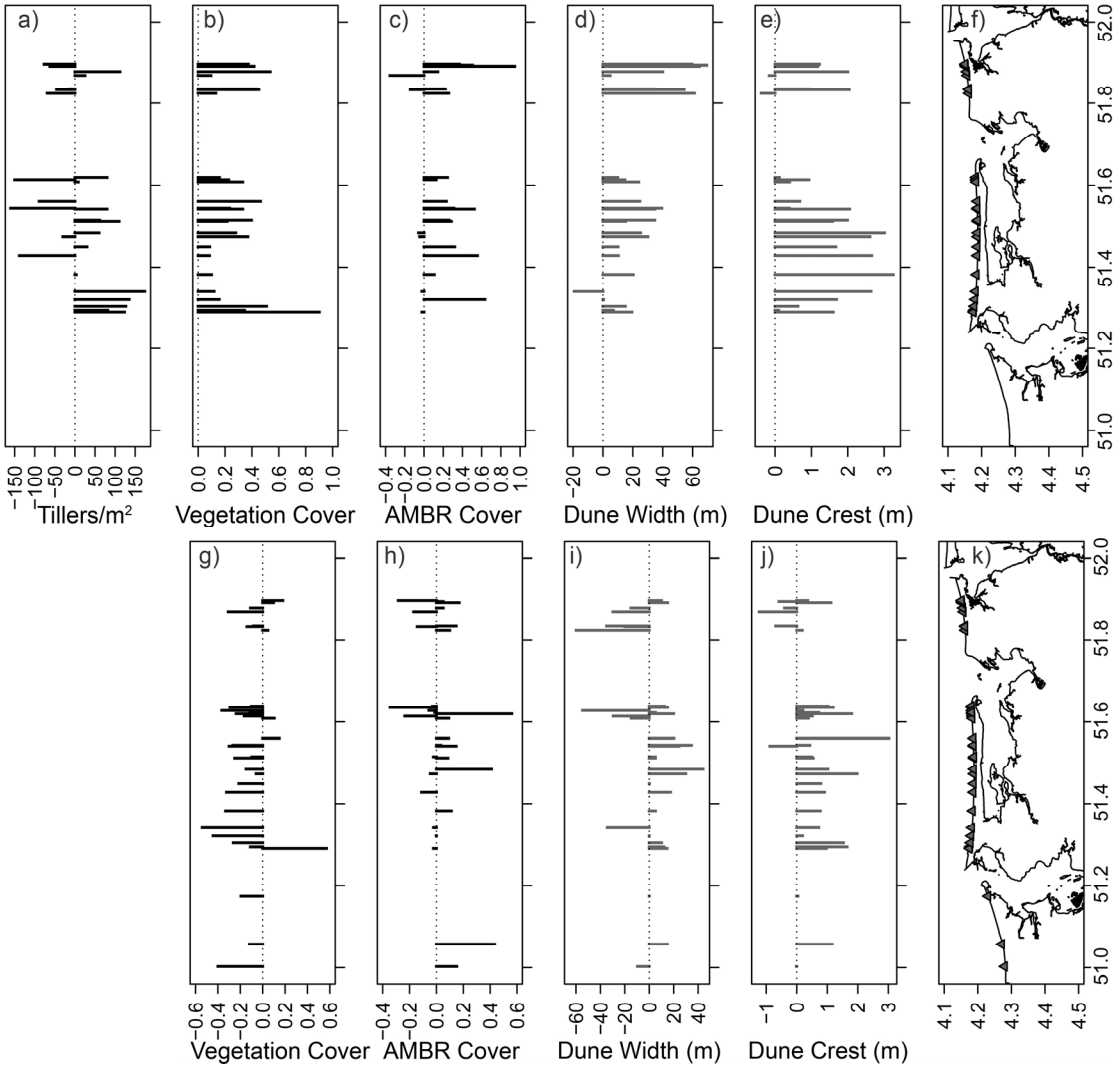


Figure 2.4. Changes in biological variables across the CRLC from 1988 to 2009 (a-c), and from 2006 to 2009 (g, h). Foredune shape change is shown in panels (d, e) for 1988 to 2009 and (i, j) for 2006 to 2009. Panels (f) and (k) are reference maps with UTM coordinates (x 100,000 m) showing the locations of the vegetation transects where these data were collected. Tiller data was absent from 2006.

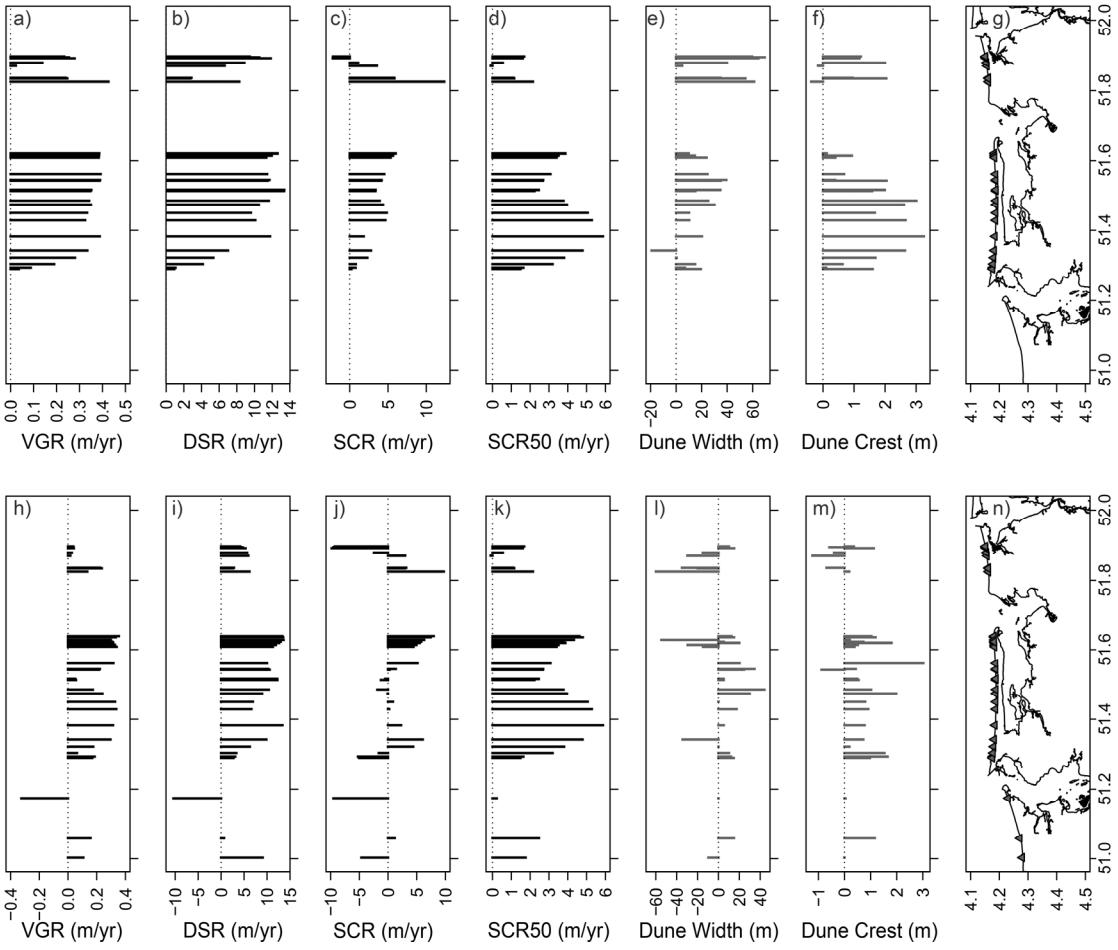


Figure 2.5. Changes in physical variables (sediment supply rates) across the CRLC from 1999 to 2009 (a-c), from the 1950's/1967 to 2002 (d, k), and from 2006 to 2009 (h-j). Panels (e, f) and (l,m) are changes in foredune width and height for 1988 to 2009 (e, f) and 2006 to 2009 (l, m). Panels (d) and (k) are both long term shoreline change rate (SCR50), from 1950/67 to 2002. Panels (g) and (n) are reference maps with UTM coordinates (x 100,000 m) showing the locations of the vegetation transects where these data were collected (foredune shape), or calculated/interpolated (sediment supply rates).

3 – Biophysical feedback mediates effects of invasive grasses on coastal dune shape

Phoebe L. Zarnetske, Sally D. Hacker, Eric W. Seabloom, Peter Ruggiero, Jason R. Killian, Timothy B. Maddux, Daniel Cox

In review

ABSTRACT

Vegetation at the aquatic-terrestrial interface can alter landscape features through its growth and interactions with sediment and fluids. Even similar species may impart different effects due to variation in their interactions and feedbacks with the environment. Consequently, replacement of one species by another may cause significant change in the physical environment. Here we investigate the species-specific ecological mechanisms influencing the geomorphology of U.S. Pacific Northwest coastal dunes. Over the last century, this system changed from open, shifting sand dunes with sparse vegetation (including native beach grass, *Elymus mollis*), to densely vegetated continuous foredune ridges resulting from the introduction and subsequent invasions of two non-native grass species (*Ammophila arenaria*, and *A. breviligulata*), each of which is associated with different dune shapes and onshore sediment supply rates along the coast. Here we propose a biophysical feedback responsible for differences in dune shape, and investigate two, non-mutually exclusive ecological mechanisms for these differences: (1) species differ in their ability to capture sand, and (2) species differ in their growth habit in response to sand deposition. To investigate sand capture, we used a moveable bed wind tunnel experiment and found that increasing tiller density increased sand capture efficiency, and that under different experimental densities, the native grass had higher sand capture efficiency compared to the *Ammophila* congeners. However, the greater densities of non-native grasses under field conditions suggest that they have greater potential to capture more sand overall. We used a mesocosm experiment to look at plant growth responses to sand deposition, and found that in response to increasing sand supply rates, *A. arenaria* produced higher density, vertical tillers (characteristic of higher sand capture efficiency), while *A. breviligulata* and *E. mollis* responded with lower density, lateral tiller growth (characteristic of lower sand capture efficiency). Combined, these experiments provide evidence for a species-specific effect on coastal dune shape. Understanding how dominant ecosystem engineers, especially non-native

ones, differ in their interactions with abiotic factors is necessary to better parameterize coastal vulnerability models and inform management practices related to both coastal protection ecosystem services and ecosystem restoration.

3.1 INTRODUCTION

Aquatic-terrestrial interface environments are dynamic systems mediated by strong feedbacks among sediment (e.g., silt, mud, sand), a fluid medium (air or water), and vegetation. These biological and physical interactions and feedbacks modify system dynamics leading to striking landscape features such as marsh platforms and channels, river topologies, and coastal dunes (Fisher et al. 2007, Murray et al. 2008, Gutierrez et al. 2011). To understand how these features evolve, it is important to investigate the interplay between ecomorphology – an organism's form and function – and geomorphology – a physical landform and its function. Understanding this interplay is necessary to anticipate the ecological and physical changes that can occur with species invasions, land use alterations, and climate change (Hacker and Dethier 2006, Murray et al. 2008, Koch et al. 2009, Gutierrez et al. 2011).

Species that physically modify a variety of abiotic materials through their own structure and growth habit (Jones et al. 1994, Jones et al. 2010) are particularly influential within interface environments as they cause changes to the structure, function, and services provided by these environments (Barbier et al. 2011). For example, vegetation in river systems can alter river geomorphology, specifically channel braiding patterns and bank structure, which in turn mediates effects of flow, increases bank stability, and reduces erosion – all key to future vegetation growth (Murray and Paola 2003, Tal and Paola 2010). Vegetation in estuarine and subtidal environments (e.g., seagrasses, cordgrasses, mangroves, algae) captures and stabilizes sediment, creating intertidal habitat complexity for diverse aquatic species (Duarte 2000, Langlois et al. 2003, Kirwan and Murray 2007, Aburto-Oropeza et al. 2008), and also attenuates waves through its structure, reducing coastal vulnerability

(Danielsen et al. 2005, Barbier et al. 2008). Some of the best examples come from aeolian environments where vegetation (e.g., grasses, sedges, shrubs, forbs) captures wind-blown sediment, creating dunes (Hesp 1989, 1991, Arens et al. 2001), speeding ecological succession (Cowles 1899), and increasing coastal protection by reducing wave overtopping (Sallenger 2000).

Changes in the physical environment in turn can influence ecological changes in community composition, succession trajectories, and vegetation growth form (Corenblit et al. 2008, Murray et al. 2008, Bouma et al. 2010, Hacker et al. 2011). Variations in the frequency or intensity of physical forces such as wind velocity, sediment supply, and near and onshore wave conditions, can lead to further modification of the physical and biological environment. Many of the landscape features we observe today are the result of numerous feedbacks between shifting species compositions and environmental conditions. Therefore, understanding the relative roles of ecological versus physical forces in the context of interface environments is necessary to make robust predictions about the future of these environments under intense human influence.

Here we investigate a dune interface environment on the Pacific Northwest coast of North America that is highly invaded by non-native grasses. In this system, vegetation, sand, wind, ocean currents, and waves interact to form landscape features that provide important functions and services along the coast. The vegetation in this system is dominated by three sand-binding beach grass species (two non-native invaders, *Ammophila arenaria* and *Ammophila breviligulata,* and one native, *Elymus mollis*). The purposeful introduction and subsequent spread of *Ammophila* species led to the development of vegetated and stabilized foredune ridges, replacing the open shifting dunes characterized by low density native vegetation (Cooper 1958). Today, these foredune ridges provide coastal protection from wave overtopping and inundation for communities and infrastructure on and behind the dunes (Sallenger 2000) but also have implications for native dune species and habitat conservation

(Seabloom and Wiedemann 1994, Wiedemann and Pickart 1996, Zarnetske et al. 2010, Hacker et al. 2011).

The introductions of the two *Ammophila* species are linked to variability in dune geomorphology. Dunes dominated by *A. arenaria* tend to be taller and narrower than dunes dominated by *A. breviligulata* (Seabloom and Wiedemann 1994, Hacker et al. 2011). Species-specific morphological differences (e.g., vertical vs. lateral growth habit) suggest that the three species may vary with respect to their ability to capture sand and in their growth response to subsequent sand deposition (Hacker et al. 2011). However, the species-specific mechanisms involved in sand capture and foredune development have not yet been measured in this system.

These observations are potentially confounded by co-varying gradients in sediment supply along the Oregon and Washington coast (Hacker et al. 2011, Ruggiero et al. 2011). Along the southern Washington and northern Oregon coast, where foredunes are typically low and wide, sediment supply is variable but mostly positive, and *A. breviligulata* is the dominant foredune grass. In contrast, along the central and southern Oregon coast, where the foredunes are taller and narrower, sediment supply is lower and more stable, and *A. arenaria* is the dominant foredune grass. Differences in sediment supply play a strong role in controlling coastal dune geomorphology (Hesp 1989, Psuty 1992). However, Hacker et al. (2011) found that with similar sediment supply conditions (as measured by shoreline change rates (SCR) ± 2 m/yr, where SCR is a proxy for sediment supply), dunes dominated by *A. arenaria* were taller than those dominated by *A. breviligulata*. These results imply an ecological control on dune shape.

Here we experimentally decouple the effects of species identity from sand supply to determine the ecological mechanisms responsible for dune shape variability. We propose the following biophysical feedback to explain differences in dune shape. First, differences in the form (structure and growth habit) of species lead to initial differences in function (sediment capture ability) (Fig. 3.1a). Second, species vary in

their growth response to sediment deposition. Third, deposition-induced changes in plant growth alter sediment capture. We suggest that this feedback reinforces species-specific sediment capture ability, eventually resulting in differences in dune shape with *A. arenaria* building taller, narrower dunes, *A. breviligulata* building lower, wider dunes, and *E. mollis* building the shortest, widest dunes (Fig. 3.1b).

Within the context of the feedback hypothesized above, we propose two non-mutually exclusive mechanisms: (1) species differ in their ability to capture sand, and (2) species differ in their growth habit in response to sand deposition. We controlled sand supply in two experiments to investigate the ecological mechanisms important to dune shape. First, we used a moveable-bed wind tunnel to investigate the influence of species and tiller density on sand capture ability. Second, we used a mesocosm experiment to investigate the effects of sand supply on the growth response of species.

3.2 METHODS

We used three species of beach grasses in the study – *A. arenaria* (originally from Europe) and *A. breviligulata* (originally from the east coast of North America and the Great Lakes) and *Elymus mollis* (native to the Pacific coast of North America). Superficially, these species appear similar, but each differs in a variety of plant morphological and growth habitat features (Appendix B, Hacker et al. 2011). Specifically, *A. arenaria* has numerous tillers with stiff blades and grows in a tussock form while *A. breviligulata* has moderate numbers of tillers with more flaccid blades, and grows in a less clumped distribution. Finally, *E. mollis* produces few tillers with limp blades, and grows in a more even distribution.

3.2.1 Assessing sand capture efficiency

We constructed a moveable bed wind tunnel at the O. H. Hinsdale Wave Research Laboratory (HWRL), Corvallis, Oregon, to perform sand capture efficiency experiments (see Appendix C for details on tunnel design and instrumentation). We

collected 3,000 adult tillers with intact rhizomes of each of the three grass species from the foredune face at Fort Stevens State Park, Clatsop Plains, Oregon (46˚ 09' 46" N 123˚ 58' 15" W) in May 2008 and planted them in 28, 1 m^2 x 0.3 m tall boxes filled with Oregon beach sand (median grain size 0.24 mm) at HWRL. Species were planted at three density blocks (125, 250, 500 tillers/m^2, Appendix C), reflecting a range of field densities on coastal foredune faces in the Pacific Northwest (Appendix B). In total, we used 28 boxes (3 replicates per species by density combination, 1 sand-only box).

We controlled the abiotic components of the experiment (supply of dry beach sand, wind velocity), so that we could isolate biotic factors influencing the sand capture outcome. Prior to an experimental run, each box was leveled to its surface with dry beach sand and placed into the wind tunnel test section. Windward (upstream) of the test section, a loaded bed of dry sand simulated a ground-level backshore beach environment, and unidirectional air flow transported sand toward the test section (downstream). To assess sand capture during low versus high wind conditions, we subjected each box to each of the following conditions, in random order: (1) 6 m/s wind for 4800 s, and (2) 9.5 m/s wind for 1200 s. We used test runs to determine these speed and duration combinations such that total sediment supply from the upstream sand bed (in kg/m/s) remained approximately constant across each experimental run. We calculated the sand provided to each test box (s_{in}) as the difference between the mass of the upstream load of sand before and after each experimental run, s_0 minus s_1. The proportion of sand captured (sand capture efficiency, *CE*) in the test box was the box's sand gain (in kg) divided by the amount of sand provided to the box, $CE = (b_1 - b_0)/s_{in}$, where b_0 is initial box mass, and b_1 is final box mass. Therefore, 1- *CE* is the proportion of sand transported through the test box. We computed the volumetric sediment transport rate per unit tunnel width, q, by dividing sand mass, s_{in}, by the density of sand (ρ_s = 1600 kg/m^3) per experimental run time (1200 or 4800 s) per tunnel width (1.0 m).

We normalized the sand capture efficiency for each experimental run such that we could compare results across species and densities, but within a wind velocity. We normalized *CE* to CE_{norm} (CE/q^*), by the non-dimensional volumetric sediment transport rate (q^*):

$$q^* = \frac{q}{D\sqrt{\frac{\rho_s - \rho_a}{\rho_a} gD}}$$

where q is the dimensional volumetric sediment transport rate, ρ_a is the density of air (1.2 kg/m^3), D is the median grain size (2.4e^{-4} m), and g is the acceleration of gravity (9.81 m/s).

We also investigated the response variable, highest sand deposition (cm): H_{max}. We measured this metric from vertical sand deposition around the tillers. At the start of the experiment, we marked sand level on each grass tiller with black permanent marker at the box surface, re-leveled prior to the second wind velocity experimental run. Following the experimental run, we re-marked each tiller with a colored marker at the final sand level (blue for 6 m/s, red for 9.5 m/s). After both wind velocity experiments occurred, we gridded off the boxes into 100, 10 cm^2 sections, clipped the tillers below the sand, and measured the gain or loss in sand level on up to 3 tillers per 10 cm^2 section, and calculated H_{max}.

We determined grass morphological characteristics for each box by measuring the longest blade, blades per tiller, and tiller circumference at initial sand level, for the same 3 tillers per 10 cm^2 section. For each box, we tallied the total number of tillers, and obtained dry biomass for plant material above the initial sand level by drying grasses to a constant mass in a 38˚C drying room for 24 hours. Further, we measured the average proportional flexure of vegetation in each box and velocity combination by measuring the vertical height of 3 random blades bent by the wind and dividing this value by the natural standing height of those random blades prior to turning on the fan.

3.2.2 Assessing the effects of sand deposition

We used a mesocosm experiment to assess the growth response of the three grass species to different levels of sand deposition. At Hatfield Marine Science Center, Newport, Oregon, we planted 41, 1 x 1 m^2 x (expandable) 2 m tall permeable geotextile bags with grass mixtures (3 species) or monocultures in 30 cm of beach sand in spring 2007. In this constant density mesocosm experiment, 5 adult plants per species from the Clatsop Plains foredune in Oregon, were planted in each of the mixture bags while 15 adult plants were planted in each of the monoculture bags (an adult plant=1 rhizome with varying number of tillers). Plants were allowed to establish for 3 months prior to sand deposition. Of the 41 bags, 8 mixture replicates (32 bags) were each subjected to different treatments of vertical beach sand deposition (0, 0.15, 2.20, and 4.20 cm) every 2 weeks for 1 yr (0, 3.6, 52.8, 100.8 cm deposition per year), and 3 monocultures of each species (9 bags) were each subjected to the non-zero deposition treatments. From bi-weekly sand level measurements in the bags, natural settling yielded vertical sand accumulation (or loss) rates of -3.0 cm/yr, 9.4 cm/yr, 31.0 cm/yr, and 46.3 cm/yr, and reflected a range of field vertical rates in the Pacific Northwest from 1997-2009 (Ruggiero et al. 2005, Ruggiero et al. 2011).

We measured growth responses for each species in each bag at the start and end of the experiment. These included tillers/m^2, tiller growth form (determined by the tiller angle from the main rhizome – an acute angle was deemed vertical, a right angle was deemed lateral), total plant dry biomass/m^2, and rhizome internode lengths (a proxy for growth response to deposition – measured on the first 16 internodes on the rhizomes of 4 random tillers per species-bag combination).

3.2.3 Statistical analyses

We used R version 2.12.1 for all statistical analyses (R Development Core Team 2010). Natural log transformations were applied to variables to conform to the

assumptions of linear regression (e.g., ln(CE_{norm})). Only non-correlated explanatory variables (|r|<0.6) were used together within one model.

To assess the mechanism responsible for varying sand capture efficiency, we ran mixed-effects models in R package nlme (Pinheiro and Bates 2000, R Development Core Team 2010) on the sand capture efficiency response vs. explanatory variables including species identity, morphology, and density. Each box was run at two wind velocities, and randomly ordered run number (1 or 2) was included as a random effect. Fixed effects always included a velocity term (6 m/s or 9.5 m/s; e.g., lme(ln(CE_{norm}) ~ velocity+species, random = ~1|run order), and additional factors including species identity and plant morphological characteristics (means per tiller, or per box, see Appendix D). We used likelihood ratio tests and Akaike's information criterion (AIC) for top model selection (Burnham and Anderson 2002, Zuur et al. 2009). We applied top models to 2009 tiller densities (tillers/m^2) on the foredune face to predict ln(CE_{norm}) and H_{max} for field densities (see Appendix B for field tiller data methods). For these predictions, we used mean blade flexure values per species-velocity combination (Appendix D).

To assess evidence for the growth response mechanism, we ran generalized linear models (GLMs) with associated ANOVAs on the plant growth response variables from the sand deposition experiment, and the sand deposition treatment rates (each with +0.01 offset to remove zero: 0.01, 3.61, 52.81, and 100.81 cm/yr). For these models we combined species mixture and species monoculture data after finding that the mixture/monoculture designation did not explain variation in these response variables.

3.3 RESULTS

3.3.1 Sand capture efficiency among grass species

Across all wind tunnel experiment densities, higher ln(CE_{norm}) was associated with lower wind velocity (6 m/s), higher tiller density, lower blade flexure (i.e., more

rigid tillers), and species identity (Table 3.1 model A, Fig. 3.2a). Blade flexure and tiller density were somewhat negatively correlated at both wind velocities (6 m/s r=-0.488, p=0.010; 9.5 m/s r=-0.559, p=0.002). For a given density, ln(CE_{norm}) was usually highest for *E. mollis*, followed by *A. breviligulata*, and *A. arenaria* (Fig. 3.2a), but only differed between *E. mollis* and *A. arenaria* at each wind velocity (fixed effects models per wind velocity: ln(CE_{norm})~species, Tukey HSD test: only *E. mollis* and *A. arenaria* comparison $p<0.05$). Many of the plant structural characteristics differed by species (Appendix D) but did not explain the variation in ln(CE_{norm}) across all experimental densities in mixed-effects models (Table 3.1). Tiller circumference, tiller cross-sectional area, biomass per tiller, overall above-sand biomass, blades per tiller, and tiller length were largest in *E. mollis*, moderate in *A. breviligulata*, and smallest in *A. arenaria* (Appendix D). Blade flexure explained variation in ln(CE_{norm}), even though it only differed between *E. mollis* and each *Ammophila* species at 6 m/s (Table 3.1, Appendix C). Predictions of ln(CE_{norm}) from the top model of all wind tunnel experiment densities (Table 3.1 model A), applied to field tiller densities show that *A. arenaria* can achieve higher ln(CE_{norm}) than the other species (Fig. 3.2b). For both wind velocities, the lowest vegetation density block (125 tillers/m^2) for each species had substantially higher ln(CE_{norm}) than the sand-only box (separate linear models for 6 m/s, 9.5 m/s: ln(CE_{norm})~ sand or species: Tukey HSD test: all sand - species comparisons $p<0.005$).

When we considered only wind tunnel experiment density blocks that represented field densities of species ("density blocks per species" – *E. mollis* 125/m^2, *A. breviligulata* 250/m^2, *A. arenaria* 500/m^2), ln(CE_{norm}) was almost equivalent among species (Table 3.1). However, mixed effects models for these densities showed that species identity did not explain ln(CE_{norm}) (fixed effects model: ln(CE_{norm})~ velocity+species, ANOVA: species $F=2.71$ (2,13), $p=0.108$, Tukey HSD test: all species comparisons $p>0.05$). Instead, after accounting for velocity, blade flexure and

tiller cross-sectional area were the most important (but not significant) variables (Table 3.1 model B).

Within the timeframe of the experiment, the highest sand deposition ($\ln(H_{max})$) was explained by higher wind velocity (9.5 m/s) and more tillers/m^2 across all wind tunnel experiment densities (Table 3.1 model C, Fig. 3.2c). Predictions of $\ln(H_{max})$ from the top model of all wind tunnel experiment densities (Table 3.1 model C), applied to field tiller densities show that *A. arenaria* can achieve higher $\ln(H_{max})$ than the other species (Fig. 3.2d). For the density blocks per species, $\ln(H_{max})$ was slightly higher for *A. arenaria* compared to *A. breviligulata* and *E. mollis* (Table 3.1). However, $\ln(H_{max})$ was not explained by species identity (fixed effects model: $\ln(CE_{norm})$~ velocity+species, ANOVA: species $F=0.937$ (2,13), $p=0.417$, Tukey HSD test: all species comparisons $p>0.05$), but was explained by higher velocity and fewer blades per tiller (Table 3.1 model D). Blades per tiller were highest for *E. mollis*, then *A. arenaria*, and *A. breviligulata*, and differed between *E. mollis* and each *Ammophila*, but not between *Ammophila* (Appendix D).

3.3.2 Growth responses of grass species with different sand deposition regimes

We found that growth habit and tiller density differed among species and sand deposition treatments (Table 3.2, Fig. 3.3). Final tiller density varied by species (Fig. 3.3a), with *A. arenaria* producing more tillers in response to higher sand deposition rates than *A. breviligulata* or *E. mollis*, both of which decreased tiller production with increasing sand deposition rate (Fig. 3.3a,b). Although all species increased biomass with increasing sand deposition rate, *A. arenaria* put on the most biomass at high sand deposition rates (Table 3.2, Fig. 3.3c). Vertical tiller growth was highest in *A. arenaria*, and increased relative to lateral tillers, especially as sand deposition rate increased (Table 3.2, Fig. 3.3d-f). Lateral tiller growth was greater than vertical tiller growth in both *A. breviligulata* and *E. mollis*, although the number of lateral tillers/m^2 declined as sand deposition rate increased (Table 3.2, Fig. 3.3d-f). Finally, mean

internode length (and maximum, not shown) increased for each species as sand deposition rate increased (Table 3.2, Fig. 3.3g).

3.4 DISCUSSION

Together, the wind tunnel and mesocosm experiment results provide evidence for a biophysical feedback among plant growth form and sand deposition, leading to differences in the shapes of dunes dominated by the two grass invaders along the Pacific Northwest coast. The dense, vertical growth habit of *A. arenaria* allows it to capture more sand, produce more vertical tillers, and build taller, narrower dunes, while the less dense, lateral growth habit of *A. breviligulata* is more suited for building shorter but wider dunes. Although *Ammophila arenaria* has been assumed to be a superior dune building species by coastal managers and engineers over the last century (as reflected in the widespread planting of *A. arenaria* around the world), this is the first study to directly measure the dune building capacities of multiple grass species exposed to similar environments. This is also the first study known to connect these mechanistic findings of species-specific sand capture and growth responses with observed gradients in sediment supply, vegetation, and dune geomorphology in the field.

Our wind tunnel experiment showed that the highest sand capture efficiencies ($\ln(CE_{norm})$) belong to the native *E. mollis* compared to the two invasive *Ammophila* species (Fig. 3.2a). Under controlled tiller density manipulations, it appears that the tillers and biomass of *E. mollis* provide greater surface area, thus impeding the movement of sand grains, resulting in greater sand deposition around the tillers (Appendix D). In support of this mechanism, *A. breviligulata* also has slightly thicker tillers and more biomass per tiller compared to *A. arenaria* (Appendix D) and it too has slightly higher $\ln(CE_{norm})$ than its congener (Fig. 3.2a). However, these plant morphological characteristics did not explain differences in $\ln(CE_{norm})$ as they were

either not significant in top models, or did not appear in any competing top models (Table 3.1).

The effect of tiller morphology is mitigated by tiller density. In fact, except for wind velocity (where decreased velocity resulted in greater ln(CE_{norm})), tiller density was the most important explanatory variable influencing sand capture efficiency (Table 3.1 model A, Fig. 3.2a). Another important variable was blade flexure, with lower flexure (stiffer blades) resulting in greater overall capture efficiencies (Table 3.1 model A). This result makes sense because blade flexure is likely a consequence of tiller density, where surrounding blades provide increased structural support (Appendix B, C2). Our finding that higher vegetation density increases and sediment capture and deposition agrees with other research (Hesp 1989, Arens et al. 2001, Murray et al. 2008, Burri et al. in press). Nonetheless, for a given density used in the wind tunnel experiment, the native grass is slightly better at capturing sand than the invasive species.

To explore the sand capture results further, we applied the top wind tunnel experiment model (Table 3.1 model A) to field tiller densities to predict field ln(CE_{norm}), under the experimental timeframes and velocities (Fig. 3.2b). We find that, because *A. arenaria* and *A. breviligulata* both have much higher tiller densities in the field than *E. mollis*, the two invasive grasses are capable of much higher sand capture efficiencies (3.7 to 5.1 times at 6m/s and 3.5 to 4.8 times at 9.5m/s) compared to the native grass. For example, *E. mollis* can reach as high as 250 tillers/m^2 on the foredune face, but lower tiller densities are more common (mean: 44.45 ± 5.04, Appendix B), suggesting that it never reaches densities in which it can capture as much sand as the two congeners (Fig. 3.2b). On the other hand, the field densities of *A. arenaria* tillers can be high, reaching upwards of 1110/m^2 (mean: 203.08 ± 27.26) thus potentially allowing *A. arenaria* to capture more sand than the other species under natural conditions (Fig. 3.2b).

Moreover, our field data suggest that the differences in natural growth form could play an important role in sand capture efficiencies being higher for *A. arenaria*. While random tiller placement in the wind tunnel allowed us to separate the effect of species from tiller density, this tiller arrangement does not necessarily reflect the natural growth form in the field. In nature, *A. arenaria* develops a high density, tussock-like tiller growth, where multiple vertical tillers grow from proximal rhizomes in a clumped manner (Appendix D, Greig-Smith et al. 1947, Gemmell et al. 1953, Huiskes 1979). Conversely, *A. breviligulata* has a lower density, lateral, and less clumped tiller growth pattern, especially in regions of high sediment supply (Appendix D, Maun and Lapierre 1984, Baye 1990). Thus, these differences in growth form could create variability in capture efficiencies in the field that are not reflected in the wind tunnel. Further, wind tunnel studies with cylinder arrays (rather than living plants) support our hypothesis for larger differences in species-specific sand capture, based on differences in tiller morphology. Studies with high cylinder aspect ratios (height/diameter) – analogous to *A. arenaria* tillers – require lower densities to achieve the same sand capture as cylinders with lower aspect ratios. Within higher aspect ratio cylinder arrays, higher threshold wind velocities are necessary to mobilize sand (Musick et al. 1996). Conversely, an array with lower cylinder aspect ratios – analogous to *A. breviligulata* tillers or, with even lower aspect ratios, *E. mollis* tillers – requires higher densities to achieve the same sand capture. Thus at higher field densities, the greater tiller aspect ratio of *A. arenaria*, combined with its vertical growth should yield more efficient sand capture than natural densities of *A. breviligulata* or *E. mollis*.

Sand capture is one measure of how the grasses may influence dune geomorphology but growth response to sand deposition is potentially more important. Evidence from the mesocosm experiment shows that species differ in their growth response to sand deposition rates. Across sand deposition rates, *A. arenaria* outpaced *A. breviligulata* and *E. mollis* in tiller growth (especially in vertical tiller growth) and

in biomass (Table 3.2, Fig. 3.3). All species increased their internode lengths with increasing sand deposition rate (Table 3.2, Fig. 3.3g). However, while the increased internode length of *A. arenaria* contributes to vertical growth in tussock-like form, the increased internode lengths of *A. breviligulata* and *E. mollis* combined with their lower tiller density and higher proportion of lateral tillers, shows that their growth strategy is distinctly horizontal and spreading (Table 3.2, Fig. 3.3).

The combination of species-specific growth response to sand deposition, differences in tiller density and arrangement in nature, and projected sand capture should all reinforce a dune growth positive feedback, leading to differences in dune shape (Fig. 3.1b). Specifically, taller, narrower dunes along the Pacific Northwest coast are dominated by high-density, vertical *A. arenaria* tillers and typically occur in regions of fairly neutral shoreline change rates (Hacker et al. 2011). Under these conditions, a relatively neutral overall beach sediment budget combined with sediment available for transport to the foredune, leads to long-term sand accumulation on the dune (Psuty 1993). Wind-blown sand is captured on the foredune face by high-density, vertical *A. arenaria* tillers which increase the sand transport threshold wind velocity, thus promoting sand deposition (Bagnold 1941, Lancaster and Baas 1998). The dune elevation increases with the positive feedback of continued sand capture and deposition, and a growth response of more vertical, tussock-like tillers that result in higher tiller density per area (Fig. 3.1b, Baye 1990, Maun 1998, de M. Luna et al. 2011). Conversely, lower, wider dunes are dominated by lower-density, lateral *A. breviligulata* tillers and typically occur in regions of positive shoreline change rates. Under these conditions, the shoreline extends seaward as large amounts of sand deposit on the beach, and wind-blown sand is carried farther inland due to the relatively minor obstruction of a low elevation foredune (Psuty 1993). Sand that does deposit on the dune encounters lower density vegetation, with less efficient capture ability (Bagnold 1941, Lancaster and Baas 1998). This high sediment supply, in turn, promotes a positive feedback with *A. breviligulata* to send out lateral tillers which

decreases tiller density per area and thus sand capture efficiency, resulting in a low, wide foredune shape (Fig. 3.1b, Baye 1990, Hacker et al. 2011). Although no *E. mollis* dominant foredunes exist along the coast, our results show that its low density, lateral tiller growth would yield low, broad foredunes across sediment supply rates (Fig. 3.1b).

Our findings suggest that the growth response of *A. breviligulata* to sediment supply, and the resulting low, wide dunes, are causes for concern for dune restoration and coastal vulnerability. Its apparent constant growth across sediment supply gradients (Table 3.2, Fig. 3.3) suggests that it is more indifferent to the range of sediment supplies than *A. arenaria*, and thus may be more difficult to control. Further, our field data show that through time, *A. breviligulata* has displaced *A. arenaria* along the Pacific Northwest coast (Seabloom and Wiedemann 1994, Hacker et al. 2011). Thus, the apparent constant growth of *A. breviligulata* across multiple sediment supply regimes, its ability to generate shorter dunes, and its possible superior competitive effects on *A. arenaria* and native species diversity, implies that it could have negative effects on coastal protection and native species conservation (Hacker et al. 2011).

Our study used sand capture and sand deposition experiments to characterize the ecological mechanisms responsible for variation in foredune shape along the Pacific Northwest coast. Our results suggest that a species-specific biophysical feedback between sand deposition, growth habit, and growth-habit-mediated sand capture efficiency has led to distinctly different dune geomorphologies. This knowledge can be incorporated into dune building models (Pattanapol et al. 2008, de M. Luna et al. 2011) that expand the plant-scale sediment capture mechanisms to ecosystem-scale dynamics. These models in turn, can assist in coastal management, restoration, and engineering decisions through the resulting dune geomorphology predictions. Given that vegetation plays an important role in foredune evolution, it will also be important to include vegetation parameters in models predicting risk to wave overtopping and coastal vulnerability, especially in light of the range of possible

climate change influences on sea level rise (Bindoff 2007) and increased storm intensity. More generally, understanding how dominant ecosystem engineers differ in their interactions with abiotic factors is necessary to make predictions of changes to physical environmental features, to guide ecosystem restoration efforts, and to inform decision-making that balances the need for ecosystem services and ecosystem conservation.

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Table 3.1. Top linear mixed effects models (LME) from the wind tunnel experiment (using restricted maximum likelihood methods). Variables were transformed based on residual vs. fitted plots, and normal quantile plots. All models contain a Gaussian link function, and non-correlated explanatory variables ($|r|<0.6$). For top model selection, we used AIC and likelihood ratio tests (LR=likelihood ratio). For competing models within $\Delta AIC = 2$, we chose the most parsimonious model. "All Wind Tunnel Densities" are data from all experimental units (n=27)); "Density Blocks per Species" are data from experiment density blocks reflecting field densities (*A. arenaria* (AMAR) 500 tillers/m^2 (n=3), *A. breviligulata* (AMBR) 250 tillers/m^2 (n=3), and *E. mollis* (ELMO) 125 tillers/m^2 (n=3)). For Density Blocks per Species, $\ln(CE_{norm})$ was almost equivalent among species (AMAR 6m/s: 9.316 ± 0.063; 9.5m/s: 6.811 ± 0.103; AMBR 6m/s: 9.210 ± 0.061; 9.5m/s: 6.689 ± 0.193; and ELMO 6m/s: 9.191 ± 0.063; 9.5 m/s: 6.474 ± 0.047), as was $\ln(H_{max})$ (AMAR 6m/s: 1.315 ± 0.107; 9.5m/s: 1.678 ± 0.094; AMBR 6m/s: 1.104 ± 0.203; 9.5m/s: 1.587 ± 0.147; and ELMO 6m/s: 1.314 ± 0.084; 9.5 m/s: 1.358 ± 0.130).

Response Metric	**Fixed Effects Model**	**Model Results**	**LME ANOVA F-stat, p-value**
(A) All Wind Tunnel Densities: $\ln(CE_{norm})$	$\ln(CE_{norm})$ = 13.110 -0.677[Velocity] +0.003[Tillers/m^2] -1.0978[Blade Flexure] -1.066[AMAR] -0.441[AMBR]	df=47 AIC=60.907 ΔAIC=1.956 LR= 0.045, p=0.8321	Velocity: F=999.55 (1,47), p<0.0001 Tillers/m^2: F=160.34 (1,47), p<0.001 Blade Flexure: F=5.74 (1,47), p=0.021 Species: F=50.68 (2,47), p<0.0001
(B) Density Blocks per Species: $\ln(CE_{norm})$	$\ln(CE_{norm})$ = 14.374 -0.724 [Velocity] -3.511[Tiller Cross-Sectional Area] -2.207[Blade Flexure] +9.260[Tiller Cross-Sectional Area * Blade Flexure]	df=12 AIC=1.698 ΔAIC=0.447 LR= 4.447, p=0.108	Velocity: F=858.17 (1,12), p<0.0001 Tiller Cross-Sectional Area: F=0.20 (1,12), p=0.664 Blade Flexure: F=2.02 (1,12), p=0.180 Tiller Cross-Sectional Area * Blade Flexure: F=1.19 (1,12), p=0.297

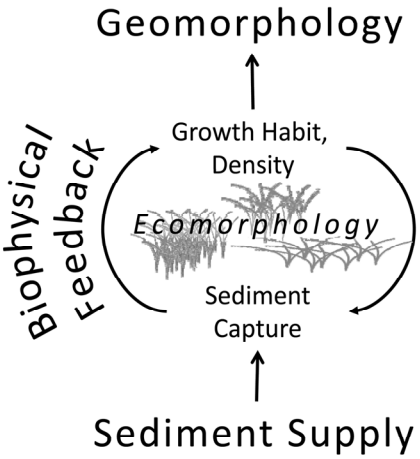
(C) All Wind Tunnel Densities: $\ln(H_{max})$	$\ln(H_{max}) = 0.694 + 0.074$ [Velocity] $+ 0.0005$ [Tillers/m^2]	df=50 AIC=7.202 ΔAIC=0 LR=9.315, p=0.002	Velocity: F=26.203 (1,50), p<0.001 Tillers/m^2: F=8.907 (1,50), p<0.001
(D) Density Blocks per Species: $\ln(H_{max})$	$\ln(H_{max}) = 1.873 + 0.088$ [Velocity] $- 0.227$ [Blades per Tiller]	df=14 AIC=13.112 ΔAIC=0.583 LR=2.583, p=0.108	Velocity: F=11.197 (1,14), p=0.005 Blades per Tiller: F=6.319 (1,14), p=0.025

Table 3.2. Top generalized linear models (GLM) for the mesocosm experiment. Response or explanatory transformations were applied based on residual investigations (residual vs. fitted plots, normal quantile plots). All models contain a Gaussian link function. Models contain only non-correlated explanatory variables ($|r|<0.6$). For top model selection, we used Akaike's information criterion (AIC). Letters preceding response metrics align with Fig. 3.3 plot letters. Multiple top models are shown as "M1" and "M2". In models, sand is the treatment deposition (cm/yr), where 0.01 was added to each deposition value (0.01, 3.61, 52.81, 100.81 cm/yr).

Response Metric	Fixed Effects Model	Model Results	GLM ANOVA F-stat, p-value
(A) ln(Final Number Tillers/m^2)	M1: ln(Tillers) = 4.289 +1.143 [AMAR] +0.637 [AMBR] – 0.002 [Sand]	df =101 AIC=148.12 ΔAIC=0	Species: F=50.594 (2,101), p<0.001 Sand: F=2.310 (1,101), p=0.132
	M2: ln(Tillers) = 4.220 +1.143 [AMAR] +0.637[AMBR]	df =102 AIC=148.49 ΔAIC=0.37	Species: F=49.952 (2,102) p<0.001
(B) ln(Relative Gain in Tillers/m^2)	ln(Relative Gain) = 3.774 + 1.310[AMAR] + 0.841 [AMBR]	df=102 AIC=237.52 ΔAIC=0	Species: F=28.733 (2,102), p<0.001
(C) ln(Relative Gain in Dry Biomass, g/m^2)	ln(Relative Gain) = 3.427 + 0.368[AMAR] +0.327[AMBR]+ 0.003[Sand]	df=101 AIC=146.49 ΔAIC=0	Species: F=6.377 (2,101), p=0.002 Sand: F=9.594 (1,101), p=0.003
(D) ln(Final Number Lateral Tillers/m^2)	ln(Laterals) = 2.871 -1.733 [AMAR] + 0.061 [AMBR]	df=102 AIC=313.79 ΔAIC=0	Species: F=32.738 (2,102), p<0.001
(E) ln(Final Number Vertical Tillers/m^2)	ln(Verticals) = 3.533 + 1.816 [AMAR] +1.091[AMBR]	df=102 AIC=265.00 ΔAIC=0	Species: F=41.994 (2,102), p<0.001

(F) ln(Gain in Vertical Tillers/Gain in Lateral Tillers)	M1: ln(Gain) = 0.793 + 0.970 [AMAR] +0.864 [AMBR] – 0.002 [Sand] +0.014[AMAR*Sand] – 0.003 [AMBR*Sand]	df=99 AIC=352.96 ΔAIC=0	Species: F=13.188 (2,99), p<0.001 Sand: F=0.385 (1,99), p=0.536 Species*Sand: F=3.165 (2,99), p=0.047
	M2: ln(Gain) = 0.721 + 1.536 [AMAR] +0.737 [AMBR]	df=102 AIC=353.85 ΔAIC=0.89	Species: F=12.725 (2,102), p<0.001
(G) Mean Internode Length (cm)	Length = 3.938 +0.013 [Sand]	df=100 AIC=320.97 ΔAIC=0	Sand: F=23.279 (1,100), p<0.001

A)



B)

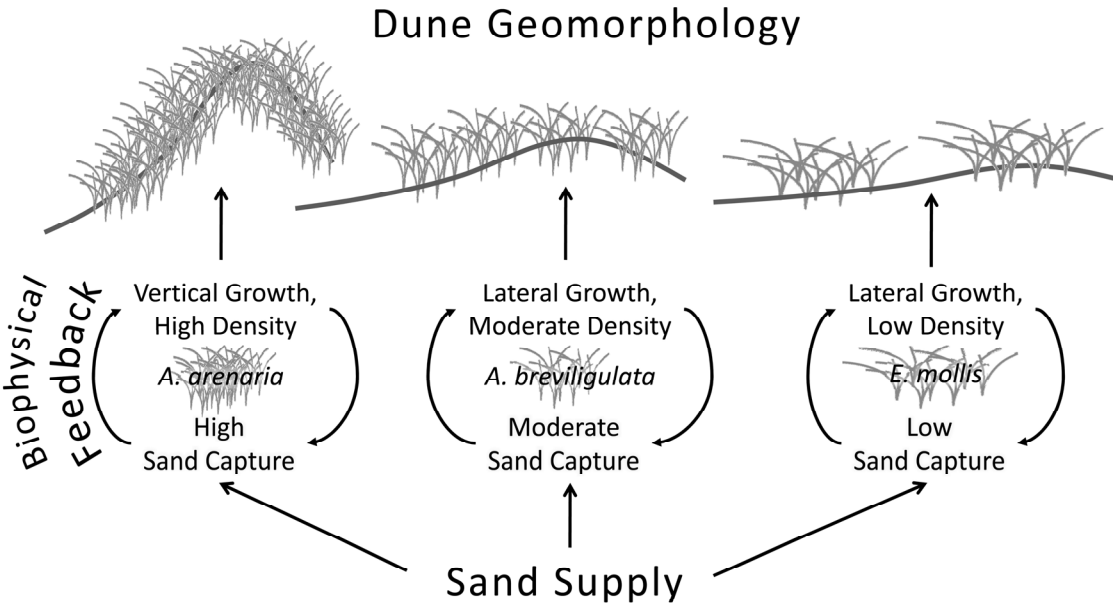


Figure 3.1. A) Conceptual diagram showing the important biophysical feedback between vegetation and sediment. Vegetation characteristics (growth habit, density) and sediment supply form the basis for the sediment capture process, which is continually modified through feedbacks between vegetation growth and sediment capture. B) Expected feedbacks and resulting dune geomorphology for the study system.

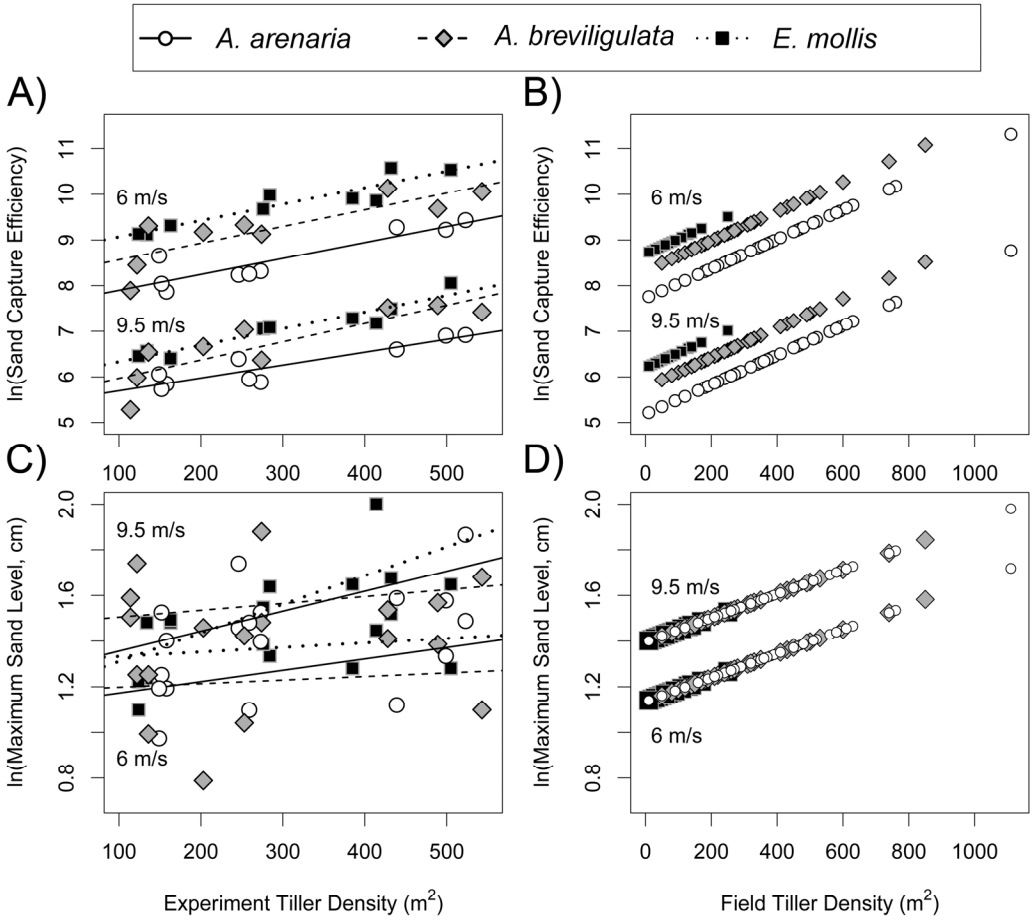


Figure 3.2. For low (6 m/s) and high (9.5 m/s) wind velocity, A) natural log of normalized sand capture efficiency ln(CE_{norm}) for grass species, across all experiment densities, B) predictions of ln(CE_{norm}) for maximum natural field tiller densities at 6 m/s and 9.5 m/s wind velocities, using Table 3.1 model A, applied to natural field densities on the foredune face (Appendix B), and mean blade flexure values from Appendix D, C) maximum sand deposition level (cm) (H_{max}) within each box, across all experiment densities (multiple regression lines are shown but species do not differ within velocity), D) predictions of H_{max} for maximum natural field tiller densities at 6 m/s and 9.5 m/s wind velocities, using Table 3.1 model C applied to natural field densities on the foredune face (Appendix B).

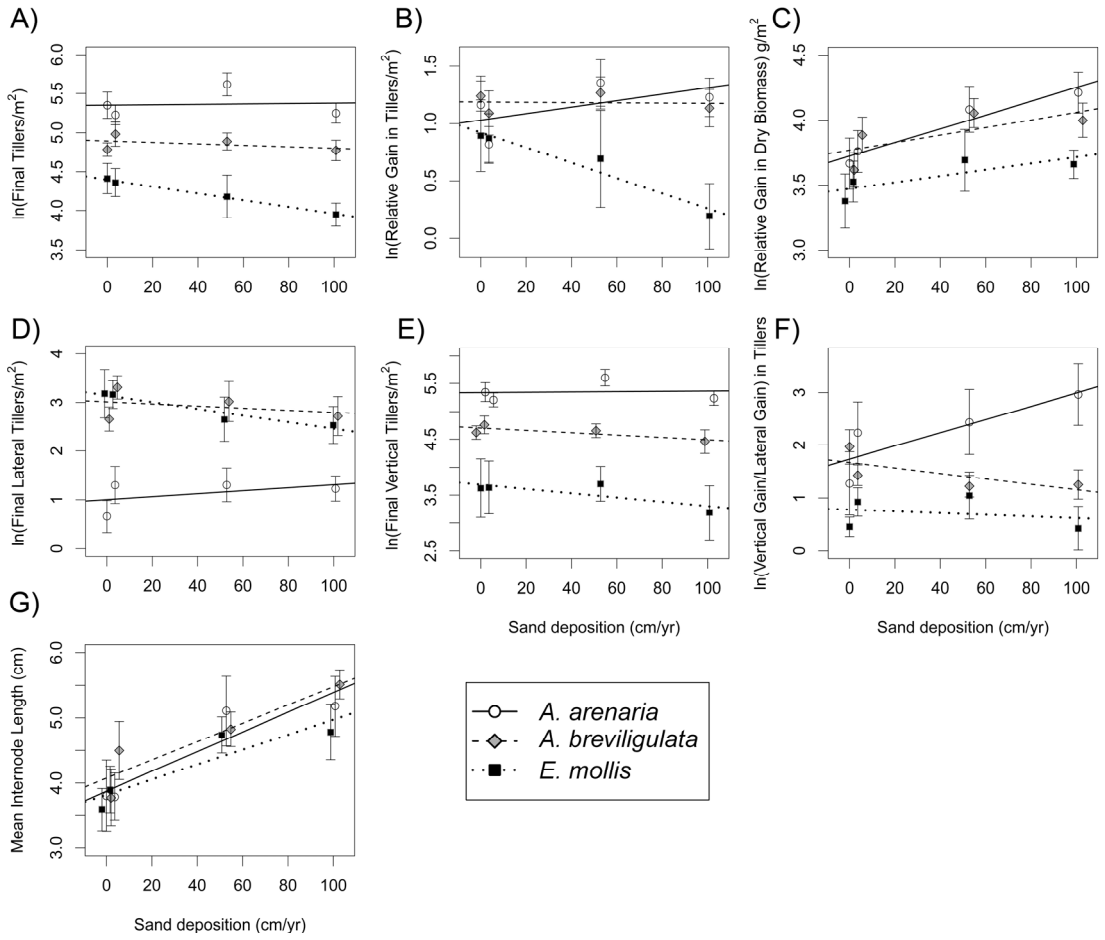


Figure 3.3. Grass species growth responses from sediment deposition treatments in the mesocosm experiment (0, 3.6, 52.8, 100.8 cm deposition per year). Plant data from the experiment are scaled to 1 m^2. All data points are mean ± 1SE: A) ln(final number of tillers/m^2), B) ln(relative gain in tillers/m^2) = ln((final tillers/m^2 - initial tillers/m^2)/initial tillers/m^2), C) ln(relative gain in dry biomass g/m^2) = ln((final dry biomass/m^2 – initial dry biomass/m^2)/initial dry biomass/m^2), D) ln(final number of lateral tillers/m^2), E) ln(final number of vertical tillers/m^2), F) ln(gain in number of vertical tillers/gain in number of lateral tillers), G) mean internode length. See Table 3.2 for model statistics matching these figures.

4 – Indirect effects, facilitation, and sand supply gradients mediate coexistence on coastal dunes

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ABSTRACT

Recently ecologists have revisited species coexistence theory to emphasize the notion that co-occurring species may not coexist at equilibrium. In reality, communities are likely composed of both transitionally co-occurring and species that may coexist at equilibrium – knowing the difference can be especially important in invasion ecology because invaders that can coexist, can invade and persist in the community. We use a 3-species Lotka-Volterra model parameterized with experimental and long-term field data to determine (1) whether patterns in species co-occurrence equate to coexistence, (2) whether native - non-native coexistence is context dependent, (3) the mechanisms mediating coexistence, and (4) whether non-native species can invade new regions. Our system consists of three dominant Pacific Northwest coastal dune building grass species (two non-native invaders: *Ammophila arenaria*, *A. breviligulata*, and one native *Elymus mollis*). Our results indicate that although sand supply increased the strength of facilitation and indirect effects, it had little impact on community structure. Indeed, regardless of sand supply, all species could coexist in communities dominated by *A. breviligulata*. The model analysis and simulation suggests that if *A. breviligulata* were introduced to new coastal regions, it would invade and become the dominant foredune species. Such an invasion may reduce the coastal protective services afforded by tall dunes currently dominated by *A. arenaria* because *A. breviligulata* is an inferior dune building species.

4.1 INTRODUCTION

The ability of novel species to establish in a new community depends on an array of direct and indirect interactions among species and their environment (see (Menge 1995, Mack et al. 2000, Shea and Chesson 2002, Mitchell et al. 2006 for reviews). The strength and direction of these species interactions are context dependent and their outcome depends on such factors as resource supply, physical stress, disturbance, and life history stage (e.g., see Callaway and Walker 1997).

Ultimately, once a novel species makes it to a resident community, its long term persistence will depend on its ability to coexist with other species (Seabloom et al. 2003).

Coexistence has been a cornerstone of ecology since the 1930's (Gause 1934), and provides a means to investigate the factors responsible for native and non-native species to live together in one place. Species are only able to coexist indefinitely if they have a positive per capita growth rate when they are rare and their competitor is at equilibrium abundance - termed the "invasibility criterion" for coexistence (MacArthur 1972, Holt 1997, Chesson 2000); this holds even if the mechanism for coexistence is not known (Siepielski and McPeek 2010). Recently, ecologists have revisited coexistence theory to emphasize that co-occurring species are not necessarily coexisting species, and to suggest ways to improve the rigor in determining coexistence (including adopting the use of the invasibility criterion (Siepielski and McPeek 2010, Gravel et al. 2011)). Coexisting species are a special subset of co-occurring species. Co-occurring species can be in a transitory state that ultimately leads to the extinction of some species either through random neutral processes (Hubbell 2001) or by other species (Leibold and McPeek 2006), or that ultimately maintains species via incoming dispersers within the context of source-sink dynamics (Pulliam 1988). In reality, communities are likely composed of both co-occurring and coexisting species (Siepielski and McPeek 2010) – determining which species can coexist identifies those which are more likely to remain in the community despite interactions with other species, and improves our understanding of community regulation.

Several mechanisms may lead to equilibrial coexistence between species. Research on the mechanisms leading to native - non-native coexistence has focused on competition avoidance mechanisms (Shea and Chesson 2002), apparent competition (Borer et al. 2007), and the role of spatial heterogeneity (Melbourne et al. 2007). There is also evidence that facilitation (Bertness and Callaway 1994, Hacker and

Gaines 1997, Bruno et al. 2003) and indirect effects (Holt 1977, Menge 1995) are key mechanisms of community regulation and coexistence. However, evidence is only beginning to accumulate on facilitative interactions promoting native - non-native coexistence (Palmer and Maurer 1997, MacDougall and Turkington 2005, Rodriguez 2006, Wolkovich et al. 2009, Altieri et al. 2010), and there is a knowledge gap regarding indirect effects as a mechanism for native - non-native coexistence. In reality, the mechanisms driving native - non-native coexistence are likely to be complex – including a combination of positive and negative direct and indirect interactions that are context dependent.

Here we use field data, experiments, and modeling and simulation to explore the mechanisms of native - non-native coexistence across environmental gradients to ask 1) whether the co-occurrence of species equates to their coexistence, 2) whether coexistence is mediated by the environment, 3) what mechanisms are important for coexistence to occur, and 4) whether non-native species can invade new areas following an introduction. Our study system is composed of beach grass communities found along the Pacific Northwest (PNW) coastal dunes. These dunes are dominated by three beach grass species – the native grass, *Elymus mollis*, and two non-native grasses, *Ammophila arenaria*, and *A. breviligulata*. Both non-native species were introduced for sand stabilization to the PNW beginning over a century ago (*A. arenaria* late 1800's, *A. breviligulata* 1935) and subsequently invaded dune backed beaches which comprise nearly 50% of the coastline (Seabloom and Wiedemann 1994, Wiedemann and Pickart 2004). Each invader has different effects on native community composition (Hacker et al. 2011) and dune geomorphology (Zarnetske et al. in review). The primary environmental gradient in this system is ocean-derived sand supply to the beach and dunes (Cooper 1958, Ruggiero et al. 2005, Ruggiero et al. 2011).

The three beach grass species co-occur in some regions of the coast but not others (Hacker et al. 2011). Since its introduction, *A. breviligulata* expanded its range

into foredunes with moderate to high sand supply rates (previously dominated by *A. arenaria*) where it now dominates but co-occurs with *E. mollis* and to a lesser extent, *A. arenaria* (Seabloom and Wiedemann 1994, Hacker et al. 2011). Today, *A. breviligulata* remains largely absent from foredunes with low sand supply rates (where *A. arenaria* is dominant and co-occurs with *E. mollis*) but it is unclear whether this is a consequence of dispersal limitation, species interactions, different physiological tolerance of sand supply, or some combination of these factors (Hacker et al. 2011). The spread and distribution of *A. breviligulata* has also been correlated with lower dunes (Seabloom and Wiedemann 1994, Hacker et al. 2011), and our recent research suggests that it is inferior to *A. arenaria* in terms of its ability to capture sand and build dunes (Zarnetske et al. in review). Thus, we are interested in whether *A. breviligulata* can coexist with the other two grass species across sand supply rates, and if so, what mechanisms are responsible for this coexistence. The answers to these questions will help determine if *A. breviligulata* can invade new sections of coastline, which may have implications for dune shape and the coastal protective properties of these important barriers to wave inundation.

4.2 METHODS

We assessed coexistence of PNW native and non-native beachgrass species across three sand supply regimes, using a 3-species Lotka-Volterra model for each sand supply rate, parameterized with experimental and observational data. We used three forms of constraints to simultaneously determine the best fit model and best fit parameters within a nonlinear optimization technique with a built-in ordinary differential equation solver. The three constrained components included: a time series of five abundance datapoints (t_0 to t_4) per sand supply, the structural constraint of the Lotka-Volterra model, and bounded constraints per given sand supply regime on each Lotka-Volterra parameter. These constraints are described below, following the data collection descriptions.

4.2.1. Data collection

Species interaction experiment

We manipulated species and sand supply rate to measure the effect of sand supply on species interactions and coexistence. We performed this experiment outside, at Hatfield Marine Science Center (HMSC), in Newport, Oregon. The experiment consisted of 41, 1 m x 1 m x 2 m permeable geotextile bags planted with 3-species grass mixtures or monocultures in 30 cm beach sand in May 2007. Plant density was constant, with 5 individual adult plants of each species planted in mixtures, and 15 individual adult plants per species, planted in monocultures. All plants came from the foredune in Clatsop Plains, Oregon. We define an adult plant as 1 rhizome with varying number of tillers. Of the 41 bags, 8 mixture replicates (total=32 bags) were each subjected to a different treatments of vertical beach sand deposition (0.15, 2.20, and 4.20 cm) every 2 weeks, consecutively for 1 yr, beginning in July 2007, and ending in July 2008. We completed the experiment in September 2008, and removed the plants for processing. Three monocultures of each species (total=9 bags) were each subjected to the same sand deposition treatments. In this manner, we applied vertical sand supply rates of 3.6 cm/yr (low), 52.8 cm/yr (mid), 100.8 cm/yr (high) that, after accounting for sand settling via bi-weekly measurements (9.4 cm/yr, 31.0 cm/yr, 46/3 cm/yr), reflected a range of dune vertical growth rates on fronts of foredunes along the Pacific Northwest Coast from 1997-2009 (Ruggiero et al. 2005, Ruggiero et al. 2011).

Our abundance response metric for each species was total dry biomass. To obtain dry biomass, we counted the number of tillers at the initial time (t_0), at 5 months (t_1), and at 15 months at the end of the experiment (t_2). To estimate dry biomass from tiller numbers at t_0 and t_1, we counted the number of tillers per species and determined the ratio of live to dry biomass of 10 extra plants per species at t_0 and applied a live-to-dry ratio to the live biomass per tiller. We ran linear models on these data and applied the best model to estimate dry biomass at t_0 and t_1 from the known tiller counts in each bag (Appendix E, Appendix A.1). We used actual dry biomass for

the values at the end of the experiment (t_2). We obtained dry biomass by drying samples at 38° C for 24 hrs.

Field data

In summer 2009, we recorded tiller numbers per species within 20 x 50 cm quadrats placed on the foredune front at 5 m intervals along 84 vegetation transects across the PNW (see (Hacker et al. 2011) for transect methodology). Of these 84 transects, we used 48 where at least 2 species co-occurred on the foredune front. We then binned these transect locations by low, mid, and high dune vertical growth rates (VGR) to match low, mid, and high sand supply treatments from the experiment. Dune vertical growth rate is the average rate of vertical dune growth in m/yr from 1999-2009, computed at the horizontal location of the end year crest elevation, and obtained with either (1) high resolution GPS survey techniques taken quarterly from 1999 to 2009, and spaced approximately every 1 km along the coast north of Seaside, Oregon (and interpolated to our vegetation transect locations), or (2) a regression between VGR and its proxy, shoreline change rate, calculated directly at all vegetation transects south of Seaside, Oregon (Ruggiero et al. 2005, 2011) (Appendix E).

We determined abundance at t_3 and t_4 by counting the number of tillers per species and sand supply treatment at the end of the species interaction experiment (t_2) and running linear models on the number of tillers and their dry biomass. We applied the best model per species and sand supply to estimate field abundance (dry biomass) at t_3 and t_4 from the field tiller counts (see Appendix A.1).

4.2.2. Model development

Data time series

We constructed an abundance time series for each species (*A. arenaria, A. breviligulata, and E. mollis*) and sand supply rate (low, mid, high). Data from the species interaction experiment captured exponential growth (datapoints t_0 to t_2) and

data from the field represented long term trends (datapoints t_3 and t_4). For each species and sand supply rate, the first 3 abundance datapoints were the mean dry biomass/m^2 of the corresponding 8 replicate mixture mesocosm units (see Appendix E). The last 2 abundance datapoints for each species and sand supply rate came from the corresponding mean field biomass across foredune fronts (see Appendix E). We varied the first long-term data point t_3 over 10 linearly spaced time points (between t_2 + 1 yr and t_4 – 1 yr) to allow species to take different amounts of time to achieve long term field abundances (Appendix E, F). However, we fixed the final datapoint (t_4) according to the mean lifespan of a foredune in each sand supply regime (i.e., the time from foredune initiation to completion), and thus the time that a grass would exist on that same foredune (Appendix E).

3-species Lotka-Volterra competition model

We used the per-species abundance from the experiment and field to generate parameters for our models. Below we describe how we obtained each of the parameters in the following set of equations comprising the 3-species Lotka-Volterra model:

for *A. arenaria*: $$\frac{dN_A}{dt} = r_A N_A \left(1 - \left(\frac{N_A + \alpha_{AB}N_B + \alpha_{AM}N_M}{K_A}\right)\right)$$

for *A. breviligulata*: $$\frac{dN_B}{dt} = r_B N_B \left(1 - \left(\frac{N_B + \alpha_{BA}N_A + \alpha_{BM}N_M}{K_B}\right)\right)$$

for *E. mollis*: $$\frac{dN_M}{dt} = r_M N_M \left(1 - \left(\frac{N_M + \alpha_{MA}N_A + \alpha_{MB}N_B}{K_M}\right)\right)$$

Our abbreviations for species are based on their species name: A is *A. arenaria* (AMAR), B is *A. breviligulata* (AMBR), and M is *E. mollis* (ELMO). The system of equations above was repeated for each of 3 sand supply rates – low, mid, and high. For a given species A, B, or M, N is its abundance, K is its carrying capacity, r is its intrinsic rate of growth, and α_{ij} is the per capita effect of species j on species i where

$\alpha_{ij}>0$ is a negative effect of species *j* on *i*, and $\alpha_{ij}<0$ is a positive effect of species *j* on *i*. The value of $|\alpha_{ij}|$ is the strength or magnitude of the interaction.

Parameter constraints

All parameter values and their constraints were derived from experimental and/or field data (Appendices E, G). We constrained the *K* and *r* parameters by allowing them to vary between two endpoints specific to each sand supply rate. The *K* of each species per sand supply rate varied between the corresponding (1) final experimental monoculture biomass (at t_2), and (2) the mean biomass of field monocultures (Appendix H, H.1). The *r* for each species varied between the rate at zero, solved from (1) an exponential curve fit between the t_0 monoculture and t_1 monoculture biomass, and (2) a linear curve between the same points (Appendix H, H.2). The α values were unconstrained but were given a starting estimate in the optimization procedure based on the experimental interaction strengths (Appendix G).

4.2.3. Model analysis

Best-fit parameters

We used a nonlinear optimization method based on the simplex search algorithm described by Lagarias et al. (1998) to find the model parameter estimates (K, r, α) that minimized the difference between the observed abundance time series of all species and those predicted by the 3-species Lotka-Volterra model (i.e., the cost function) for each of the three sand supply rates. To generate the model time series for each set of parameter values, we used a stiff numerical solver to compute the dynamics of the 3-species Lotka-Volterra model. In this manner, we obtained best-fit parameters (Appendix I).

Sensitivity and local stability analysis

We used the optimization method to determine the sensitivity of (1) the parameter estimates, and (2) the equilibrium solution to the time species take to reach their long-term abundance (t_3) for each sand supply rate (Appendices J-L). Although

changes in the time that species take to reach their long-term abundance (t_3) did not have a strong effect on the parameter estimates for either r or K, they did have a strong impact on the estimates for α and ultimately led to different stable equilibrium solutions, and therefore, different community outcomes (Appendix K). All 10 low sand supply simulations converged and resulted in two possible community outcomes (a 2-species community with *E. mollis* extinct, and a 3-species equilibrium with *A. breviligulata* > *A. arenaria* > *E. mollis*), 8 of 10 mid sand supply simulations converged and resulted in the same two community outcomes, and 8 of the 10 high sand supply simulations converged with the same two community outcomes (Appendix L).

Based on these simulation results, we selected the most common 2- and 3-species community outcomes for each sand supply rate (Appendix J). For each of these communities, we computed the normalized sensitivity index to determine the relative influence of K and α on the equilibrium abundance of each species (Appendix L). Finally, we include a dimensional analysis of the 3-species Lotka-Volterra model as it relates to this study (Appendix M), as well as a local stability analysis from which we determined the invasibility criterion for each species under all equilibrium conditions (Appendix N).

4.3 RESULTS

Across all sand supply rates, coexistence among all three species was the most common outcome (Fig. 4.2 a-c). The exclusion of the native, *E. mollis*, and coexistence of both *Ammophila* invaders was the second most common outcome (Fig. 4.2). The system never resulted in the exclusion of all three species, nor the exclusion of any two together (Fig. 4.2). The time to reach long-term field abundances influenced whether a community was composed of 2 or 3 species, and altered the relative abundances of the three species (Fig. 4.2, Appendix J). At low sand supply, with one exception at t_3 = 24 mo., all communities at equilibrium had all 3 coexisting

species (Fig. 4.2 a, d). Regardless of the time to reach long term abundance, the relative abundances in low sand communities were consistent: *A. breviligulata* > *A. arenaria* > *E. mollis* (Fig. 4.2 d). At mid sand supply, if species achieved their long-term abundances before or after 98 months, they all coexisted, and if those abundances were achieved at 52 months, *E. mollis* overtook *A. arenaria* in abundance (Fig. 4.2 e). However, at 98 months, *E. mollis* was excluded, but could co-exist at other time points before and after this time period (Fig. 4.2 e). At high sand, if the species achieved their long term abundances before or after 61 months, all 3 species coexisted; at 61 months, *E. mollis* was excluded from the community by the two invaders (Fig. 4.2 f). *A. arenaria* could dominate the community if the species took 35 months to achieve their long term abundances, but at all other times, *A. breviligulata* dominated the community (Fig. 4.2 f).

The species interaction mechanisms enabling 2- or 3-species coexistence were largely facilitative, but indirect interactions (both positive and negative) involving both native and invasive species also played important roles (Fig. 4.3). Direct competition was least common (Fig. 4.3). Although both *Ammophila* species coexisted in both communities, they differed slightly in their interactions across community type. In both communities, *A. breviligulata* directly facilitated *A. arenaria* in low sand supply but competed against *A. arenaria* at high sand supply, while *A. arenaria* increasingly facilitated *A. breviligulata* with increasing sand supply in the 3-species community, but only strongly facilitated *A. breviligulata* at the mid sand supply in the 2-species community (Fig. 4.3).

Although the sand supply gradient did not affect the final outcome of coexistence, it did mediate the strength of the underlying α species interactions (Fig. 4.3), and magnitudes of parameters r and K (Appendix K). Specifically, we found that greater sand supply rate reduced the intrinsic rate of growth (r) for all species, reduced carrying capacity (K) for both *Ammophila* invaders in the 3-species community, and increased the strength of species interactions across both communities (Fig. 4.3,

Appendix K). The dynamics of the stable 2- and 3-species communities at equilibrium show consistent dominance by *A. breviligulata* across sand supply rates (Fig. 4.4). *E. mollis* was consistently excluded in the 2-species community because at low and mid sand supplies it received stronger competition from *A. arenaria* (which was promoted through facilitation by *A. breviligulata*) than direct facilitation from *A. breviligulata*, and at high sand supply, experienced direct and indirect competition from *A. breviligulata* (Fig. 4.3, Appendix J). *E. mollis* was the lowest abundance species in the 3-species community (Fig. 4.4), and there were no stable solutions that led to *E. mollis* dominance (Fig. 4.3, Appendix J).

Sensitivity analyses also showed that sand supply mediated the relative influence of inter- and intraspecific interactions on community composition. The abundance of *A. arenaria* in the 2-species community was most sensitive to interspecific interactions at low sand supply (facilitation from *A. breviligulata*), intraspecific interactions at mid sand supply (i.e., its own carrying capacity), and both inter- and intra-specific interactions at high sand supply (i.e., competition from *A. breviligulata*, and its own carrying capacity) (Fig. 4.3, Appendix L). Conversely, in the same 2-species community, the abundance of *A. breviligulata* was more sensitive to its own carrying capacity at low and high sand supply, and interspecific facilitation from *A. arenaria* at mid sand supply (Fig. 4.3, Appendix L). The abundance of each species in the 3-species community was most sensitive to its own carrying capacity at low sand supply, but became increasingly sensitive to interspecific interactions in mid sand supply (facilitative) and high sand supply (both direct and indirect, positive and negative) (Fig. 4.3, Appendix L).

Species abundances varied by sand supply rate, owing to the sand supply mediated interactions (Fig. 4.4). In both communities, *A. breviligulata* achieved its highest long term abundance at mid sand supply rate, while in the 2-species community, *A. arenaria* achieved its highest long term abundance at low and mid sand supply, and at mid sand supply in the 3-species community (Fig. 4.4). The direct and

indirect interactions enabled species to exceed their carrying capacities at long-term equilibrium (Fig. 4.4). In the 2-species community, direct and indirect positive interactions enabled *A. breviligulata* and *A. arenaria* to exceed their carrying capacities at low and mid sand supply rates, while direct and indirect competition from *A. breviligulata* reduced the abundance of *A. arenaria* to levels far below its carrying capacity at high sand supply rates (Fig. 4.3, 4.4). In the 3-species community, direct and indirect facilitation enabled *A. breviligulata* and *E. mollis* to exceed their carrying capacities across sand supply rates (Fig. 4.3, 4.4). In contrast, direct and indirect competition restricted the long-term abundance of *A. arenaria* near its carrying capacity in low and mid sand supply rates, and only at high sand supply did direct and indirect facilitation enable it to exceed its carrying capacity over the long term (Fig. 4.3, 4.4).

4.4 DISCUSSION

Understanding the processes responsible for natural patterns of species distributions is critical for predicting the assembly and dissolution of communities in response to environmental change and species invasions. Here we used the Lotka-Volterra model parameterized with experimental and field data to determine the effect of species interactions and abiotic processes (sand supply) on the distribution and coexistence of coastal dune-building beach grasses.

We found strong evidence for coexistence among all three species of beach grass on foredune fronts across sand supply rates in the Pacific Northwest (Fig. 4.2). However, the model prediction of all species coexisting differs from the observed co-occurrence patterns. Although both *Ammophila* species occasionally co-occur on foredune fronts across the region, and across sediment supplies, they are more likely to be found separately (although co-occurring with *E. mollis*) (Fig 4.1a, Hacker et al. 2011). Therefore, other factors may play a role in determining the species distribution patterns along the coast, including other interacting species, dispersal limitation, the

distribution of other resources, or the timing and intensity of major disturbances (e.g., wave overtopping events or variation in sediment supply). Even so, the Lotka-Volterra model framework provided key insight into the species interactions that regulate community composition, and also provided a means to determine invasibility through coexistence.

Our model suggests that the relative abundance of beach grass species will remain largely consistent across sand supply rates, with *A. breviligulata* > *A. arenaria* > *E. mollis*, a pattern which is especially evident at low sand supply rates (Fig. 4.2). These results show that not only can *A. breviligulata* invade under all three sand supply regimes, but it can become the dominant species in each case. Our results suggest that the current distribution of *A. breviligulata* is not due to a physiological intolerance to certain sand regimes because the models show that it can coexist with the other two species across all sand supply rates. Rather, its current distribution pattern is more likely due to dispersal limitation to the southern region where sand supply rates are low. If *A. breviligulata* is introduced to these regions via natural dispersal or human means, its resulting dominance may have important implications for coastal protection services (Hacker et al. 2011, Zarnetske et al. in review).

Exclusion of the native species, *E. mollis*, by the two *Ammophila* invaders only occurred in 4 of 30 cases (Fig. 4.2). *E. mollis* is found across the PNW, but on foredune fronts it is always in low abundance within small patches (Fig. 4.1). Our model shows that its low abundance and occasional exclusion is potentially due to direct and indirect competition from the two invaders. However, *E. mollis* is an important facilitator for the two invaders, and is often similarly facilitated by them (Fig. 4.3). In fact, many of the species interactions varied depending on whether the community trajectory maintains coexistence of all species (a 3-species community), or whether the subordinate native was excluded (a 2-species community). These results suggest that even rarer species in communities can influence the relative abundance of more dominant species. More recent research is showing instances of native and

invasive species facilitating one another, and this could be one reason why we rarely see invaders completely excluding native species (Palmer and Maurer 1997, MacDougall and Turkington 2005, Rodriguez 2006, Wolkovich et al. 2009, Altieri et al. 2010). For example, Davis et al. (2011) have emphasized that native-invasive interactions rarely end with the extinction of native species. Our study demonstrates that this is indeed the case in the PNW coastal dunes. There is also evidence that species diversity may increases after an invasion (Davis 2003). We have anecdotal evidence that the invasions of the *Ammophila* species increased species richness on the dunes through their sand stabilizing properties which promote the establishment of both native and non-native grassland, shrubs, and trees (Seabloom and Wiedemann 1994, Wiedemann and Pickart 1996, Hacker et al. 2011). However, species richness differs depending on the dominant grass, suggesting that they have different facilitative effects on community structure (Hacker et al. 2011).

Our results indicate that a strong environmental gradient plays a significant role in regulating the community such that the coexistence mechanisms and abundances of species were highly context dependent. However, sand supply did not directly determine coexistence (or whether the outcome was a 2- or 3-species community). Instead, it strongly mediated the species interaction mechanisms leading to coexistence via altering their strength, direction, and mode (direct/indirect) (Fig. 4.3). For both a 2- and 3-species communities, greater sand supply rate increased the strength of species interactions (especially facilitation), and sometimes changed the direction of these species interactions (Fig. 4.3 c, f). Further, the importance of indirect effects regulating the community increased with sand supply, especially within the 3-species community (Fig. 4.3). The relative influence of inter- and intraspecific interactions was context dependent because the community types and often the abundance of each species within them, were sensitive to different types of interactions at different sand supply rates (Appendix L).

Facilitation, whether direct, or indirect, is the predominant mechanism for species coexistence in this system, but its importance to each species is dependent on the resident-community context, and sand supply stress gradient. For example, facilitation allowed *A. arenaria* to far exceed its carrying capacity at low sand supply in a 2-species community (Fig. 4.3a, 4.4a) and coexist despite competition from *A. breviligulata* at high sand supply in a 3-species community (Fig. 4.3f, 4.4f). In contrast, facilitation allowed *A. breviligulata* to far exceed its carrying capacity at high sand supply rates in a 3-species community (Fig. 4.3f, 4.4f). The overall importance of facilitation appears to increase with greater sand deposition and thus more stressful conditions, which aligns with studies on other systems as well as coastal dunes in other regions (Bertness and Callaway 1994, Hacker and Gaines 1997, Callaway et al. 2002, Franks and Peterson 2003)

The species interactions within the model can provide possible explanations for historical trends in species abundance and distributions. For example, the small increase in *E. mollis* abundance within the last two decades of concurrent *A. breviligulata* invasion may be explained by the direct facilitation from *A. breviligulata*, especially where it recently invaded mid sand supply rates (i.e., Fig. 4.3d). After 1935, *A. breviligulata* spread into regions with high sand supply rates, becoming the dominant foredune species there; more recently, *A. breviligulata* spread into mid sand supply regions, becoming a co-dominant or dominant species there (Seabloom and Wiedemann 1994, Hacker et al. 2011). At high sand supply rates in particular, *A. breviligulata* concurrently receives facilitation from *E. mollis* and competitively dominates *A. arenaria* (Fig. 4.3e), enabling it to exceed its carrying capacity in these regions (Fig. 4.3, 4.4). Whereas, the more recent (perhaps slower) expansion of *A. breviligulata* into mid sand supply regions may reflect its reduced direct and indirect facilitation from *E. mollis* and *A. arenaria*. *A. arenaria* once occurred throughout much of the Pacific Northwest as the dominant foredune sand-binding species but currently only dominates the foredunes in low sand supply regions

(Fig. 4.1). Our model suggests that the contracted distribution of *A. arenaria* on foredunes may reflect its inferior ability to compete directly against *A. breviligulata* combined with its direct and indirect facilitation of *A. breviligulata* across sand supply rates (Fig. 4.3).

We can also use the model to determine potential future changes in community composition. Our model suggests that following initial establishment (via planting or successful propagule dispersal from wind or ocean currents), *A. breviligulata* can grow when rare, and therefore, can invade regions where it is currently absent. Over the long term in low sand supply regions, our model shows that *A. arenaria* would become a near co-dominant species to *A. breviligulata* (Fig. 4.4). The potential invasion of *A. breviligulata* into new regions will undoubtedly have ecological implications – not only in terms of the direct or indirect positive or negative impacts on *A. arenaria* and *E. mollis*, but also potentially some negative impacts on species richness, especially for native plant species (Hacker et al. 2011). Potentially, the facilitation it receives from *A. arenaria* and *E. mollis*, combined with its lateral spreading growth (Maun and Lapierre 1984, Baye 1990, Zarnetske et al. in review) will result in *A. breviligulata* covering more area, thus imparting larger negative effects on other dune species not considered here. *A. breviligulata* dunes have lower species richness (of native species in particular) as compared to *A. arenaria* dunes (Hacker et al. 2011), thus, there is anecdotal evidence that *A. breviligulata* may negatively affect the resident dune plant community.

A paramount concern with the potential invasion of *A. breviligulata* into new regions is its effect on dune geomorphology – especially dune height (Seabloom and Wiedemann 1994, Hacker et al. 2011, Ruggiero et al. 2011, Zarnetske et al. in review). In other experimental work (Zarnetske et al. in review), we have shown that through its lateral spreading growth habit, *A. breviligulata* generates lower, wider dunes. Although this growth response is more profound at high sand supply rates (resulting in lower tiller densities which capture less sand), it still maintains its lateral growth at

lower sand deposition (Zarnetske et al. in review). Therefore, if *A. breviligulata* invades taller foredunes in low sand supply regions of the coast where *A. arenaria* dominates, dune height may decline over time, compromising coastal protection from overtopping of large waves generated by storms and tsunamis (Sallenger 2000, Liu et al. 2005, Mascarenhas and Jayakumar 2008, Zarnetske et al. in review). However, our model also predicts that *A. arenaria* will be a near co-dominant to *A. breviligulata* under lower sand supply, and thus this coexistence might help to mediate a large change in dune shape.

Our study provides evidence for a strong environmental gradient mediating the strength and direction of species interactions, which ultimately determined community composition and coexistence. Our study combined long-term field data and interaction experiments within a parameterized model to determine coexistence and invasion potential. With this approach, we were able to identify the context-dependent species interaction mechanisms underlying the patterns of beach grass species co-occurrence. Uncovering these mechanisms will enable more robust predictions concerning the causes and consequences of potential future invasions.

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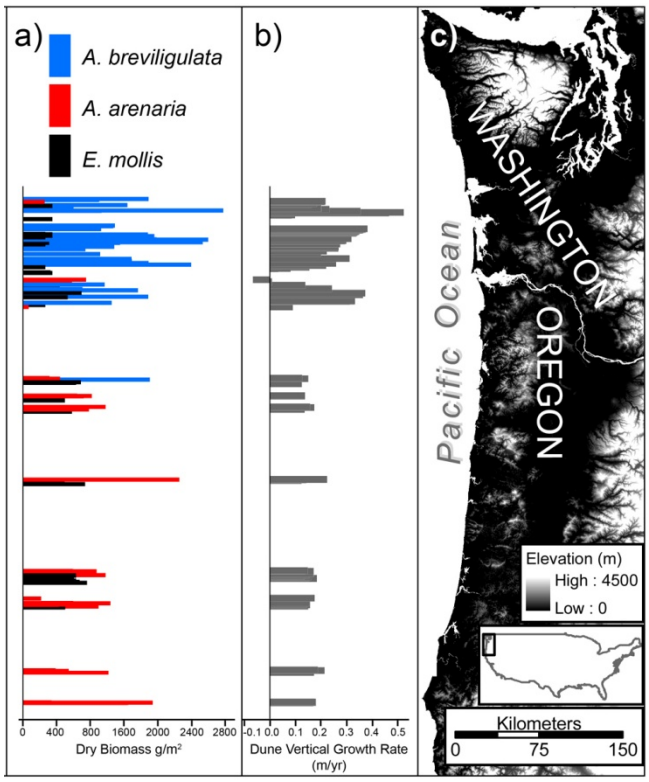

Figure 4.1. Distribution of (a) two non-native grasses, *Ammophila arenaria* and *A. breviligulata*, and the native grass, *Elymus mollis* (as mean dry biomass g/m^2 from 81 transects along the front of the foredune in 2009) and (b) sand deposition (measured as dune vertical growth rate from 1997-2009 (m/yr)) along the Oregon and Washington coasts.

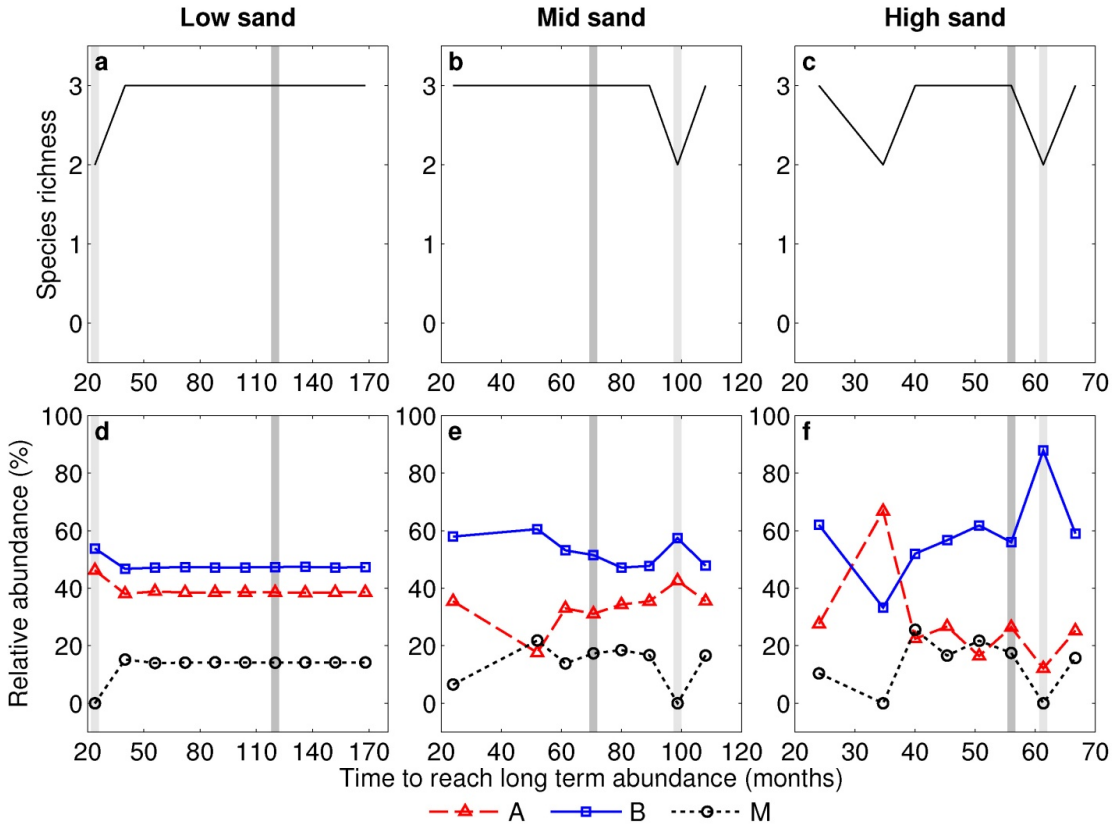

Figure 4.2. Species coexistence and relative abundance patterns, across time to reach long term abundances, per sand supply rate. Panel (a-c) shows species richness by sand supply rate. Panels (d-f) show the relative abundance of each species by sand supply rate. Two- and 3-species communities per sand supply rate were selected for further assessments – the 2-species communities are highlighted with light grey bars, and the 3-species communities are highlighted with dark grey bars.

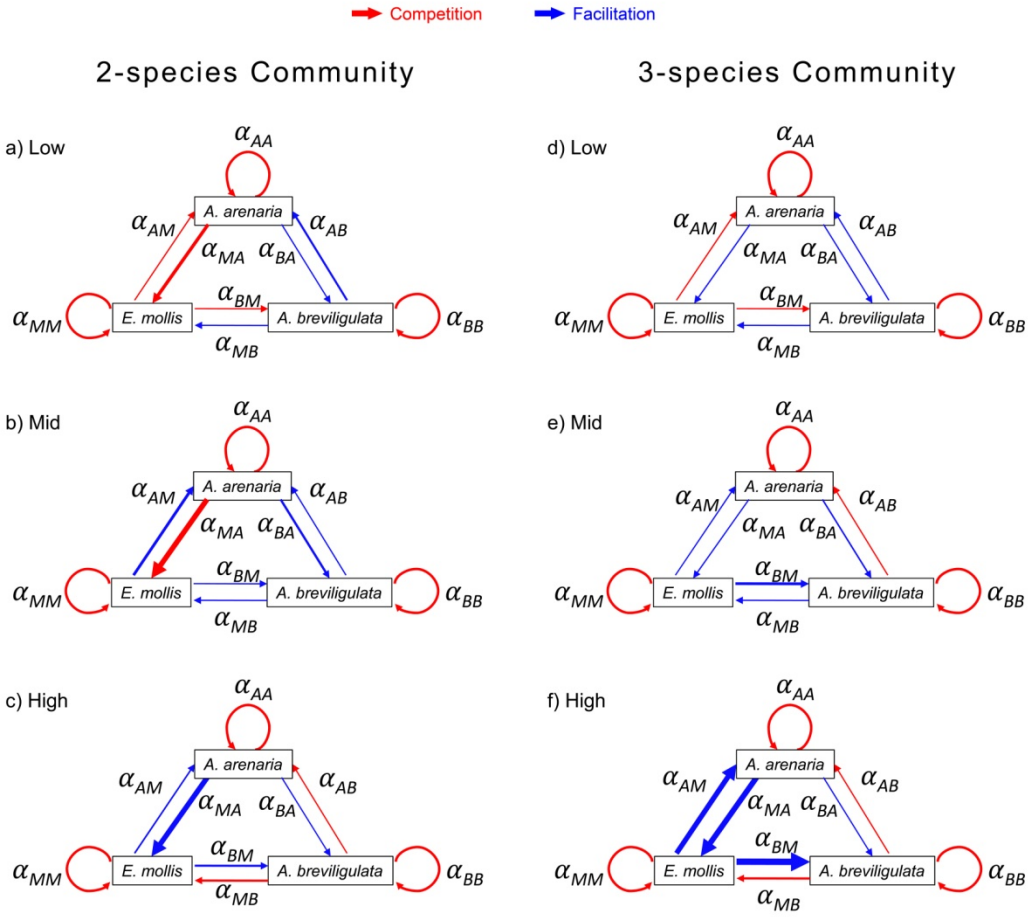

Figure 4.3. Path diagrams for 2- and 3-species communities per sand supply rate, showing the strength and direction (blue=facilitation, red=competition) of all α values (both inter- and intra-specific interactions where α_{AA}, α_{BB}, α_{MM} all equal 1).

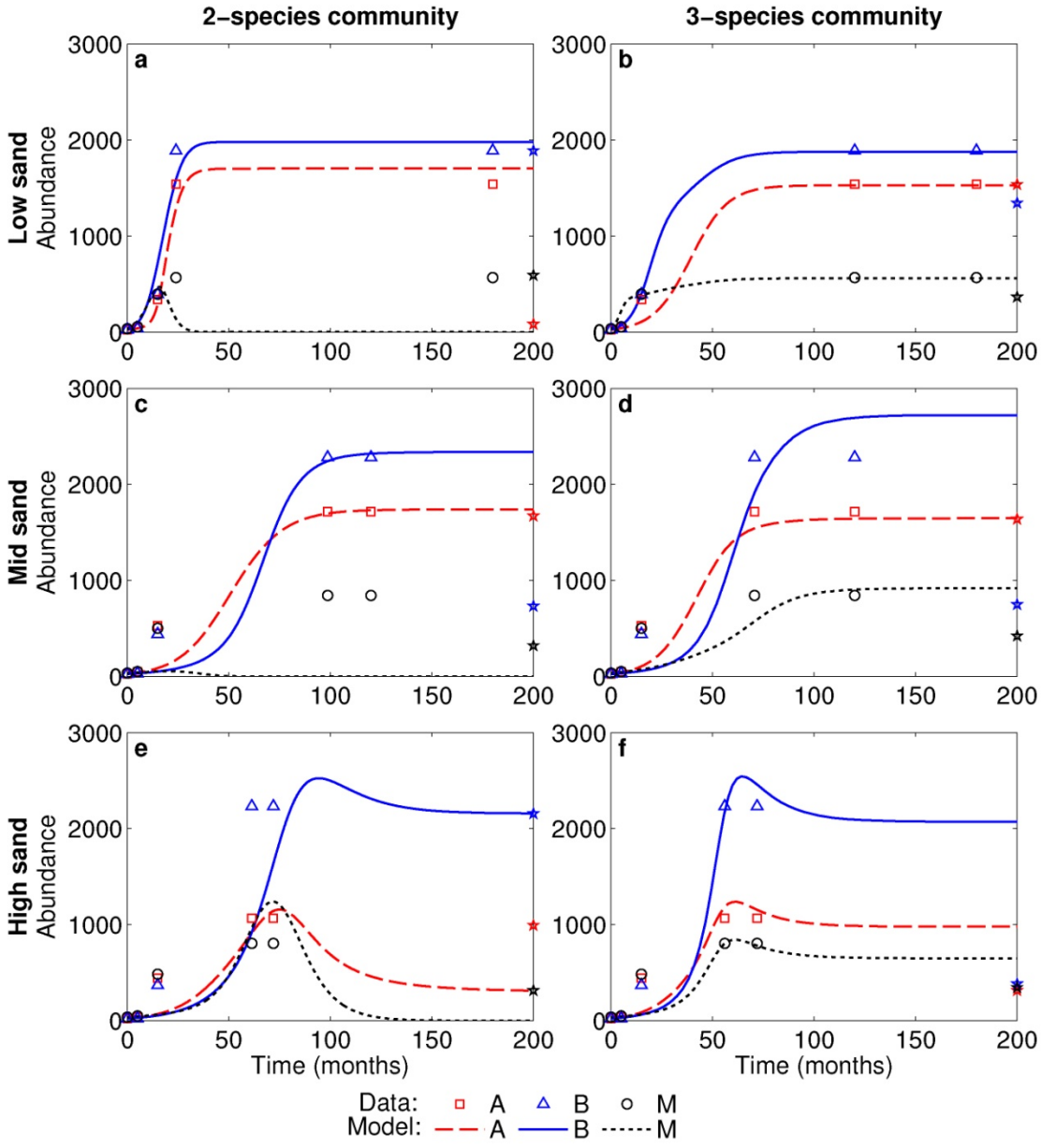

Figure 4.4 Three species Lotka-Volterra model dynamics for low, mid, and high sand supply rates, by 2-species communities (light grey bars in Fig. 4.2) and 3-species communities (dark grey bars in Fig. 4.2) which represent different types of coexistence outcomes. Pentagrams represent the carrying capacity of each species, which varies by sand supply rate. The first three data point abundances (t_0, t_1, t_2) are from the species interaction experiment (capturing the exponential portion of the abundance curves), while the last two data point abundances are from field

abundances, representing long term growth (see Appendices E and F). The time points of the t_3 abundance were selected from stable equilibrium solutions from a suite of time point scenarios, while the t_4 time point was fixed based on the lifespan of a foredune for each sand supply rate (Appendix J). *E. mollis* is consistently the zero abundance species in the 2-species equilibria (a, c, e). *A. breviligulata* dominates the community under most cases (a-d, f), except for the 2-species equilibrium under high sand supply rate (e).

5 – Non-target effects of invasive species management: beachgrass, birds, and bulldozers in coastal dunes

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ABSTRACT

Alteration of ecosystem processes by invasive species can lead to the decline of native species. Management actions targeted at removing these invaders and restoring native populations may have knock-on effects on non-target native species and ecosystems. For example, coastal dunes in the Pacific Northwest of North America are nearly monocultures of the introduced beach grasses, *Ammophila arenaria* and *Ammophila breviligulata*. These invasive grasses have converted open, low-lying sand dunes with a sparse covering of native plants to tall, densely-vegetated ridges dominated by the two invaders. As a result, the critical open-sand habitat of the federally threatened Western Snowy plover (*Charadrius alexandrinus nivosus*) has declined along with populations of several native dune plant species. Here we investigate how nearly 20 years of management targeted at the removal of *Ammophila* for plover recovery are impacting native plant species and dune morphology along 500 km of coastline in Oregon and Washington, USA. Despite increased plovers and decreased *Ammophila* in treated areas, plover habitat restoration also has had the unintentional effect of reducing the richness and abundance of native dune plants. Additionally, frequent *Ammophila* removal has prevented the re-establishment of the natural disturbance regime and dune function. Based on these findings, we suggest that the Pacific Northwest coastal dune ecosystem would benefit from a more synthetic community-wide management approach.

5.1 INTRODUCTION

Invasive species are a leading cause for biodiversity decline and ecological community modification worldwide (Wilcove et al. 1998, Stein et al. 2000, Pimental et al. 2005, National Invasive Species Council 2008). Invasive species that modify the physical environment, such as ecosystem engineers, generate particularly severe impacts (Cuddington and Hastings 2004, Dukes and Mooney 2004, Hacker and Dethier 2006, Hastings et al. 2007). As a consequence, rare, threatened, or endangered

species can be made more vulnerable to extinction from habitat loss or modification caused by invasive species (Seabloom et al. 2006); those experiencing extreme population declines resulting from invasive species may receive state and/or federal mandated protection and monitoring (e.g., the United States Endangered Species Act; ESA). These recovery efforts aim to ensure the listed species' long-term survival (ESA 1973), often through restoration of critical habitat as outlined in recovery plans.

Although federal recovery plans can include habitat improvements, the primary focus is on reversing the decline of the listed species, sometimes at the expense of co-occurring species or important ecosystem functions (Hobbs and Humphries 1995, Myers et al. 2000, Zavaleta et al. 2001). While 'whole ecosystem' approaches, such as multispecies recovery plans, are desirable, they can be less effective, due to their broad-based coverage and less explicit linkage between the biology and recovery goals of each species (Boersma et al. 2001, Clark and Harvey 2002, Taylor et al. 2005, Rahn et al. 2006). To be successful, single or multispecies plans must explicitly integrate species biology into the recovery efforts (Tear et al. 1995, Boersma et al. 2001, Clark and Harvey 2002, Clark et al. 2002). This 'target-species' approach may boost the endangered species populations, while potentially (and often unintentionally) neglecting other species and ecosystem functions.

Managing invasive species removal commonly requires a targeted approach as well. National invasive species legislation (Executive Order 13112 – Invasive Species (Clinton 1999) , National Invasive Species Council 2008) mandates federal agencies to "detect and respond rapidly to and control populations" of species whose "introduction does or is likely to cause economic or environmental harm or harm to human health" (EO 13112 Sec. 1 & 2). Although this Executive Order contains provisions "for restoration of native species and habitat conditions in ecosystems that have been invaded" (Sec. 2), the practice of controlling invasive species is primarily based on target-species management, not on the legacy effects of the invader (Hobbs

and Humphries 1995, Hacker and Dethier 2009) or ancillary effects of the control itself (Simberloff and Stiling 1996, Myers et al. 2000, Roy 2004).

Whether focused on a threatened or invasive species, target-species management may have unintended consequences for non-target species, such as the loss or gain of habitat or resources, that may result in population declines or increases. Positive, non-target effects may arise if the target is a wide-ranging species whose habitat and resource requirements include those of many other species (i.e., an umbrella species; (Wilcox 1984, Groom et al. 2006), but see (Andelman and Fagan 2000, Roberge and Angelstam 2004) for critiques of the application of umbrella species concept). In contrast, negative indirect effects from invasive species management appear to be more common than positive ones (Bergstrom et al. 2009, Rinella et al. 2009, Zipkin et al. 2009). Biological control is perhaps "the poster child" of non-target effects of species management with abundant literature documenting these effects (Howarth 2000, Myers et al. 2000, Louda and Stiling 2004). The potential for non-target effects of invasive and imperiled species management demonstrates the need for integrated management plans.

Here we present a case study of the non-target effects of managing for a threatened shorebird living on the dunes and beaches of the Pacific Northwest coast of the USA. Coastal dunes comprise 45% of Oregon and Washington's coastline (Cooper 1958) and have been modified dramatically by two invasive grasses, European beachgrass (*Ammophila arenaria* (L.)) a native of mainland Europe and the British Isles, and American beachgrass (*Ammophila breviligulata* (Fern.)) native to the U.S. East Coast and Great Lakes). These grasses have changed the dunes from open, sparsely vegetated and low-lying, mobile systems to large, continuous, and highly stable, foredunes (linear dune ridges parallel to the shoreline), since their introductions in the late 1800's (*A. arenaria*) and 1935 (*A. breviligulata*) (Cooper 1958, Seabloom and Wiedemann 1994, Wiedemann and Pickart 2004, Hacker et al. 2011). *Ammophila* driven foredune development has led to decreased sand supply to backdune areas,

further stabilization, soil formation, a decline in native dune fauna and flora, and an increase in invasive and native grassland, coastal scrub, and wetland species (Wiedemann and Pickart 2004).

The most prominent threatened species in this system is the federally-threatened Western Snowy plover, (*Charadrius alexandrinus nivosus*, hereafter, "plover"), while the invasive species targeted for removal are the two grasses (*A. arenaria* and *A. breviligulata*) that have contributed to the decline of plovers (USFWS 2007). Although habitat improvement efforts focus on the plover, other ground dwelling birds such as the Streaked Horned lark (*Eremophila alpestris strigata*, a candidate for listing on the ESA) also benefit from *Ammophila* removal (Pearson and Altman 2005). In addition, a number of dune plants endemic to the Pacific Northwest have declined due to the grass invasion (Pavlik 1983, Miller 1993, Seabloom and Wiedemann 1994, Wiedemann and Pickart 2004, USFWS 2007, Hacker et al. 2011). Of these, only *Abronia umbellata* ssp. *breviflora* (pink sand verbena) is listed as endangered by Oregon and Washington states.

Western Snowy plover recovery plans focus on removing the invasive *Ammophila* species that interfere with the bird's feeding and breeding success (USFWS 1993, 2007). *Ammophila* is removed from hundreds of hectares of foredune each year using mechanical (e.g., bulldozing), chemical (herbicides), and manual (hand pulling) techniques. To assess how beach grass removal impacts foredune communities, we collected information on management actions and response metrics (i.e., abundance and diversity) for plovers, invasive beach grasses, and other non-native and native dune plants. We also measured foredune morphology at eight plover habitat restoration areas on the Oregon and Washington coastlines. To understand how plover recovery efforts affect the system as a whole, we asked the following questions: (1) How does the removal of *Ammophila* affect plover recovery, target and non-target plant species' community structure, and foredune structure and function?, and (2) Do

particular treatment and management techniques improve plover or native plant recovery outcome?

5.2 METHODS

5.2.1 Study species

The Western Snowy plover (*Charadrius alexandrinus nivosus*) is a small, open-ground nesting shorebird. The plover breeding season occurs from mid-February or early March to the end of July, with nests created on flat, bare, and dry sand near objects such as shell, driftwood, or kelp (Widrig 1980, Wilson 1980, Stenzel et al. 1981, Wilson-Jacobs and Meslow 1984, Warriner et al. 1986). Thus, they prefer bare or sparsely vegetated beaches, dune-backed beaches, sand spits, lagoon and estuary salt pans, and river mouths, where they are either year-round residents or migrants (Wilson 1980, Stenzel et al. 1981, Warriner et al. 1986). This open sand habitat provides access to the beach for foraging and reduces predator habitat - thus invasion of *Ammophila* severely reduces plover habitat and likely led to their population decline (USFWS 1993, 2007).

The Pacific Coast population of the Western Snowy plover (i.e., individuals nesting within 50 miles of the Pacific Ocean in the United States and Baja California, Mexico, but which are not genetically distinct from inland western populations (Gorman 2000., Funk et al. 2007, USFWS 2007)) was listed on March 5, 1993 as a federally threatened species under the 1973 Endangered Species Act (USFWS 1993), and recent attempts to delist the species have failed (USFWS 2006, Jones and Stokes 2007, USFWS 2007). Further protection exists at state levels (USFWS 2007). The majority of breeding and wintering locations occur within California, but individuals mix across the entire Pacific Coast, and an important section of the population resides in Washington and Oregon (USFWS 2007). Habitat restoration areas (HRAs) along the Pacific Northwest Coast were established as early as 1990 for plover recovery and consist of habitat improvement through invasive species removal, population

monitoring, and predator control (USFWS 2007). Western Snowy plover critical habitat was designated across California, Oregon, and Washington (USFWS 2005), and a final recovery plan outlines recovery objectives aimed at removing the plover from the Federal List of Endangered and Threatened Wildlife and Plants (USFWS 2007).

5.2.2 Habitat restoration areas

Ten plover HRAs were included in this study, ranging from Leadbetter Point (46 ° 38 ' 36.11 " N, -124 ° 4 ' 9 " W) in Washington to Elk River (42 ° 47 ' 20.39 " N, -124 ° 31 ' 27.98 " W) in southern Oregon (Fig. 5.1, Appendix O). Depending on the HRA, habitat restoration techniques involved (1) different types of *Ammophila* removal (i.e., bulldozing, plowing, disking, herbicide application, hand-pulling, salt water application, or burning), (2) predator exclosures surrounding plover nests (i.e., wire cages with mesh sizes large enough for plover movement), (3) predator control (i.e., baiting or shooting), (4) oyster shell additions (i.e., to help with nest camouflage), and (5) beach closures during the breeding season (extending from early March to the end of September to allow for the completion of nesting, hatching, and fledging) (USFWS 2007). Landowners (e.g., Bureau of Land Management, Army Corps of Engineers, USFWS, U.S. National Forest Service, and State of Oregon) carry out the habitat restoration and USFWS oversees plover monitoring. Two sites, Sutton Beach and Siltcoos River, were not surveyed for vegetation or dune morphology but were included in the plover analyses.

5.2.3 Ammophila removal treatments and plover metrics

Ammophila removal treatments and plover metrics were compiled for each HRA from annual reports on population and management for Western Snowy plovers in Oregon and Washington (e.g., (Lauten et al. 2007, Pearson et al. 2008a), and from

information provided by HRA managers and biologists. All data were kept at the original reported resolution; some HRAs such as Coos Bay North Spit had multiple sections with different plover management and grass removal treatments. We compiled metrics of management actions and plover responses for each HRA section in each year (Appendix P). We analyzed a subset of the plover response metrics that were not highly correlated with each other (i.e., values with a Pearson correlation coefficient < 0.6). HRA boundaries and habitat cover types (i.e., intact vegetated foredune, open beach or sand spit, and unvegetated HRA treated area) were digitized in ArcMap 9.3 (ESRI 2008)from true color, 1-meter resolution 2006 United States Department of Agriculture National Agricultural Imagery Program (NAIP) ortho-rectified aerial photos (NAIP 2008). We used these digital maps to calculate area-based metrics such as natural (untreated) plover nesting habitat area and proportion of habitat treated (Appendix P).

We assigned an *Ammophila* removal treatment intensity value to each HRA section across all years, using two methods: (1) high versus low mechanical impact to the ecosystem (highest impact=10; lowest impact=0), and (2) principle components analysis (PCA). For (2), each removal type per hectare was summed by HRA section across years, creating a cumulative treatment metric per hectare at each site. PCA was performed on these cumulative metrics, generating a site-specific PCA treatment intensity variable with the first two components (PC1, PC2) explaining 43.5% and 34.6% of the variance in the original ten variables, respectively. PC1 correlates with (positive) disking and plowing per hectare and (negative) bulldozing per hectare, while PC2 correlates with (positive) shells and bulldozing per hectare and (negative) herbicide per hectare (Appendix Q).

5.2.4 Dune plant community and dune morphology surveys

To assess the impact of *Ammophila* removal, we measured plant community composition and foredune morphology both within the *Ammophila* removal areas

(termed "treatment" areas) and adjacent to the removal areas (termed "control" areas) immediately after the 2007 plover breeding season in eight of the ten HRAs in Oregon and Washington. We randomly placed three transects in both treatment and control areas at each site in Oregon (and four transects each for Washington's Leadbetter Point because of its large size). Treatment and control transects began at the seaward extent of vegetation, ran perpendicular to the shoreline, over the foredune crest to the lowest elevation between the foredune and secondary dune (or, in the absence of a foredune at treatment sites, for 100 m). We measured dune height using a survey rod and hand level (± 1 cm) and percent cover of each plant species and ground type (e.g., sand, litter, shell, wood) within a 20 by 50 cm quadrat every 5 m along the transect. We assigned a 1% cover value for those species observed within 2 m of the quadrats, to capture rare plant species that might be present but did not fall within the quadrats.

We investigated the restoration treatment effects on (1) *Ammophila* spp. alone, (2) plant species non-native to the Pacific Northwest ("non-native plants", including *Ammophila* spp.), (3) plant species native to the Pacific Northwest ("PNW native plants"), and (4) plant species endemic to the Pacific Northwest dunes ("PNW endemic dune plants"). We separated native and non-native species in this manner so as to account for the effect of *Ammophila* invasion and removal on endemic dune plants versus native or non-native plants, which likely colonized after the *Ammophila* introduction. For these vegetation classifications, plant relative abundance (individual species cover divided by total summed cover of vegetation) and species diversity metrics (i.e., richness and evenness) at the site level (by treatment and control sites) were generated from percent cover data at the quadrat level. For relative abundance, we calculated the mean of the quadrat data within each transect, and then calculated the mean of the transect means to form a site mean and standard error. We calculated diversity metrics at the transect level, and then calculated the mean of the transect means to form a site mean and standard error. We further assessed diversity metrics

with and without *Abronia umbellata* ssp. *breviflora*, a threatened PNW dune endemic, which was actively seeded or planted in several HRAs.

5.2.5 Statistical analyses

We used mixed-effects models (R package nlme) for each plover metric to determine whether plover populations had improved over time. We treated year as the fixed effect and HRA site as the random effect (e.g., lme(plover metric~year, random=~1|site)). Predator management has been shown to increase plover numbers (USFWS 2007)and began in some of the HRAs in 2000. We tested the effects of predator management on plovers using mixed-effects models (here the fixed effect was the presence or absence of predator management, year and year by predator management interaction. The random effect was the HRA site). Elk River was excluded from these mixed-effects models because no plovers were recorded. To determine how plovers responded to the first *Ammophila* removal treatment effort, we ran Pearson correlation tests on the gain in plover metrics following the first time *Ammophila* was removed (first post-*Ammophila* removal minus pre-*Ammophila* removal, per metric) and the change in *Ammophila* relative abundance in 2007 (site mean treatment *Ammophila* relative abundance minus site mean control *Ammophila* relative abundance). We treated this 2007 *Ammophila* change metric as a proxy for the historical change. Most plover metrics (Appendix P) were unavailable for this analysis so only fledglings per male and hatch rate were used.

To further investigate how *Ammophila* removal impacts target and non-target components of the plover habitat restoration projects, plovers, vegetation, and dune morphology were assessed for response to overall treatments using HRA sites as replicates. Treatment effects on plovers in 2007 were assessed using one-sample t-tests on mean response metrics with the null hypothesis that the true mean was equal to 0, less than 0.5, or less than 1, depending on the metric. Treatment effects on 2007 vegetation and dune morphology were assessed using log response ratios. Mean

response metrics per site were converted to log response ratios (log (site treatment response /site control response)) followed by one-sample t-tests, with the null hypothesis that the true mean is equal to 0. In this manner, positive log ratio values indicated an increase in response to treatment while negative values indicated a decrease in response to treatment.

If target and non-target species responded similarly to *Ammophila* removal treatments in 2007 we would expect them to be correlated. Therefore, plover metrics were correlated with other responses (mean *Ammophila* relative cover, mean bare ground relative cover, and mean relative cover and richness of: non-native plants, PNW native plants, and PNW endemic dune plants) inside treated areas using two-sided Pearson correlation tests and linear regression.

Finally, we constructed linear regression models (with generalized linear models) to investigate how year 2007 and cumulative habitat treatment (e.g., bulldozing, herbiciding) and plover management techniques (e.g., human patrols) explain the variability of each of the year 2007 response categories (plover metrics, mean *Ammophila* relative cover, and mean relative cover and richness of: non-native plants, PNW native plants, and PNW endemic dune plants). Presence or absence of predator control was a potentially confounding variable with plover response, so only sites with predator control (all sites except Leadbetter Point) were used in this analysis. Top models were chosen for each response category based on extra sum of squares F-tests. In the aforementioned 2007 analyses, not all explanatory variables were measured at all HRA sections in 2007, hence degrees of freedom fluctuates depending on the explanatory variable. All analyses were performed in R 2.10.1 (R Development Core Team 2009).

5.3 RESULTS

5.3.1 Ammophila removal effects on dune morphology and plant community structure

Dunes in *Ammophila* removal areas were roughly 3 m shorter (Fig. 5.2A) and 7 m longer (Fig. 5.2B), largely as a result of bulldozing, which occurred between 1 and 11 times at each site. *Ammophila,* PNW endemic dune plants, PNW native plants, and non-native plants all declined in relative abundance in the removal areas (Fig. 5.3A, B, Table 5.1). *Ammophila* removal led to a decline in plant species richness and evenness for PNW endemic dune plants (when excluding *Abronia umbellata* ssp. *breviflora*; Fig. 5.3C, D, Table 5.1, Appendix R) and a decrease in PNW native dune plant species evenness (Fig. 5.3D, Table 5.1). *Ammophila* relative abundance did not vary with any particular removal type or intensity, but did correlate with lower proportion of HRA natural (open sand) habitat and higher HRA treatment proportion (Table 5.2). PNW endemic dune plant relative abundance and richness were positively correlated with cumulative saltwater/ha and cumulative ripping/ha (Table 5.2).

5.3.2 Ammophila removal effects on plovers

Plovers responded positively to overall habitat treatment over time throughout the region (Fig. 5.4) [mixed-effects models: fledglings per male $p<0.001$; hatch rate $p=0.019$; number of nests $p<0.001$; number of adults $p<0.001$; unexclosed (open) nest success rate $p=0.037$], although exclosed (closed) nest success rate ($p=0.810$) did not increase through time. Plover response was mixed through time after predator management was initiated at each HRA; some metrics showed strong improvement [number of nests $p=0.039$; number of adults $p<0.001$; unexclosed (open) nest success rate $p=0.046$] while others showed strong decline [exclosed (closed) nest success rate ($p=0.003$)]; and still others had no strong effect [fledglings per male ($p=0.619$) and hatch rate ($p=0.724$)].

Plovers did not appear to respond positively immediately following the first year of *Ammophila* removal treatment (Fig. 5.5); the change in plover metrics from pre- to post-*Ammophila* removal did not correlate with the proxy for first time change in *Ammophila* relative abundance (Pearson R-squared correlation; fledglings per male = -0.019, t=-0.038, df=4, p=0.972; egg hatch rate = 0.140, t=0.245, df= 3, p=0.822). A variety of treatments were applied for the first time at different sites and predator control did not occur at any sites until 2000.

Most plover metrics responded positively to the overall habitat restoration efforts across sites as measured in 2007 (Table 5.1). Mean fledglings per male, number of nests, and exclosed nest success rate were all considerably above null mean values, while unexclosed nest success rate, was not sufficiently higher than null means. Plover fledglings per male in 2007 did not appear to respond differently to any particular treatment type or intensity (whether in 2007 or cumulative across HRA section history); they were slightly positively associated with the sum of treatment intensity (1 way ANOVA; F=3.394, df = 10, p=0.095), as this sole metric comprised the top linear model (Table 5.2). Unexclosed nest success was positively correlated with treated hectares and negatively correlated with both cumulative bulldozing/ha and handpulling/ha whereas exclosed nest success was positively correlated with the proportion of natural habitat and hectares of natural habitat at the site (Table 5.2).

5.3.3 Generalities in response metrics

Plover metrics in 2007 did not correlate with most of the other response variables (i.e., relative abundance of *Ammophila,* bare ground, and PNW endemic dune plants) within treated areas. The only strong correlation was negative between exclosed nest success rate and mean PNW endemic dune plants relative abundance (two-sided Pearson correlation test, R=-0.975, t=-7.575, df=3, p=0.005). From these results, plovers, *Ammophila*, and PNW endemic dune plants did not respond similarly to overall treatments.

5.4 DISCUSSION

We found that management efforts were successful for the target species (plovers and *Ammophila*) but had negative consequences on the non-target components (native plants, restoration of dune function). Removing the invasive beach grass, *Ammophila*, increased plover populations (Fig. 5.4, Table 5.1) but concurrently reduced native plant species abundance (Fig. 5.3, Table 5.1). We found that all removal treatments were effective at reducing *Ammophila* cover and had similar results for plover recovery (Table 5.2). However, plover recovery was not correlated with the reduction of *Ammophila* cover following the first *Ammophila* removal event (Fig. 5.5), suggesting that plover recovery likely depends on a combination of repeated beach grass removal over time, and other measures such as predator control, nest exclosures, and human patrols (Neuman et al. 2004, Lauten et al. 2006, USFWS 2007). Increasing habitat area should also improve plover response, as is reflected by higher nest success rates correlated with more hectares and a higher proportion of natural habitat in 2007 (Table 5.2).

Although habitat improvement benefited plovers (i.e., *Ammophila* removal, increasing habitat area, nest exclosures, predator control, addition of human patrols, increased signage and fencing, and public education (USFWS 2007)), we found little evidence to support using any one particular type of management technique. For example, fledglings per male only was explained by the sum of *Ammophila* removal treatment intensities, the success rate of nests in predator exclosures only was explained by proportion and total hectares of natural habitat available, and the variation in the success rate of open nests exposed to predators was explained by treated hectares and cumulative bulldozing and handpulling per hectare (Table 5.2).

From these results, it appears that plovers are more likely responding to the result of the *Ammophila* removal (that is, more bare ground and less vegetation) than the type of removal. Measurements of vegetation cover in *Ammophila* removal areas

(1-18%; Fig. 5.3) are similar to those in preferred plover nesting habitat in California (6-18% vegetation cover (Powell et al. 1995, Powell et al. 1996)), suggesting that plovers are responding to the overall barren ground, with some vegetation left for brood cover. Additionally, plovers appear to be attracted to areas with oyster shell application on bare ground (USFWS 2007, Pearson et al. 2008b), although shell addition was not a significant explanatory variable in our analysis.

A disconnect between habitat restoration and portions of plover life history could explain why fledglings per male was not strongly associated with any treatment metric (Table 5.2). Broods often leave the nesting area before fledging, so after hatching, plovers become less associated with local-scale habitat restoration area conditions, and more susceptible to broad-scale variables such as predators, habitat and food availability, inclement weather, and human disturbance outside of the HRA (Warriner et al. 1986, Stern et al. 1990). For example, in some instances, plover broods were found up to 6.4 km from their nesting area (Casler et al. 1993, USFWS 2007). This movement points to the need for suitable conditions outside of the HRA – although beaches are signed and patrolled to reduce human disturbance, predators could hide in the densely vegetated dunes outside of treatment areas.

Regardless of the manner in which *Ammophila* is removed, it is clear that removing this grass is an important first step for plover recovery. However, *Ammophila* removal has negative consequences for native plants. We found that the abundance of PNW endemic dune and native plants declined in treated areas, even with the removal of the competitively dominant *Ammophila* (Fig. 5.3, Table 5.1, Appendix R). Richness of PNW endemic dune plants declined in treated areas as well – when we removed the state listed threatened *A. umbellata* ssp. *breviflora* (which is hand-seeded or planted in many HRAs) from the analysis there was a significant decline (from a mean of 1.70 species in treated areas with *A. umbellata* ssp. *breviflora* to a mean of 1.27 species without *A. umbellata* ssp. *breviflora*, Table 5.1). This decline is clearly due to the frequent (sometimes twice per winter) and intense

(flattening of the foredune) mechanized treatments at most HRAs, which creates a disturbance that is likely hard for any plant to overcome. Endemic dune plants have evolved to withstand severe disturbance and stress including sand scour, low nutrient levels, and high winds (Moreno-Casasola 1986, Yura and Ogura 2006, Gilbert et al. 2008), but likely not at the levels experienced in these restoration areas. The rarity of PNW endemic dune plants, and the positive effect of seeding even one species, supports the need for whole-community management.

Ammophila removal treatments in HRAs also affected dune geomorphology. The repetitive and intensive mechanical treatments flattened foredunes (Fig. 5.2). Coastal dunes in the Pacific Northwest were dynamic, transgressive, wind-controlled systems prior to *Ammophila* introductions (Cooper 1958, Wiedemann and Pickart 2004), and dunes in the HRAs start to revert to their natural dynamic forms between bulldozing. However, this natural progression is halted each year as mechanized *Ammophila* removal resumes.

Lower-intensity treatments would allow the coastal dune system to regain more of its endemic vegetation and natural topography. Although we could not identify sites with mostly low intensity treatments (because each site history includes bulldozing or excavating prior to lower intensity treatments), use of low intensity treatments (e.g., targeted herbicide or hand-pulling of *Ammophila*) should cause less harm to endemic vegetation. We know from other studies that hand-pulling is very effective for *Ammophila* removal (Pickart and Sawyer 1998), has immediate positive response in plovers (Peterlein and Roth 2003, USFWS 2007), and also benefits native dune plants (Pickart and Sawyer 1998). Additionally, targeted, herbicide treatments on invasive, sand-binding dune plants have proven beneficial for native plant diversity and abundance (Wootton et al. 2005).

Switching from frequent and intense mechanized removal that removes the grass and flattens the foredune, to hand-pulling or targeted herbiciding could help restore the functional attributes of the dune as well as native species if *Ammophila*

removal results in the mobilization of sand. This could be especially important to larger HRAs where *Ammophila* removal appears to be less successful (Table 5.2) but where the remobilization of large volumes of sand could have a greater effect in thwarting the grass. However, the legacy of *Ammophila* may be context dependent, similar to what has been shown for other ecosystem modifying invaders (Hacker and Dethier 2009). In some areas where large foredunes have developed, the legacy effect of the foredune structure (potentially maintained by *Ammophila* roots) may hinder natural disturbance regime recovery. In these areas, one initial bulldozing treatment could be followed by less intense removal techniques and concurrent native species plantings. It is conceivable that this whole-system restoration approach could be self-sustaining if overwashing by larger storm waves occurs frequently enough to dampen dune grass re-growth.

Initial emphasis of this whole-system restoration on sand spits, river mouths, and other natural winter flooding areas further employs natural disturbance processes that reduce vegetative re-growth and promote open-ground conditions. We think this could be promising for larger natural areas where *Ammophila* is lower in abundance (Table 5.2), potentially because sand is more mobile and natural overwash is more common. These features are recognized as preferred plover habitat and thus would likely have a positive effect on the birds as well (Wilson 1980, Stenzel et al. 1981, Page et al. 1995). In these areas, oyster shell additions should become less essential as sand scour maintains shell, driftwood, and other habitat heterogeneity. Continued plover management techniques such as predator control, nest exclosures, and human patrols will still be necessary to ensure plovers continue to rebound, but restoring the natural disturbance regime in combination with regular, non-mechanized *Ammophila* removal should provide the positive feedback necessary to maintain open, shifting habitat which is so necessary for plover and endemic plant success.

The ‘acute’ phase of the *Ammophila* invasions is largely in the past, but the ‘chronic’ phase exemplified by the shift in species composition and geomorphic

template remains. It is this later invasion stage that often spurs intensive management practices because the system has been so altered (Rinella et al. 2009). Currently, HRAs exist in a transitory state that is considerably different from either the invasion or fully-restored states (Hacker and Dethier 2009). Restoring a system following significant changes in ecosystem processes is no easy task (Zavaleta et al. 2001, Byers et al. 2006, Lambrinos 2007) especially where there are few or no reference sites for evaluating restoration success (Clewell and Rieger 1997). However, explicit attention to restoring ecosystem processes and native communities – as opposed to a single target species – should generate additional benefits for the target species under consideration or mandate. In this dune system, we encourage the development of management plans that recognize the dual goals of invasive species removal and restoration of the natural disturbance regimes and endemic species dependent on them.

We recognize that *Ammophila* is a double-edged sword. The introduction of *Ammophila* was deliberate with the goal of binding sand and building foredunes as coastal protective barriers against frequent winter storm surges (McLaughlin 1939, Wiedemann and Pickart 2004, Hacker et al. 2011). *Ammophila*-created foredunes increase coastal protection in the Pacific Northwest (Ruggiero et al. 2001). In addition, *Ammophila* may have increased native species diversity through creating wetland habitats and decreasing sand scouring (Wiedemann and Pickart 2004). For this reason, removing *Ammophila* from the entire coastline is undesirable as well as impractical due to the need to balance species conservation with coastal protection services. To date, all plover restoration activities occur within state or federal land, geographically separate from coastal communities. If plover habitat management expands into regions closer to human development, restoration plans ideally will need to leave the foredune structure intact while removing *Ammophila* using low-intensity techniques that would restore plovers and native plants (as discussed in Pickart and Sawyer 1998). This strategy would be an excellent example of combining both the ecosystem service and

ecosystem process components of ecosystem-based management (Christensen et al. 1996).

Here we demonstrate that targeted management practices can have suitable results for target species while negatively affecting non-target species and ecosystem functions. In conservation and management, the status of target species has been used to indicate broader ecosystem health by assuming that other associated native species and ecosystem processes share their fate and responses to perturbations and management (Landres et al. 1988, Caro and O'Doherty 1999, Andelman and Fagan 2000). Although this view recognizes the interconnectedness of species, it ignores the different ways in which species respond to the degradation and restoration of important ecosystem functions. To promote recovery of all species, management of target species will need to include management of target ecosystem functions as well.

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researchers, and the public in March, 2008. An overview of the workshop is online at: <http://www.science.oregonstate.edu/~zarnetsp/PNW_Dunes_Website/index.html>.

Table 5.1. Year 2007 t-test results for dune morphology and plant community structure log response ratios in treatment vs. control areas (log(response metric treatment/response metric control)), and t-test results for plover metrics in treatment areas according to plover recovery plan goals.

Response metric	T-test results	Estimated mean
Dune morphology		
Maximum elevation	t = - 4.360**	- 1.260
Dune length (toe to crest)	t = 1.119	0.176
Bare ground cover	t = 4.836**	0.502
Community structure		
All vegetation cover	t = - 5.994***	- 1.791
Ammophila spp. grass cover	t = - 5.526***	- 1.842
PNW endemic dune plant cover	t = - 3.122*	- 1.559
PNW native plant cover	t = - 2.798*	- 2.255
Non-native plant cover	t = - 5.834***	- 1.650
PNW endemic dune plant richness	t = - 0.984	- 0.201
(excluding *Abronia umbellata* ssp. *breviflora*)	t = - 3.365*	- 0.467
PNW native plant richness	t = - 1.750	- 3.416
Non-native plant richness	t = - 2.261	- 0.481
PNW endemic dune plant evenness	t = - 1.280	- 1.235
(excluding *Abronia umbellata* ssp. *breviflora*)	t = - 2.514*	- 2.222
PNW native plant evenness	t = - 3.627**	- 4.107
Non-native plant evenness	t = 1.900	0.679
Plovers		
Fledglings per male †	t = 2.260*, df = 11	1.293
Number of nests ‡	t = 7.392***, df = 14	14.533
Unexclosed nest success §	t = - 2.485, df = 11	0.330
Exclosed nest success §	t = 3.525**, df = 8	0.758

Notes: For log response ratios, positive estimated means represent an increase in the metric in treatment areas while negative estimated means represent a decrease. For community structure, cover values of bare ground, PNW endemic dune plants (including or excluding manually-seeded *Abronia umbellata* ssp. *breviflora* – see Results), PNW native plants, and non-native plants (including *Ammophila* spp.) are relative to one another (i.e., relative abundance). Except for plovers, T-test null hypotheses are that the true mean is equal to zero, and df = 7. Plover null hypothesis values are set based on conditions outlined in plover recovery plans (e.g., USFWS 2007). Plover T-tests exclude Leadbetter Point (the only HRA without predator management in 2007, although including Leadbetter Point in the analysis did not alter t-test results or significance levels). Degrees of freedom fluctuate in plover models because some metrics were not available for all HRA sections in 2007. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Null hypotheses for plover response metrics are as follows:

† true mean < 1
‡ true mean = 0
§ true mean < 0.5

Table 5.2. Top generalized linear model results for year 2007 plover and plant community response variables.

Response metric	Model	GLM df, AIC	ANOVA F-stat, p-value
Ammophila spp. grass cover model	mean = 0.043 - 0.072 [natural habitat proportion] + 0.052 [treatment proportion]	6, -39.201	natural habitat proportion: 6.688, 0.041; treatment proportion: 6.035, 0.049
PNW endemic dune plant models			
Plant cover	Model 1: mean = 0.010 + 0.400 [cumulative salt/ha]	7, -55.925	cumulative salt/ha: 100.14, <0.001
	Model 2: mean = 0.015 + 0.402 [cumulative rip/ha]	7, -44.782	cumulative rip/ha: 24.065, 0.002
Plant richness	Model 1: mean = 1.483 + 6.292 [cumulative salt/ha]	7, 17.302	cumulative salt/ha: 7.295, 0.031
	Model 2: mean = 1.563 + 6.800 [cumulative rip/ha]	7, 17.735	cumulative rip/ha: 6.624, 0.037
Plover models			
Fledglings per male	mean = 0.903 + 0.034 [sum of treatment intensity]	10, 16.253	sum of treatment intensity: 3.394, 0.095
Unexclosed nest success	mean = 0.553 + 0.004 [treated hectares] - 0.208 [cumulative bulldoze/ha] - 0.498 [cumulative handpull/ha]	6, -13.353	treated hectares: 11.966, 0.013 cumulative bulldoze/ha: 14.094, 0.009 cumulative handpull/ha: 11.877, 0.014
Exclosed nest success	Model 1: mean = 0.515 + 0.015 [natural habitat ha]	6, -7.690	natural habitat ha: 16.630, 0.007
	Model 2: mean = 0.415 + 1.898 [natural habitat proportion]	6, -4.144	natural habitat proportion: 8.528, 0.027

Notes: All response variable distributions were assigned Gaussian based on model residual vs. fitted plot investigations and distributions of studentized residuals. Models contain only uncorrelated explanatory variables, and plover models exclude Leadbetter Point (the only HRA without predator management in 2007). Model selection methods included extra-sum-of-squares F-tests and Akaike's information criterion (AIC). Degrees of freedom fluctuate in plover models because some metrics were not available for all HRA sections in 2007. Cover values are relative abundance, as described in Table 5.1.

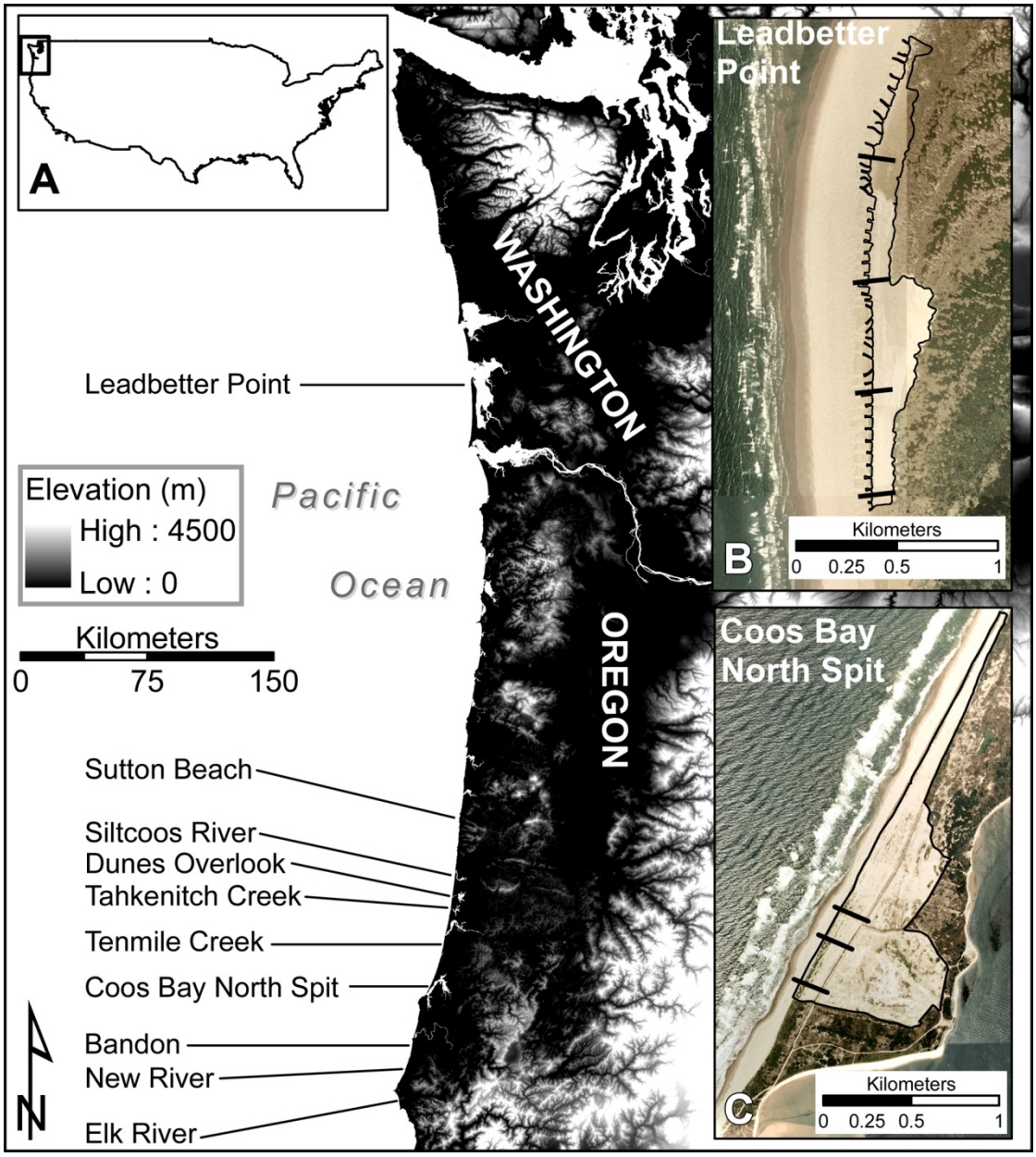

Figure 5.1. Study region (A) and example inset maps of habitat restoration areas (HRAs), showing plover nests, transects, and shell treatments in 2007. (B) Leadbetter Point, Washington, HRA; (C) Coos Bay North Spit, Oregon, HRA. See Appendix O for location details.

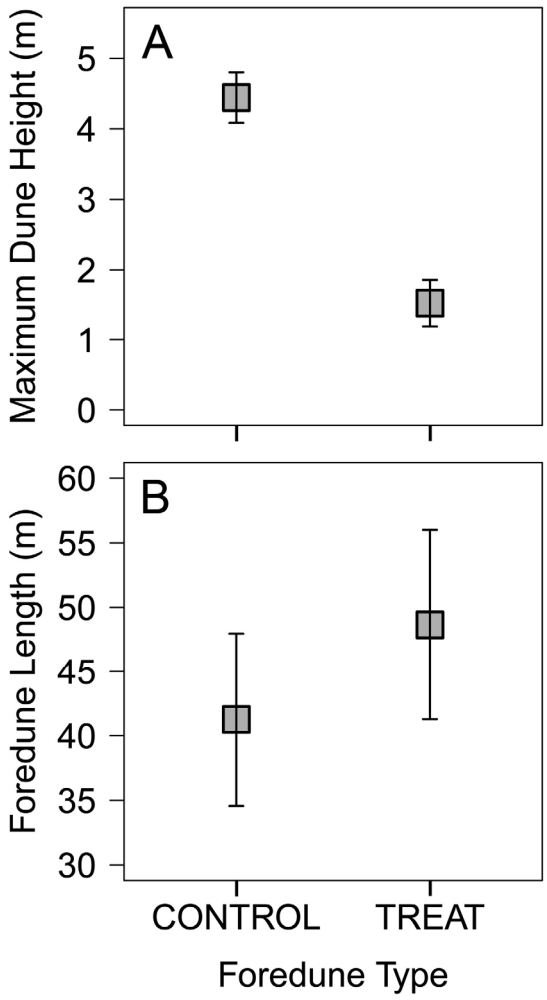

Figure 5.2. Mean dune morphology metrics ± SE of control and treatment foredunes in the Pacific Northwest coast (sites are replicates). (A) Maximum foredune height (m) is the foredune crest and (B) foredune length (m) is the longest overland distance from the dune toe to dune crest.

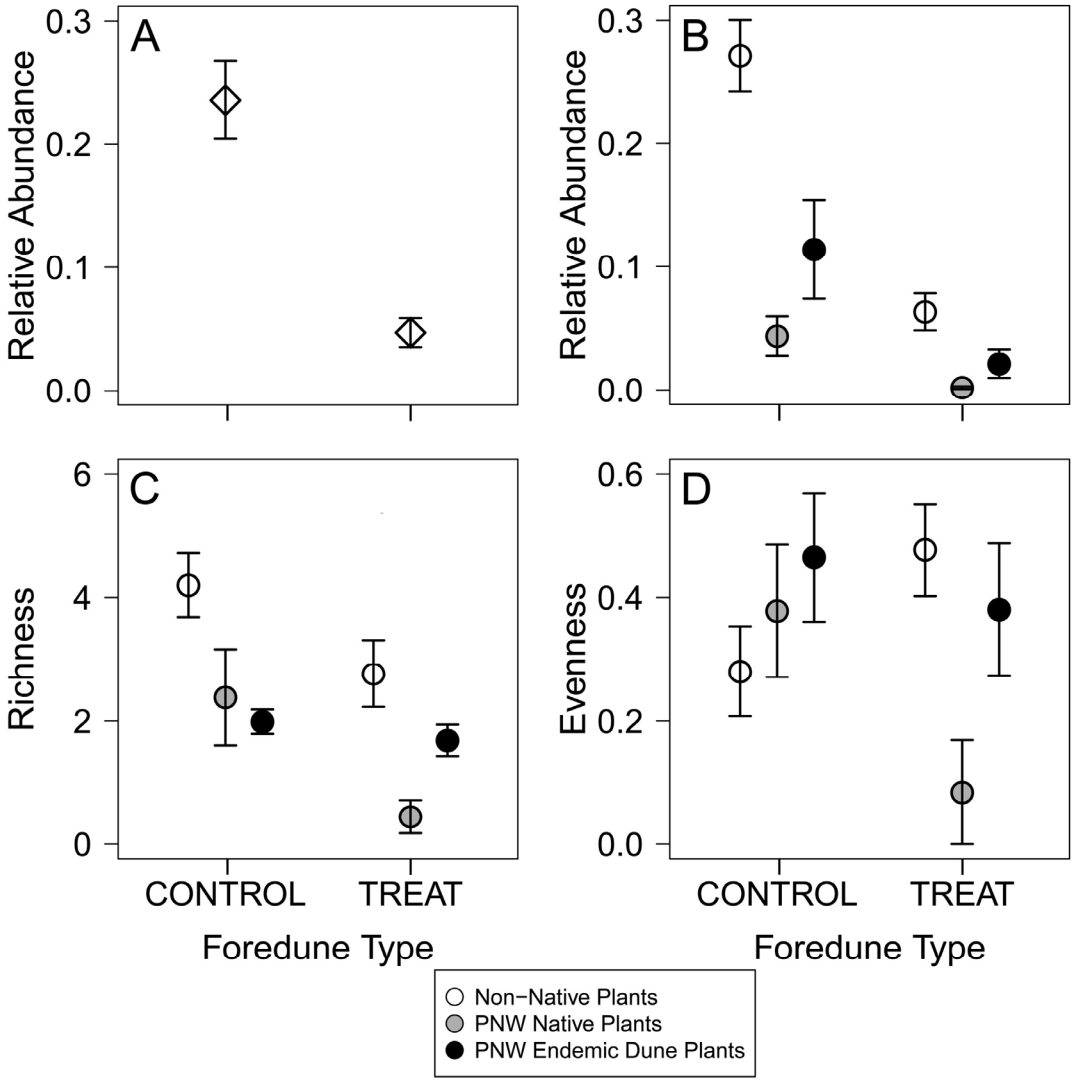

Figure 5.3. Comparison of the mean relative abundance (± SE) and diversity metrics (± SE) for plants in control and treatment areas across the Pacific Northwest coast (sites are replicates). (A) *Ammophila* relative abundance. B-D) separates all plant species into groups: "non-native plants", "PNW native plants", and "PNW endemic dune plants". See Appendix R for species list.

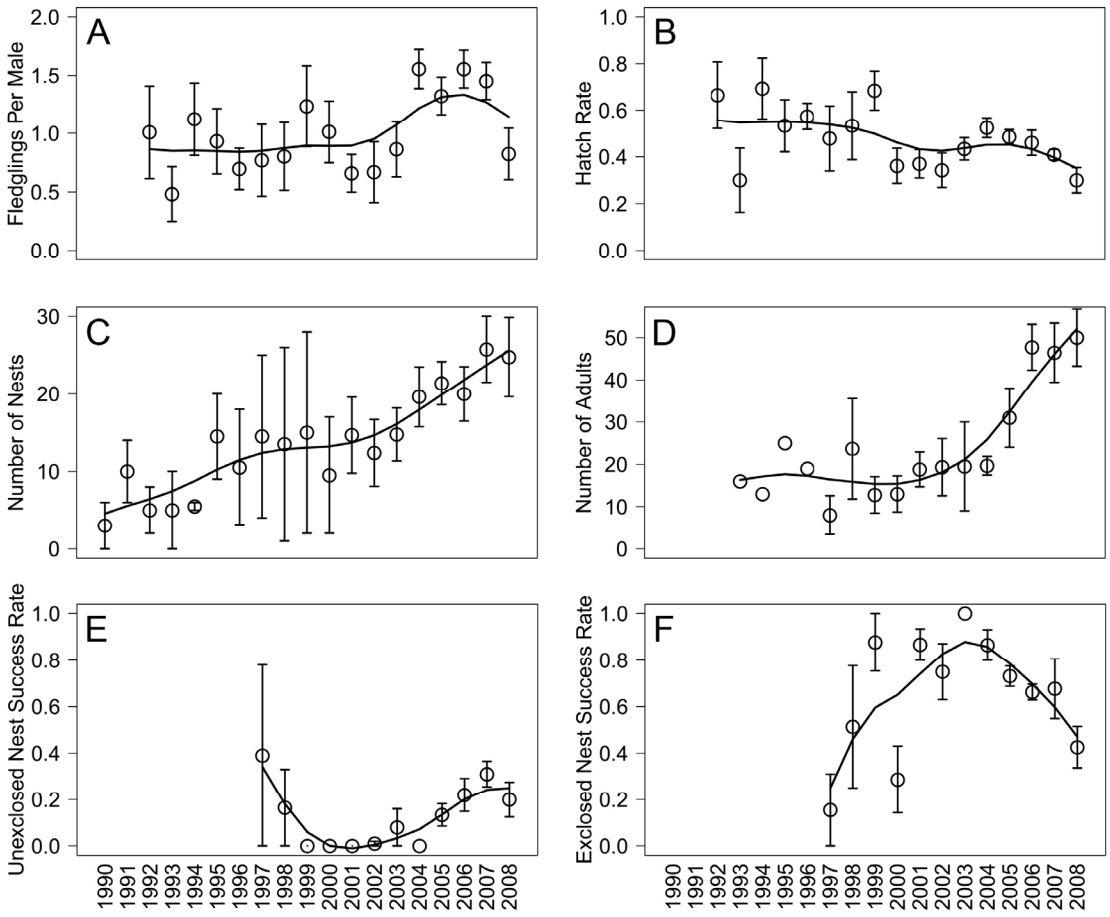

Figure 5.4. Mean ± SE plover response metrics through time across the Pacific Northwest HRAs ((A) fledglings per male, (B) egg hatch rate, (C) number of nests, (D) number of adults, (E) unexclosed nest success rate, and (F) exclosed nest success rate). Fitted curves are for illustration, and were created with a smoothing spline in R 2.10.1. Plover metrics were first recorded in 1990, and through time more HRAs were added. Predator management began in 2000 at Coos Bay North Spit.

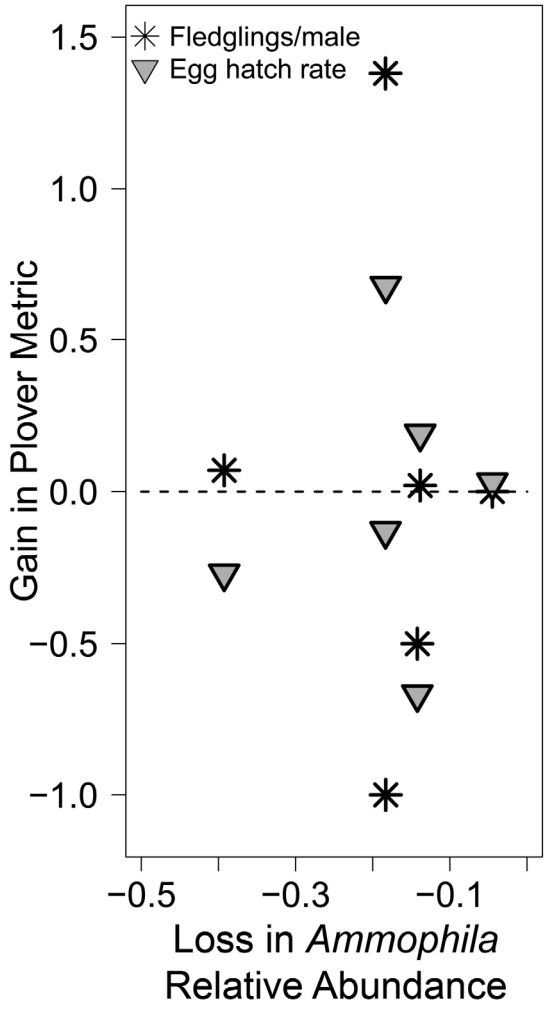

Figure 5.5. Gain in plover metrics (calculated as the metric's value after *Ammophila* removal minus pre-*Ammophila* removal) following initial *Ammophila* removal at individual HRAs. The loss in mean *Ammophila* relative abundance is calculated as control minus treatment in 2007, which is a proxy for change in *Ammophila* relative abundance following the first removal. Not all sites had these metrics for the first plover treatment year; only sites with metrics available are shown here. Fledglings per male is the number of fledglings (young that reach flying age) per male (males are brooders), and egg hatch rate is the number of eggs hatched/the number of eggs laid.

6 – Conclusion

My dissertation research examined the biophysical mechanisms and implications of beach grass invasions on Pacific Northwest coastal dunes. I used a combination of observations, experiments, and mathematical models to determine how vegetation and sediment supply interact to influence the distributions of foredune shapes and coastal dune plant communities along the coast. I gained deeper insight into the causes and consequences of beach grass invasions by merging the fields of community ecology with geomorphology, and by taking an interdisciplinary approach to these investigations.

In Chapter 2, I assessed the patterns in the spatial and temporal distributions of vegetation characteristics, foredune shape, and sediment supply rates along the Columbia River Littoral Cell and found that both vegetation and sediment supply associated with the changes in foredune shape across multi-decadal and inter-annual time scales. These results show that both biological and physical factors are important in shaping foredune features across scales, and thus adds to the growing literature on the evolution of physical features, particularly those at the aquatic-terrestrial interface (Murray et al. 2008). I found that the increase in one dominant species (*A. breviligulata*) was largely responsible for the overall vegetation signal, thus this is an relevant case study to demonstrate the large impact of a non-native ecosystem engineer (Cuddington and Hastings 2004). This assessment is the first in this study region to compare the relative biological and physical signals shaping coastal dunes over multiple time scales, and thus provides a baseline from which to investigate how further changes in the distributions of invasive beach grasses and foredune shapes are impacted by the future climatic conditions including El Niño/La Niña events, sea level rise, and increasing wave heights.

In Chapter 3, I designed and implemented two experiments to investigate the underlying mechanisms responsible for the differences in foredune shape along the coast. The combined results of the experiments demonstrate a highly coupled

biophysical feedback between the growth habit of beach grass species and sediment supply. This feedback combined with field measurements show that the species-specific differences in sand capture ability and the spatial distribution of sediment supply rates ultimately lead to different dune shapes along the coast (where *A. arenaria* builds tall, narrow dunes in the southern regions of lower sediment supply and *A. breviligulata* builds lower, wider dunes in the northern regions of higher sediment supply). The mechanistic understanding gained through this study allowed me to tease apart the underlying causes of the co-varying distributions of beach grass species, sediment supply rates, and foredune shape, and to uncover the feedbacks inherent in this system. Experiments like these that concurrently investigate the interactions among multiple species and an environmental gradient are necessary to uncover the complex causes behind observed patterns (Belovsky et al. 2004), and to make robust predictions about how a system will respond to changing conditions. In combination with Chapter 2, this mechanistic understanding can be used to guide models of dune evolution that account for differences in dominant vegetation. In turn, these predictions of dune shape enable more robust forecasting of dune vulnerability to wave overtopping, under current and future scenarios of sea level and wave heights. Further, as the foredune shape and dominant vegetation strongly influence the dunes plant community composition (Cowles 1899), understanding the mechanisms that create the shapes will inform further work on the causes of diversity and succession patterns, as well as inform dune restoration activities.

In Chapter 4, I parameterized 3-species Lotka-Volterra models using short-term data from experiments and long-term data from the field. With these models I determined whether the beach grass species co-occurrence patterns observed along the coast equated to coexistence, which species interactions led to that coexistence, and whether sand supply mediated the coexistence outcome. I showed that across all sand supply rates, the most common outcome is coexistence among all three species, and the less common outcome is *Ammophila* invaders excluding the native *E. mollis*. I also

showed that *A. breviligulata* can invade and dominate beach grass communities across the sand supply gradient, therefore, it can invade sections of coastline where it is currently absent. If this invasion occurs, it is possible that the coastal protective ecosystem services maintained by the taller *A. arenaria* dunes may be compromised owing to the different dune building ability of *A. breviligulata*. However, any change in dune shape is likely to be moderated by the predicted near co-dominance of *A. arenaria* in these low sand supply rate regions.

Importantly, in Chapter 4 I used models parameterized with both short-term experimental and long-term field data to determine coexistence. In many cases, experiments must run for extended periods of time for interactions among species to result in a coexistence or exclusion outcome, and this is especially the case with long-lived species. Thus, ecologists cannot exclusively rely on experiments to predict these outcomes. I suggest investigating coexistence and its mechanisms with a hybrid approach involving longer-term field data, experiments, and parameterized models. Further, this study shows that positive and indirect effects may often be important for the coexistence between native and invasive species, and thus, may be one explanation for the predominance of higher diversity communities following invasions (Davis 2003). Finally, this study uses the invisibility criterion to determine coexistence, and thus directly addresses recent critiques of equating co-occurrence with coexistence (Siepielski and McPeek 2010, Gravel et al. 2011).

Finally, in Chapter 5, I combined data on plover habitat restoration histories, vegetation composition, and dune shape to investigate the effects of target-species management actions on non-target species, dune shape, and the natural disturbance regime. I found that the target-species management involving *Ammophila* removal for plover population recovery was successful for the target species, but led to unintended negative impacts on the native plant community and natural disturbance regime within restoration areas. The species native to the coastal dunes, as well as the natural disturbance regime of shifting sand would benefit from restoration efforts that focus

on the ecosystem as a whole. These negative non-target effects serve as a cautionary tale for management and restoration activities as most efforts are focused on single threatened species recovery or single invasive species removal. In fact, the status of target species is often used to indicate the broader health of an ecosystem (Landres et al. 1988, Caro and O'Doherty 1999, Andelman and Fagan 2000); this study provides important evidence that sole reliance on these indicators will give a false sense of important ecosystem functions and services. If more restoration efforts across ecosystems can shift to restoring the highly coupled natural physical processes and native biological communities simultaneously, ecosystems may begin to self-repair and, therefore, potentially be less reliant on intensive human intervention. Ecosystem-based management (Christensen et al. 1996) is a preferable approach for this system, as both ecosystem functions and services can be addressed within the management framework.

The chapters within this dissertation provide key insights into the biological and physical mechanisms driving important functions and services on the coastal dunes of the Pacific Northwest. While the main players within this system are invasive species, they provide humans with protection from wave overtopping and inundation through their foredune building capacities. Further, the diversity on coastal dunes today is likely to be higher than it was prior to the *Ammophila* invasions, and even 20 years ago. These findings suggest that these grass invaders are not necessarily detrimental from an ecosystem-based management perspective, and that their dominance in this system provides both benefits and drawbacks. Positive effects from *Ammophila* invasions are important in the context of recent debates in invasion ecology over the influence of invasive species on ecosystems (Davis et al. 2011, Simberloff 2011).

In completing this research, I have integrated knowledge from a variety of fields including community ecology, invasion ecology, restoration ecology, coastal geomorphology, mathematics, statistics, and engineering. Each chapter uses an

interdisciplinary approach to gain further insight into the biophysical nature of coastal dunes. This integration was made possible by collaborations with other scientists, many of whom co-authored papers resulting from these chapters. Without this integration across fields, many of the methods would have been difficult to execute, many of the results would have been difficult to interpret, and many of the conclusions would not have been reached. Therefore, this study demonstrates that interdisciplinary research is necessary to move science forward.

In future work, it will be important to investigate how potential *A. breviligulata* invasions and changes in climate and sediment supply will impact the broader dune plant community, the shape of foredunes, the foredune coastal protection capacity, and the recovery of threatened species. These investigations will require further experimental, field-based, and modeling work of an interdisciplinary nature, as well as continued collaboration among scientific fields. It will be essential to communicate these scientific findings to the public, management, and policy realms. This connection is vital to ensure that policy and management decisions are well informed by scientific research, and that their implementation is guided by the best available science.

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APPENDICES

Appendix A.

Appendix A.1. Results from one-sample, two-sided t-tests on change metrics across each timeframe for the full dataset (multi-decadal: 1988 to 2009, and inter-annual: 2006 to 2009). In all cases, the null hypothesis was that the true means = zero. T-tests were adjusted with a Bonferroni correction for multiple comparisons (1988 to 2009: alpha = 0.005; 2006 to 2009: alpha = 0.0625). A significant test result (*) reflects the correction alpha. Degrees of freedom for 1988 to 2009 = 25; df for 2006 to 2009 = 32.

Change Metric	T-test: t statistic (p-value)	Mean of Change Metric ± SE (Range)
1988 to 2009		
CrestChg	7.066 (<0.001)*	1.385 ± 0.196 (-0.380, 3.250)
CrestRelChg	6.435 (<0.001)*	0.211 ± 0.033 (-0.049, 0.530)
WidthChg	6.341 (<0.001)*	27.062 ± 4.268 (-19.22, 69.43)
WidthRelChg	5.600 (<0.001)*	0.980 ± 0.175 (-0.382, 3.357)
TillChg	0.678 (0.504)	12.588 ± 18.560 (-160.00, 173.75)
TillRelChg	2.101 (0.046)	0.338 ± 0.161 (-0.6812, 2.623)
CovChg	8.553 (<0.001)*	0.310 ± 0.036 (0.084, 0.900)
CovRelChg	6.675 (<0.001)*	3.589 ± 0.538 (0.490, 12.857)
AMBRChg	3.815 (<0.001)*	0.207 ± 0.054 (-0.355, 0.943)
AMBRRelChg	1.732 (0.096)	7.263 ± 4.192 (-0.351, 94.332)
2006 to 2009		
CrestChg	3.994 (<0.001)*	0.603 ± 0.151(-1.230, 3.020)
CrestRelChg	4.092 (<0.001)*	0.088 ± 0.021 (-0.142, 0.468)
WidthChg	0.163 (0.872)	0.689 ± 4.237 (-59.845, 44.037)
WidthRelChg	1.974 (0.057)	0.190 ± 0.096 (-0.545, 2.038)
CovChg	-3.881 (<0.001)*	-0.145 ± 0.032 (-0.540, 0.570)
CovRelChg	-2.853 (0.007)*	-0.218 ± 0.055 (-0.701, 1.425)
AMBRChg	1.063 (0.296	0.034 ± 0.037 (-0.345, 0.561)
AMBRRelChg	1.4265 (0.163)	0.079 ± 0.077 (-0.430, 1.249)

Notes: Abbreviations are as follows:

CrestChg = change in foredune crest elevation over the model time period

CrestRelChg = change in foredune crest elevation over the model time period, relative to the first year elevation

WidthChg = change in horizontal foredune width from toe to crest over the model time period

WidthRelChg = change in horizontal foredune width from toe to crest over the model time period, relative to the first year width

TillChg = change in the number of tillers/m^2 of the three beach grass species, over the model time period

TillRelChg = change in the number of tillers/m^2 of the three beach grass species, over the model time period, relative to the first year density

CovChg = change in proportional vegetation cover (relative to bare ground) over the model time period

CovRelChg = change in proportional vegetation cover (relative to bare ground) over the model time period, relative to the first year cover

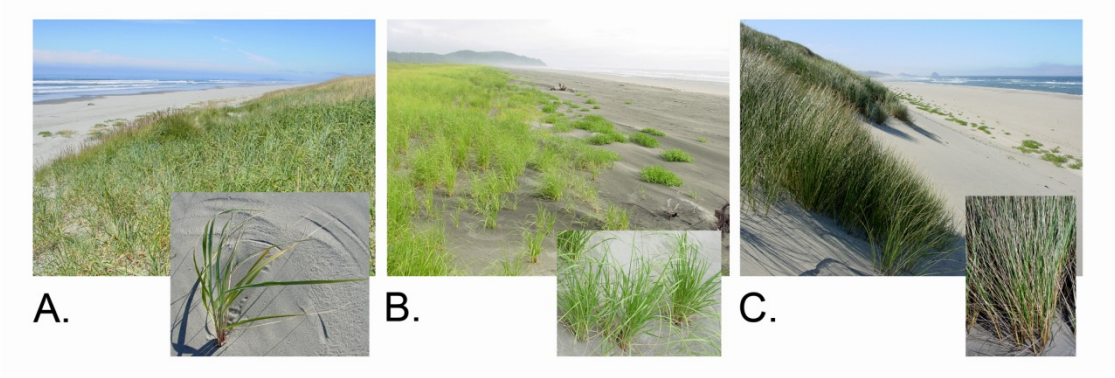
AMBRChg = change in proportional cover of *A. breviligulata* (relative to *A. arenaria* and *E. mollis*) over the model time period

AMBRRelChg = change in proportional cover of *A. breviligulata* (relative to *A. arenaria* and *E. mollis*) over the model time period, relative to the first year proportional cover of *A. breviligulata*

Appendix A.2. Results from one-sample t-tests on change metrics across each timeframe for the SCR-constrained datasets: ± 2 m/yr (multi-decadal: 1988 to 2009, and inter-annual: 2006 to 2009). In all cases, the null hypothesis was that the true means = zero. T-tests were adjusted with a Bonferroni correction for multiple comparisons (1988 to 2009: alpha = 0.005; 2006 to 2009: alpha = 0.0625). A significant test result (*) reflects the correction alpha. Degrees of freedom for 1988 to 2009 = 8; df for 2006 to 2009 = 10.

Change Metric	**T-test: t statistic (p-value)**	**Mean of Change Metric ± SE (Range)**
1988 to 2009		
CrestChg	4.452 (0.002)*	1.122 ± 0.252 (-0.160, 2.040)
CrestRelChg	3.902 (0.005)*	0.162 ± 0.041 (-0.021, 0.337)
WidthChg	4.795 (0.001)*	39.271 ± 8.191 (4.779, 69.434)
WidthRelChg	4.496 (0.002)*	1.398 ± 0.311 (0.183, 3.357)
TillChg	0.407 (0.695)	10.561 ± 25.953 (-76.67, 123.33)
TillRelChg	1.132 (0.291)	0.272 ± 0.240 (-0.421, 1.485)
CovChg	6.032 (<0.001)*	0.431 ± 0.071 (0.095, 0.900)
CovRelChg	3.953 (0.004)*	4.928 ± 1.247 (1.425, 12.857)
AMBRChg	1.436 (0.189)	0.185 ± 0.129 (-0.355, 0.943)
AMBRRelChg	1.790 (0.111)	20.156 ± 11.262 (-0.351, 94.332)
2006 to 2009		
CrestChg	0.431 (0.676)	0.112 ± 0.259 (-1.230,1.650)
CrestRelChg	0.687 (0.508)	0.024 ± 0.035 (-0.142, 0.264)
WidthChg	-0.778 (0.455)	-4.319 ± 5.552 (-34.900, 15.040)
WidthRelChg	0.560 (0.588)	0.081 ± 0.145 (-0.490, 1.022)
CovChg	-0.512 (0.620)	-0.041 ± 0.079 (-0.399, 0.570)
CovRelChg	-0.042 (0.968)	-0.007 ± 0.176(-0.701, 1.425)
AMBRChg	-0.107 (0.917)	-0.005 ± 0.044 (-0.285, 0.169)
AMBRRelChg	-0.086 (0.934)	-0.005 ± 0.058 (-0.430, 0.216)

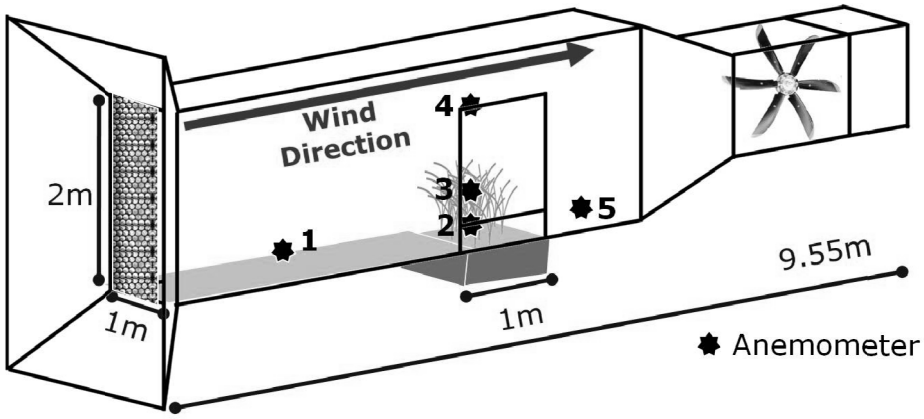
Appendix B.



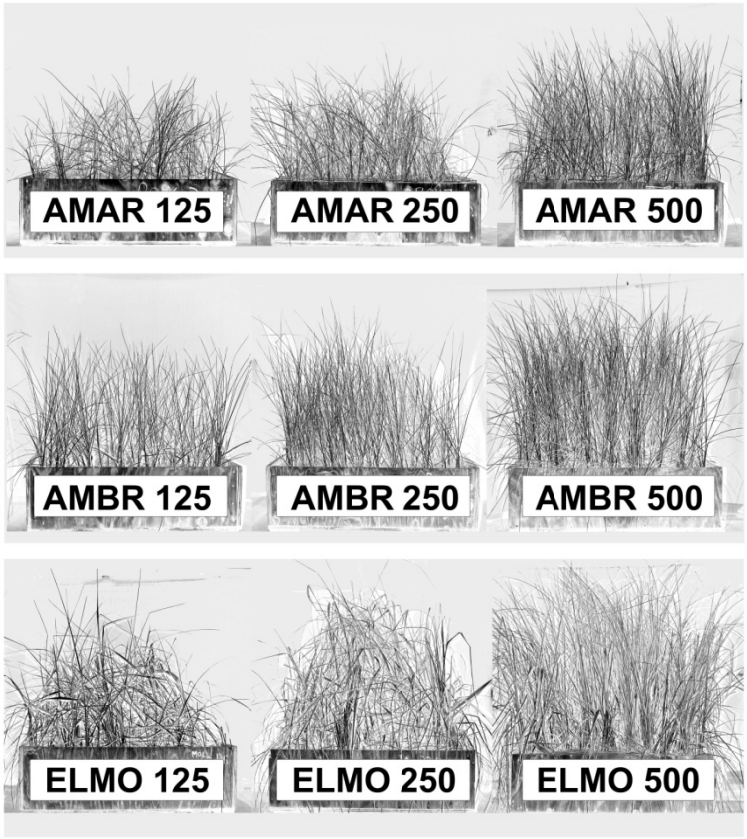
Appendix B. Field characteristics of the three beach grass species along the Pacific Northwest coast. Photos show each species with a typical foredune shape (note that *E. mollis* is pictured in a rare narrow strip on a foredune face dominated by *Ammophila*; it more often occurs in the backdune or in small patches near the dune toe). Tiller field densities were collected from the foredune face in 2009 using the methods in Hacker et al. (2011). A) *E. mollis* tillers grow in a more even distribution (tillers/m^2 variance/mean ratio: 40.98 ± 4.19), in low density (tillers/m^2 ± 1SE, mean: 44.45 ± 5.04, max: 66.14 ± 8.12, absolute max: 250/m^2) and have limp blades, B) *A. breviligulata* tillers grow in moderate clumping (tillers/m^2 variance/mean ratio: 123.84 ± 13.30), in moderate tiller density (tillers/m^2 ± 1SE, mean: 160.43 ± 10.84, max: 294.22 ± 24.53, absolute max: 850/m^2), and have less limp blades, and C) *A. arenaria* tillers grow in highly clumped tussock form (tillers/m^2 2009 variance/mean ratio: 222.32 ± 15.20), in high density (tillers/m^2 ± 1SE, mean: 203.08 ± 27.26, max: 373.04 ± 32.17, absolute max: 1110/m^2), and have stiff blades. Biomass per tiller is highest for *E. mollis*, followed by *A. breviligulata*, and *A. arenaria* (Hacker et al. 2011).

Appendix C

1)



2)



Appendix C. Wind Tunnel experimental design. 1) The flow-through tunnel was designed to pull air through PVC pipe diffusers, and across the test section, which contained live grass in sand. This design reduced turbulence so as to ensure uniform sediment transport. The tunnel interior (from diffuser to fan) measured 1m wide by 2 m high by 7.3 m long, with a 1 m^2 test section consisting of sand boxes containing live grass. Prior to each experimental run, the upstream bed (from diffuser to box test section) was loaded evenly with dry sand (length: 3.38 m, width: 1 m, sand depth: 2.54 cm). The tunnel fan (Delhi manufactured tube axial duct fan with four, 106.68 cm blades) had a capacity of 20.44 m^3/s. When placed inside the tunnel without any grass or sand, the fan could reach upwards of 20 m/s. Five anemometers (Sper Scientific 840003 digital anemometers) were hung from the tunnel ceiling, affixed to the ends of metal poles. As measured by anemometer 1, 6 m/s represents the lowest speed at which sand movement was maintained along the bed, while 9.5 m/s represents the highest consistent speed achievable with the largest, densest grass placed in the tunnel test section (*E. mollis* at 500 tillers/m^2). These wind tunnel speeds also reflect summer and winter daily high wind speeds on Oregon dune-backed beaches (6.15 m/s 1999-2009 ten-year daily mean August 85th percentile, 8.89 m/s January 85th percentile, Station NWPO3 - Newport, OR (NOAA 2010)). 2) Grass species in boxes by tiller density, where boxes measure 1 m^2 x 0.3 m tall.

Appendix D

Appendix D. Plant morphological differences from the wind tunnel experiment. Means and standard errors for each response metric are shown in the second column and are untransformed. Tukey post hoc tests (using "TukeyHSD" in Program R) were run on ANOVAs of linear models to test differences among species for each morphological characteristic (e.g., lm(response metric~species)). Tiller cross-sectional area (cm^2) was quantified from tiller circumference measurements. Natural log transformations were applied to the following response metrics in order to conform to the assumptions of linear regression: tiller circumference, dry biomass per tiller, dry above-sand biomass from entire box, blades per tiller, and tiller height. These models were generated on plant morphology characteristics from original sample resolutions (i.e., per tiller or box). All linear models except the blade flexure at 9.5 m/s model had a signficant species term.

Response Metric	Species Mean ± 1SE (n)	Tukey HSD post-hoc test difference (lower, upper 95% CI), p-value
Blade Flexure at 6 m/s	AMAR: 0.230 ± 0.011 (n=27)	AMBR-AMAR: 0.020 (-0.042,0.082), p=0.721
	AMBR: 0.250 ± 0.017 (n=27)	ELMO-AMAR: 0.085 (0.023,0.147), p=0.004
	ELMO: 0.314 ± 0.024 (n=27)	ELMO-AMBR: 0.065 (0.003, 0.127), p=0.037
Blade Flexure at 9.5 m/s	AMAR: 0.388 ± 0.014 (n=27)	AMBR-AMAR: 0.032 (-0.03,0.090), p=0.394
	AMBR: 0.420 ± 0.016 (n=27)	ELMO-AMAR: 0.044 (-0.014, 0.103), p=0.167
	ELMO: 0.432 ± 0.020 (n=27)	ELMO-AMBR: 0.013 (-0.045,0.071), p=0.861
Tiller Circumference (cm)	AMAR: 1.238 ± 0.022 (n=216)	AMBR-AMAR: 0.301 (0.230-0.371), p<0.0001
	AMBR: 1.663 ± 0.025 (n=211)	ELMO-AMAR: 0.553 (0.482-0.625), p<0.0001
	ELMO: 2.270 ± 0.068 (n=198)	ELMO-AMBR: 0.252 (0.181, 0.324), p<0.0001
Tiller Cross-sectional Area (cm^2)	AMAR: 0.130 ± 0.005 (n=216)	AMBR-AMAR: 0.602 (0.461,0.742), p<0.0001
	AMBR: 0.231 ± 0.007 (n=211)	ELMO-AMAR: 1.107 (0.964,1.250), p<0.0001
	ELMO: 0.482 ± 0.029 (n=198)	ELMO-AMBR: 0.505 (0.361, 0.649), p<0.0001
Dry Biomass/Tiller above initial sand level (g)	AMAR: 0.758 ± 0.065 (n=9)	AMBR-AMAR: 1.010 (0.646,1.373), p<0.0001
	AMBR: 2.092 ± 0.187 (n=9)	ELMO-AMAR: 1.586 (1.223,1.950), p<0.0001
	ELMO: 3.854 ± 0.499 (n=9)	ELMO-AMBR: 0.577 (0.213,0.940), p=0.002

Dry Biomass above initial sand level (g/m^2 per box)	AMAR: 240 ± 49.623 (n=9) AMBR: 605 ± 136.311 (n=9) ELMO: 1279 ± 289.953 (n=9)	AMBR-AMAR: 0.915 (0.039,1.790), p=0.040 ELMO-AMAR: 1.591 (1.714,2.466), p=0.0003 ELMO-AMBR: 0.676 (-0.020,1.552), p=0.153
Blades per Tiller	AMAR: 4.603 ± 0.198 (n=624) AMBR: 4.369 ± 0.282 (n=745) ELMO: 5.374 ± 0.083 (n=760)	AMBR-AMAR: 0.143 (0.095,0.192), p<0.0001 ELMO-AMAR: 0.098 (0.050,0147), p<0.0001 ELMO-AMBR: -0.045 (-0.091,0.001), p=0.059
Tiller Length (cm): length from tiller at sand level to longest blade	AMAR: 55.931 ± 0.385 (n=1554) AMBR: 64.215 ± 0.436 (n=1698) ELMO: 92.247 ± 0.777 (n=1571)	AMBR-AMAR: 0.131 (0.100,0.161), p<0.0001 ELMO-AMAR: 0.464 (0.433,0.496), p<0.0001 ELMO-AMBR: 0.334 (0.303, 0.364), p<0.0001

Appendices E – N

Appendices E – N. Within these appendices are descriptions of methods for assembling and analyzing the 3-species Lotka-Volterra model. These methods include: methods to obtain parameter values and time series (Appendices E-G), parameter constraints (Appendix H), and best-fit parameters (Appendix I). We also describe equilibrium solutions and associated parameter values (Appendix J, Appendix K), sensitivity analysis (Appendix L), and results for the 2-species community (Appendix L.1), and 3-species community (Appendix L.2) outcomes. Finally, we present a dimensional analysis of the 3-species Lotka-Volterra model (Appendix M) and a local stability analysis of the 3-species Lotka-Volterra model (Appendix N).

Appendix E.

Appendix E. Parameter values: linear models determining dry biomass.

Here we describe the data and models used to calculate dry biomass from live plants and/or tiller counts. We first scaled field tiller density data to $1m^2$. We restricted our use of field tiller data to the front of foredunes because these regions contain the densities important to dune building processes. Out of 84 transects across the region, we only used data from vegetation transects that contained at least 2 species co-occurring on the foredune front (n=48). We took the mean of all quadrat-level tiller densities on the foredune front by transect to generate a transect mean. These values (n=48) were used in the models described below.

We then matched experiment data per sand deposition treatment with field transect data by binning vegetation transects into corresponding low, mid, and high dune vertical growth rates (VGR). VGR is the average rate (in m/yr) of vertical profile growth from 1997-2009, as calculated from Real Time Kinematic Differential Global Positioning System (RTK DGPS) surveying technique data, taken quarterly, from 1997 to 2009, spaced approximately every 3 to 4km along this section of coastline, or calculated from a shoreline change rate (SCR) proxy (Ruggiero et al. 2005, Ruggiero et al. 2011). VGR was interpolated to each vegetation transect north of Seaside, OR; VGR for those south of Seaside, OR were predicted from a linear model relating VGR to long term SCR (calculated at exact vegetation transect locations). We binned VGR as follows: rates between -0.120 and 0.150 m/yr were assigned “low”, rates between 0.151 and 0.370 m/yr were assigned “mid”, and rates between 0.371 to 0.515 m/yr were assigned “high”.

Linear models were constructed and applied separately for each species, and where applicable, also for sand supply rates. If necessary, we used natural log

transformations to conform to the assumptions of linear regression, and back-transformed all natural log transformed output variables. The output variable indicates the response metric that the model predicted, and the model input consists of the specific data used to fit the model. Each output variable was computed for each species at low, mid, and high sand supply rates. The top model is presented per species and output variable, along with model statistics (Table E.1). See Appendix N for a dimensional analysis of the Lotka-Volterra model, as it pertains to this study.

Appendix E.1. Linear models used to calculate dry biomass output variables from live plants and/or tiller counts. No model statistics are included for the *r* models because they were fit between two datapoints (t_0 and t_1).

Species	Output Variable	Model Input Data	Model	Model Statistics (ANOVA)
AMAR	t_1 abundance (N_A)	Experiment mixture tiller and dry biomass at t_0	Dry Biomass = 3.156+1.365 [Tillers]	Tillers: F=401.22, df=1,33, p<0.0001
	t_3 and t_4 abundance (N_A)	Experiment mixture tiller and dry biomass at t_2	ln(Dry Biomass) = 2.402+0.848 [ln(Tillers)]	ln(Tillers): F=57.109, df=1,33, p<0.0001
	$r_{A(exponential)}$, $r_{A(linear)}$	Experiment monoculture abundance at t_0 and t_1	*Low sand supply exponential*: ln(Dry Biomass)=4.269+0.111[Time] *Low sand supply linear*: Dry Biomass=10.64+71.45[Time] *Mid sand supply exponential*: ln(Dry Biomass)=4.16+0.17[Time] *Mid sand supply linear*: Dry Biomass=17.59+64.02[Time] *High sand supply exponential*: ln(Dry Biomass)=3.92+0.26[Time] *High sand supply linear*: Dry Biomass=26.63+50.19[Time]	
AMBR	t_1 abundance (N_B)	Experiment tiller and dry biomass at t_0	Dry Biomass = 3.455+2.228 [Tillers]	Tillers: F=356.62, df=1,33, p<0.0001
	t_3 and t_4 abundance (N_B)	Experiment mixture tiller and dry biomass at t_2	ln(Dry Biomass = 2.502+ 0.921 [ln(Tillers)]	ln(Tillers): F= 69.59, df=1,33, p<0.001
	$r_{B(exponential)}$, $r_{B(linear)}$	Experiment monoculture abundance at t_0 and t_1	*Low sand supply exponential*: ln(Dry Biomass)=4.10+0.08[Time] *Low sand supply linear*: Dry Biomass=60.30+6.01[Time] *Mid sand supply exponential*: ln(Dry Biomass)=4.27+0.05[Time] *Mid sand supply linear*: Dry Biomass=71.45+3.78[Time] *High sand supply exponential*: ln(Dry Biomass)=4.06+0.05[Time] *High sand supply linear*: Dry Biomass=58.16+3.32[Time]	

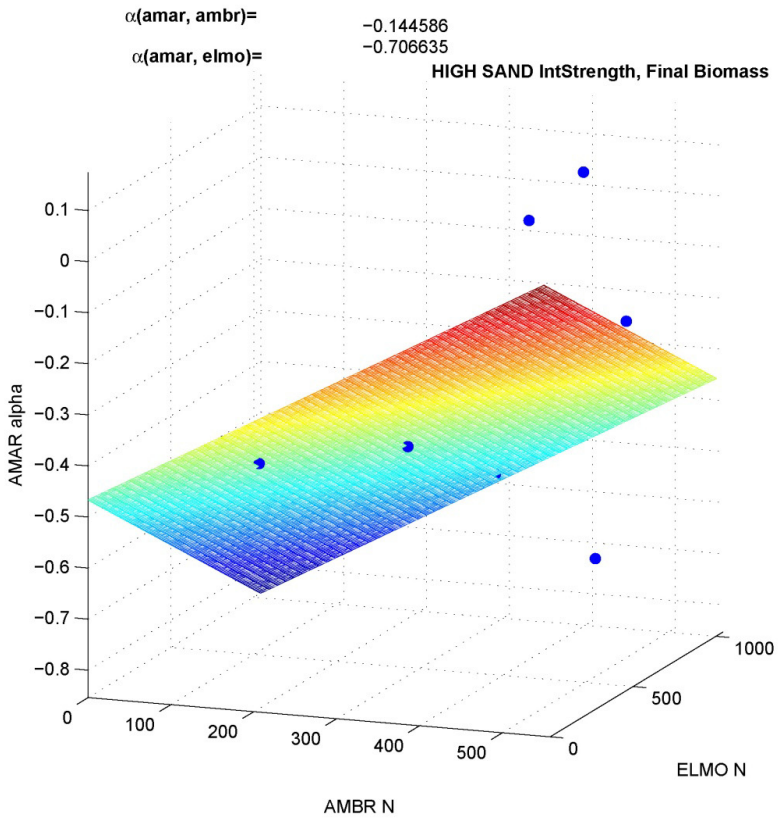
ELMO	t_1 abundance (N_M) t_3 and t_4 abundance (N_M) $r_{M(exponential)}$, $r_{M(linear)}$	Experiment tiller and dry biomass at t_0 Experiment mixture tiller and dry biomass at t_2 Experiment monoculture abundance at t_0 and t_1	Dry Biomass = 8.326+4.360 [Tillers] ln(Dry Biomass) = 4.828+0.396 [ln(Tillers)] *Low sand supply exponential*: ln(Dry Biomass)=4.63+0.07[Time] *Low sand supply linear*: Dry Biomass=102.10+8.28[Time] *Mid sand supply exponential*: ln(Dry Biomass)=4.45+0.05[Time] *Mid sand supply linear*: Dry Biomass=85.98+5.40[Time] *High sand supply exponential*: ln(Dry Biomass)=4.60+0.03[Time] *High sand supply linear*: Dry Biomass=99.14+3.64[Time]	Tillers: F=165.83, df=1,33, p<0.0001 ln(Tillers): F=10.258,df=1,33

Appendix F.

Appendix F. Parameter values: initial estimates of α

We obtained estimates of each α from the species interaction experiment with multiple regression. The experiment contained 3-species mixtures and monocultures, thus we initially generated α interaction strengths representing the per capita (per plant) effect of both *j* and *k* species on species *i* (i.e., $\alpha_{i(j,k)}$). The 2-species interaction strengths were calculated from the final experimental data as follows: [(mean of the per-plant mixture biomass) – (mean of the per-plant monoculture biomass)]/(mean of the per-plant monoculture biomass).

We plotted in 3 dimensions, 8 replicate $\alpha_{i(j,k)}$ per treatment (z-axis) vs. the corresponding N_j for interacting species *j* (x-axis), vs. the corresponding N_k for interacting species *k* (y-axis). We then fit a plane to these points using multiple regression (Appendix F.1). By setting N_j to zero, we solved for the 2 endpoints of the line that intersected the z-axis ($\alpha_{i(j,k)}$) on the plane, and the average of these two points was our estimate for the interaction effect of the species *k* on species *i*. In this manner, we estimated a total of 18, 2-species interaction coefficients (specifically: α_{AB}, α_{AM}, α_{BA}, α_{BM}, α_{MA}, and α_{MB}, for each of our 3 sand supply models).



Appendix F.1. A plane fit with multiple regression to the set of 8 replicate $\alpha_{i(j,k)}$ from the high sand deposition treatment in the species interaction experiment. In this example, AMAR (A) is the effected species, with the combined interaction strength of AMBR (B) and ELMO (M) on AMAR ($\alpha_{A(B,M)}$) plotted vs. N_B and N_M.

Appendix G.

Appendix G. Time series.

Short-term abundances from experimental data and long term abundances from field data comprised the abundance (*N*) time series for each species and sand supply rate. Short term abundances included t_0, t_1, t_2 and long term abundances included t_3 and t_4. See Appendix E for the methods involved in obtaining these values.

Table G.1. Time series of abundances per species and sand supply rate.

	LOW Sand				*MID Sand*				*HIGH Sand*			
	$N\,t_0$	$N\,t_1$	$N\,t_2$	$N\,t_{3,}\,t_4$	$N\,t_0$	$N\,t_1$	$N\,t_2$	$N\,t_{3,}\,t_4$	$N\,t_0$	$N\,t_5$	$N\,t_2$	$N\,t_{3,}\,t_4$
AMAR (N_A)	23.348	42.914	338.229	1082.019	25.106	47.691	527.627	1059.433	21.635	37.795	440.417	686.246
AMBR (N_B)	25.869	35.761	393.167	1276.370	24.112	31.027	440.443	1326.229	20.834	23.507	369.029	1201.127
ELMO (N_M)	34.287	54.647	395.092	390.347	33.543	49.197	501.167	546.838	36.901	49.742	484.092	488.676

Appendix H.

Appendix H. Parameter constraints

We used a bounded nonlinear optimization solver (fminsearchbnd) to place constraints on each parameter during the parameter optimization. See Appendix E for details on calculating these parameter values from experimental and field data.

Constraints on carrying capacity, *K*

K for each species and sand supply rate was constrained by two endpoints: the minimum and maximum values within the following set of values, (1) the final monoculture abundance per sand deposition treatment from the experiment, (2) the minimum and (3) maximum abundance from field monocultures per VGR bin (i.e., the minimum or maximum of the transect-level abundances, per VGR bin) (Appendix H.1). We used the means of both endpoints as our initial values in the parameter optimization.

Appendix H.1. Set of *K* values per sand supply rate used to constrain the possible values of the best-fit parameter, *K*, during parameter optimization and model fitting.

	LOW Sand			*MID Sand*			*HIGH Sand*		
	K_{expt}	$K_{field\ min}$	$K_{field\ max}$	K_{expt}	$K_{field\ min}$	$K_{field\ max}$	K_{expt}	$K_{field\ min}$	$K_{field\ max}$
AMAR (K_A)	672	77.7502	1540.0187	1194.4	217.1126	1715.4090	1738.9	304.2415	1068.2511
AMBR (K_B)	891.9	591.9584	1889.8487	1346.4	731.4945	2280.9873	1171.2	379.9188	2233.5187
ELMO (K_M)	639	311.1279	568.2965	1125.1	311.1279	843.2460	1306	311.1279	804.5236

Constraints on intrinsic rate of increase, r

r for each species and sand supply rate was also constrained by two endpoints: (1) the r from an exponential fit to t_0 and t_1, and (2) the r from a linear fit to t_0 and t_1 (Appendix H.2).

Appendix H.2. Set of r values per sand supply rate used to constrain the possible values of the best-fit parameter, r, during parameter optimization and model fitting.

	LOW Sand		*MID Sand*		*HIGH Sand*	
	$r_{exponential}$	r_{linear}	$r_{exponential}$	r_{linear}	$r_{exponential}$	r_{linear}
AMAR (r_A)	0.1113	0.1489	0.0809	0.0996	0.0681	0.0812
AMBR (r_B)	0.1729	0.2748	0.0469	0.0529	0.0546	0.0628
ELMO (r_E)	0.2591	0.5306	0.0502	0.0571	0.0337	0.0367

Unconstrained interaction coefficients, α: Every α was unconstrained (i.e., allowed to range between $-\infty$ and $+\infty$).

Appendix H.3. Set of α values per sand supply rate used as initial estimates for the best-fit parameter, α, during parameter optimization and model fitting.

	α_{AB}	α_{AM}	α_{BA}	α_{BM}	α_{MA}	α_{MB}
LOW Sand	0.6988	0.4184	0.8841	0.1798	1.2096	0.8879
MID Sand	-0.2190	-0.7775	0.3500	-0.2391	2.4223	-0.0489
HIGH Sand	-0.1446	-0.7066	0.0034	-0.2320	-0.7077	0.5623

Appendix I.

Appendix I. Obtaining best-fit parameters

We used a bounded nonlinear optimization method (fminsearchbnd function in Matlab) based on the simplex search algorithm described by Lagarias et al. (1998) to find the model parameter values (K, α, r) that minimized the difference between the observed time series of all species and those predicted by the 3-species Lotka-Volterra model (i.e., the cost function) for each of the three sand supply rates. We set the maximum number of iterations (MaxIter) and evaluations (MaxFunEval) to 500,000. The optimization method was insensitive to initial values such that the initial values of K (minimum K from the constrained K region), r (minimum r from the constrained r region), or α (estimates from multiple regression) did not determine the final solution. We set the maximum iterations and evaluations to 500,000. Simultaneously, we used a stiff numerical solver (ode15s function in Matlab) to compute the dynamics of the 3-species Lotka-Volterra model.

Appendix J.

Appendix J. Equilibrium solutions and associated parameter values.

For each sand supply rate, we ran the optimization and numerical solver on 10 sets of time series. Each time series differed only in the location of t_3. Here we describe the sets of time series per sand supply rate, present their equilibrium solutions, and describe how we chose two solutions per sand supply rate.

The long term data point in the time series t_4 was fixed based on the lifespan of a foredune within each sand supply rate along the coast. Specifically, t_4 is 180 mo. (15 yrs) for low sand supply rate, 120 months (10 yrs) for mid sand supply rates, and 84 mo. (7 yrs) for high sand supply rates (Ruggiero et al. 2005). We varied the first long-term data point t_3 over 10 linearly spaced time points (between t_2 + 1 yr to t_4 – 1 yr) to allow species to take different amounts of time to achieve long term field abundances. Specifically, $t_3$varied between 24 and 168 mo. (2 to 14 yrs) at low sand supply rates, 24 to 108 mo (2 to 9 yrs) at mid sand supply rates, and 24 to 72 mo (2 to 6 yrs) at high sand supply rates. All other time points (t_0, t_1, t_2, t_4) remained fixed. This resulted in 10 community time series of 5 data points for each sand supply rate that differed only in the location of t_3.

We then used the optimization method on each of the time series to determine the sensitivity of both the parameter estimates and the equilibrium solution to the time position of t_3. Below we present the ten sets of parameter estimates per sand supply rate for which we determined the locally stable equilibrium solution and the equilibrium abundance of each species (solutions that converged = plain text; solutions that did not converge = italics) (Appendices J.1-J.3). Bolded solutions indicate the 2- or 3-species community selected for further analysis. A [2] indicates the equilibrium solution for the 2-species community, and a [3] indicates the equilibrium solution for the 3-species community. We present the mean ± SE of the ten sets of parameter estimates from the locally stable equilibria that converged (Appendix J.4). Finally, we present the locally-stable equilibrium (long term) abundances for each species when t_3 is varied across different time points (Appendix J.5).

Appendix J.1. Ten parameter sets from the ten low sand supply rate equilibrium solutions.

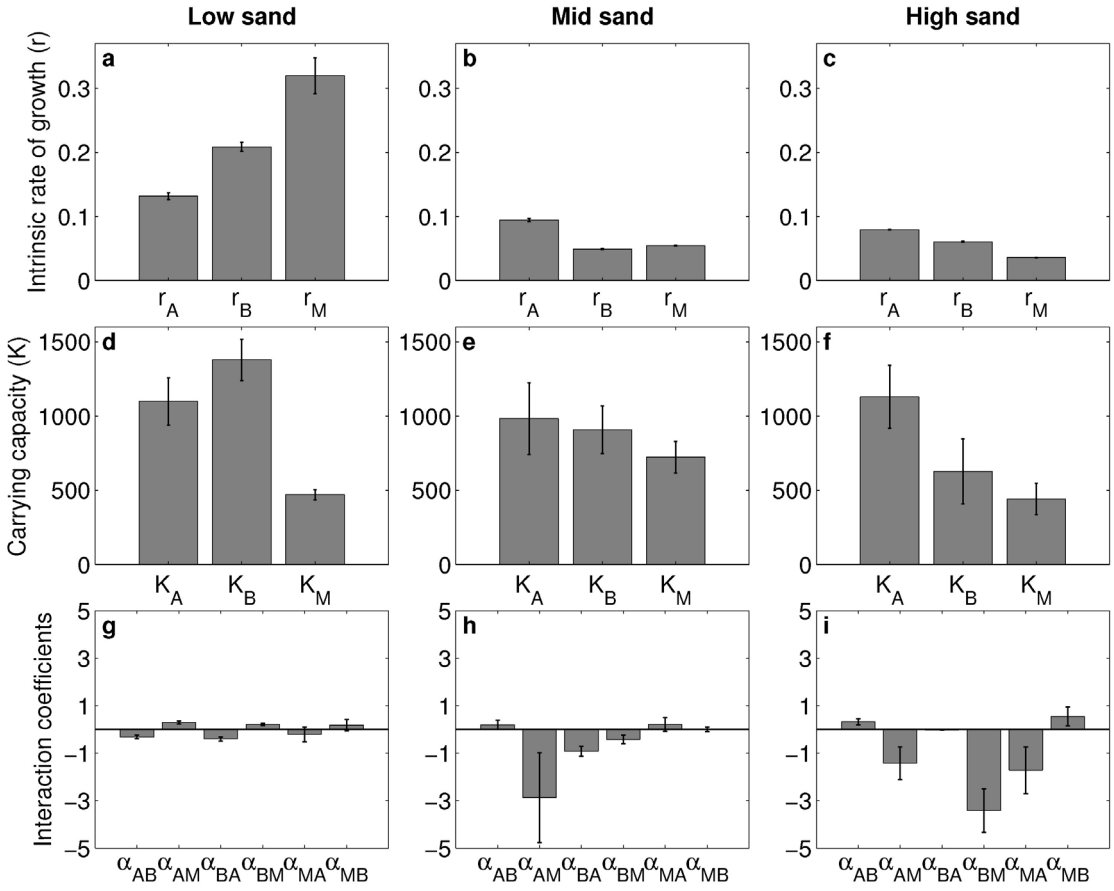
Low Sand Months	r_A	r_B	r_M	K_A	K_B	K_M	α_{AB}	α_{AM}	α_{BA}	α_{BM}	α_{MA}	α_{MB}
24 [2]	**0.116022**	**0.267667**	**0.274097**	**81.37149**	**1889.825**	**591.6314**	**-0.81819**	**0.372497**	**-0.05362**	**0.401889**	**1.341646**	**-0.45252**
40	0.114712	0.177196	0.382518	399.4456	1755.766	499.6688	-0.68218	0.230112	-0.18987	0.205394	-2.46668	1.943352
56	0.1113	0.203562	0.301047	808.9736	1877.365	320.2124	-0.54456	0.491782	-0.06363	0.145026	0.296404	-0.3728
72	0.127307	0.202282	0.266021	1447.927	823.4959	524.3613	-0.09229	0.138341	-0.78611	0.239145	-0.23087	0.163884
88	0.148826	0.201818	0.263143	1470.313	1496.656	484.3499	-0.09994	0.206992	-0.34516	0.244493	-0.50863	0.369644
104	0.148908	0.198497	0.260332	1506.155	898.4601	624.237	-0.22502	0.682815	-0.59469	-0.12791	-0.77372	0.661248
120 [3]	**0.111357**	**0.209456**	**0.525568**	**1537.733**	**1343.542**	**365.9879**	**-0.10321**	**0.361644**	**-0.41901**	**0.189564**	**-0.05101**	**-0.06148**
136	0.142529	0.216806	0.395086	1247.016	661.8369	316.3229	-0.12197	-0.09903	-0.8963	0.24845	0.568461	-0.59228
152	0.14891	0.201027	0.259101	1272.521	1490.098	539.0147	-0.25946	0.389075	-0.31164	0.142974	-0.33781	0.260125
168	0.148905	0.206173	0.264879	1210.646	1548.084	442.0507	-0.21407	0.130869	-0.35827	0.370246	0.088817	-0.13934

Appendix J.2. Ten parameter sets from the ten mid sand supply rate equilibrium solutions.

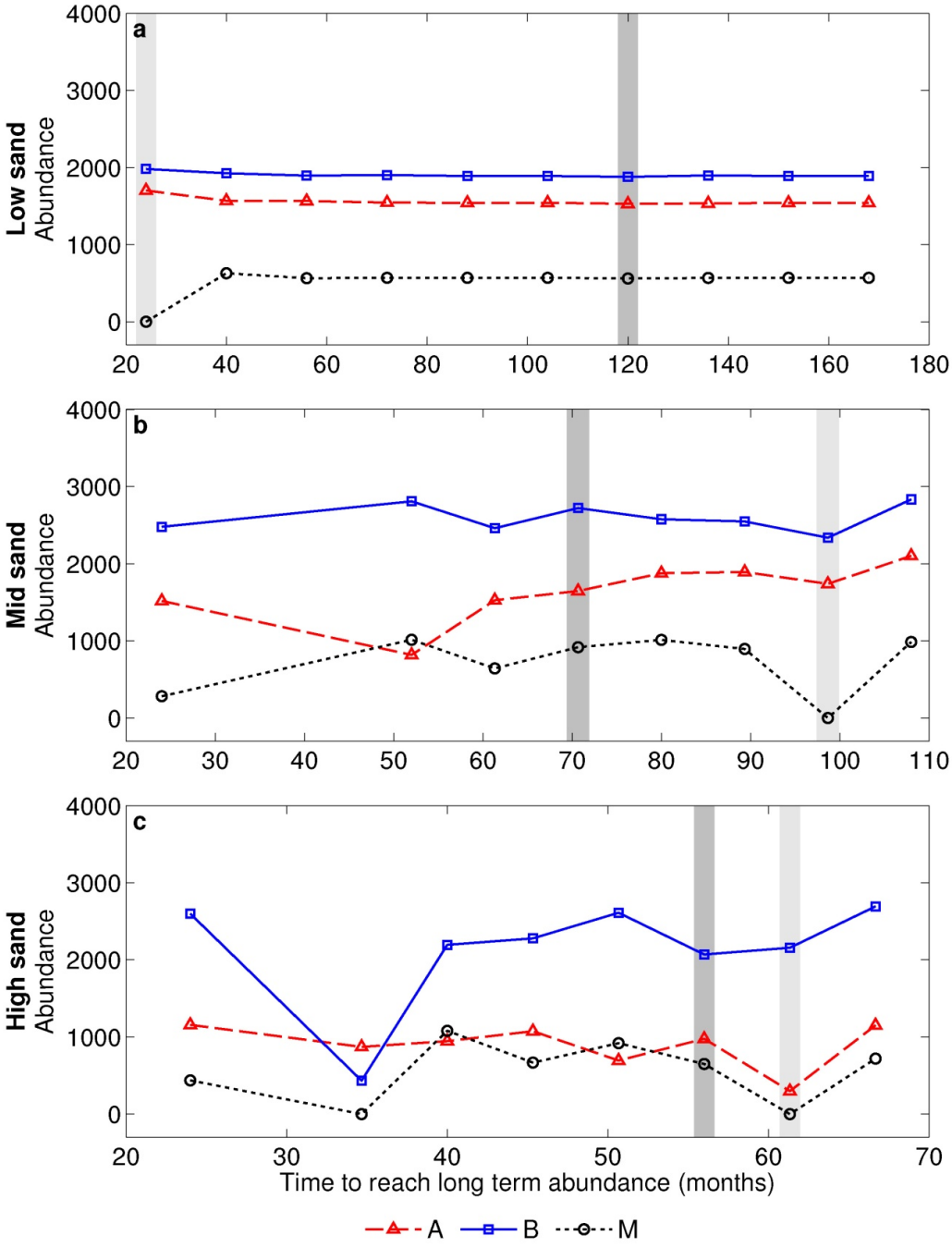
Mid Sand Months	r_A	r_B	r_M	K_A	K_B	K_M	α_{AB}	α_{AM}	α_{BA}	α_{BM}	α_{MA}	α_{MB}
24	0.096121	0.048977	0.052473	232.8701	731.8294	949.0686	1.229186	-15.436	-1.24268	0.498588	-0.35421	0.486848
33.33	*0.091985*	*0.052899*	*0.056855*	*217.2853*	*762.92*	*594.8044*	*-0.44492*	*-7.9643*	*-1.36454*	*-0.82013*	*-0.21882*	*0.408438*
42.66	*0.097951*	*0.052816*	*0.057048*	*1050.559*	*732.251*	*1088.007*	*0.026956*	*-10.8499*	*-1.60756*	*2.434785*	*1.62473*	*-0.42326*
52	0.09961	0.052835	0.05249	1714.63	731.5003	433.8799	-0.2116	1.472616	-2.18118	-0.29067	-0.23573	-0.13775
61.33	0.095299	0.048177	0.053497	225.9539	732.4041	964.3153	0.716859	-4.76545	-0.68427	-1.06377	-0.40051	0.379102
70.66 [3]	**0.097455**	**0.052292**	**0.056528**	**1637.289**	**748.9353**	**421.5649**	**0.075178**	**-0.23207**	**-0.59003**	**-1.09162**	**-0.01004**	**-0.17602**
80	0.099625	0.047069	0.056086	1398.401	740.6048	1083.66	0.159306	-0.87675	-0.75015	-0.42357	0.290039	-0.18322
89.33	0.096778	0.046946	0.057016	626.0181	804.4849	944.3662	0.048856	-1.5562	-0.76469	-0.33242	0.128136	-0.07507
89.66 [2]	**0.08085**	**0.047194**	**0.052302**	**1670.384**	**731.5864**	**319.5725**	**-0.02881**	**-1.15169**	**-0.92336**	**-0.42414**	**2.128698**	**-0.02177**
108	0.090837	0.051165	0.05333	355.6893	2030.483	668.1134	-0.45495	-0.46417	-0.26476	-0.24884	0.128788	-0.20768

Appendix J.3. Ten parameter sets from the ten high sand supply rate equilibrium solutions.

High Sand Months	r_A	r_B	r_M	K_A	K_B	K_M	α_{AB}	α_{AM}	α_{BA}	α_{BM}	α_{MA}	α_{MB}
24	0.079373	0.062753	0.036536	304.2817	379.9316	364.9963	0.19274	-3.10387	-0.00998	-5.06083	-1.30015	0.551569
29.33	*0.080061*	*0.062756*	*0.036515*	*1640.9*	*424.3976*	*1301.056*	*-0.01728*	*8.467402*	*-0.10777*	*-16.7008*	*-5.39485*	*1.666823*
34.67	*0.07933*	*0.062571*	*0.036553*	*925.782*	*379.9315*	*1174.949*	*0.128078*	*-3.8417*	*-0.06163*	*-9.02738*	*4.404139*	*-1.96758*
40	0.077804	0.06053	0.036464	1731.482	399.6406	347.3032	0.307625	0.101909	-0.01787	-1.64622	-2.0408	0.546484
45.33	0.07811	0.058315	0.036332	1313.952	381.0874	319.1322	1.154515	-3.58175	-0.02962	-2.79514	-4.55629	1.994505
50.67	0.081047	0.062741	0.03667	1738.862	550.9635	330.1041	0.140213	0.737118	-0.03027	-2.21577	-4.53254	0.980659
56 [3]	**0.081056**	**0.058404**	**0.035904**	**313.6434**	**382.4221**	**345.8999**	**0.323394**	**-2.05534**	**-0.02377**	**-2.56651**	**-2.20272**	**0.893501**
61.33 [2]	**0.078807**	**0.062762**	**0.034872**	**992.4384**	**2155.834**	**314.1976**	**0.321821**	**-0.63168**	**-0.00507**	**-0.83593**	**-2.06519**	**0.883017**
66.67	0.08073	0.056237	0.034834	1708.196	386.1003	330.1575	-0.05109	0.965563	-0.0061	-3.19748	-1.44814	0.474569
72	0.072107	0.062487	0.03659	1737.602	404.4957	969.7495	-0.54759	2.64168	-0.02823	-3.60576	4.69716	-2.83866

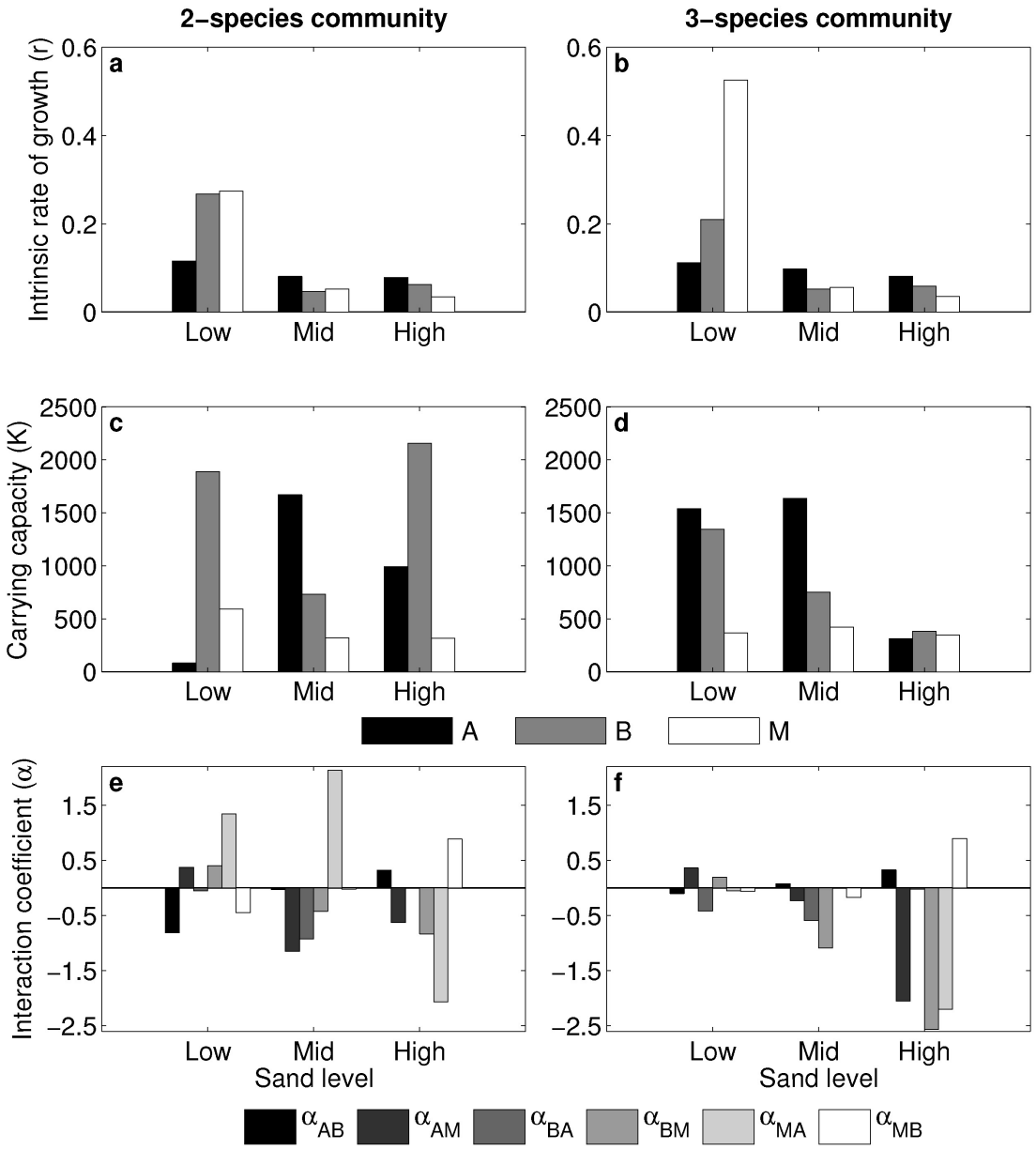


Appendix J.4. Mean ± SE of the parameter estimates from the locally stable equilibria that converged in Appendices J.1-J.3.



Appendix J.5. The locally-stable equilibrium (long term) abundances for each species when the time to reach long term abundance (t_3) is varied across different time points. Refer to Fig. 4.2 for relative abundances.

Appendix K.



Appendix K. Parameter values for the 2- and 3-species communities at equilibrium. Values of α are interpreted as follows: $\alpha_{ij}>0$ is a negative effect of species j on i, and $\alpha_{ij}<0$ is a positive effect of species j on i; the value of $|\alpha_{ij}|$ is the strength or magnitude of the interaction.

Appendix L.

Appendix L. Sensitivity analysis of 2- and 3-species communities at equilibrium.

For the selected 2- and 3-species equilibria parameters in Appendix K, we computed the normalized sensitivity index (Saltelli et al. 2000) to determine the relative influence of parameters *K* and α on the equilibrium abundance of each species. The normalized sensitivity index $S(\widehat{N}_i, \beta)$ of the equilibrium abundance $\widehat{N}_i$ of species i with respect to parameter β is defined generally as:

$$S(\widehat{N}_i, \beta) = \frac{\partial \widehat{N}}{\partial \beta}\left(\frac{\beta}{\widehat{N}_i}\right)$$

Here, the sensitivity of the equilibrium abundance ($\widehat{N}_i$) is the partial derivative of $\widehat{N}_i$ with respect to β scaled by β and $\widehat{N}_i$. These sensitivity values represent a linear estimate of the percentage change in the equilibrium abundance ($\widehat{N}_i$) caused by a one percent change in the parameter β. A positive (negative) $S(\widehat{N}_i, \beta)$ means that an increase (decrease) in the magnitude of the parameter β will lead to an increase (decrease) in $\widehat{N}_i$ (Chitnis et al. 2008). Note that this follows for both positive and negative parameter values. For example, a negative sensitivity index $S(\widehat{N}_i, \beta)$ with respect to a negative parameter (β<0) means that an increase in the magnitude of β will lead to a decrease in the equilibrium abundance ($\widehat{N}_i$). Because these sensitivity indices are normalized, the effect of the parameters on the equilibrium abundances can be compared directly even if their numerical ranges differ. Below we present sensitivity results for each of the 2- and 3-species communities at equilibrium, for each *K* and α parameter (Appendix L.1, L.2).

Sensitivity results for 2- species communities at equilibrium.

Overall, the sensitivity indices for the 2-species equilibrium solutions show that increasing sand supply rate alters the strength and direction of the species interactions and that facilitation is important more often than competition in regulating a community composed of *A. arenaria* and *A. breviligulata* (Appendix L.1).

At low sand supply rates, *A. breviligulata* strongly facilitates *A. arenaria* (α_{AB}), such that the abundance of *A. arenaria* (A) is most sensitive to α_{AB}, and the carrying capacity of *A. breviligulata* (K_B) has a stronger positive effect on *A. arenaria* than its own carrying capacity (K_A) (Appendix L.1 a). Conversely, the abundance of *A. breviligulata* (B) is slightly positively affected by *A. arenaria* (A) through α_{BA}, but is most sensitive to its own carrying capacity (K_B) (Fig. Appendix L.1 d).

At mid sand, facilitation (α_{BA}) increases such that the abundance of *A. breviligulata* (B) is most sensitive to α_{BA} (and thus K_A) and to a lesser extent to its own carrying capacity K_B (Appendix L.1 e). Here, the abundance of *A. arenaria* (A) is most sensitive to its own carrying capacity (K_A) because *A. breviligulata* barely facilitates *A. arenaria* (α_{AB}) (Appendix L.1 b).

At high sand supply rates, *A. breviligulata* competes strongly with *A. arenaria*, such that the abundance of *A. arenaria* (A) is negatively affected by increasing the magnitude of both α_{AB} and K_B (Appendix L.1 c). However, the abundance of *A. arenaria* (A) is more sensitive to its own carrying capacity, K_A (Appendix L.1 c). Here also, the effect of *A. arenaria* (A) on *A. breviligulata* (B) (α_{BA}) is strongly positive such that an increase in K_A will lead to an increase in *A. breviligulata* (B), but the abundance of *A. breviligulata* is only sensitive to its own carrying capacity, K_B (Appendix L.1 f).

Overall, these 2-species interactions result in a higher equilibrium abundance for *A. breviligulata* across sand supply rates (Fig. 4.3, 4.4 a,c). In low sand supply, *A. arenaria* far exceeds K_A via facilitation from *A. breviligulata*, while *A. breviligulata* slightly exceeds K_B due to subtle facilitation from *A. arenaria* (Fig. 4.3, 4.4 a). At mid sand supply, both species exceed their carrying capacities (Fig. 4.4 c), due to facilitation between each other, and a lack of competition from *E. mollis* (Fig. 4.3). Finally, at high sand supply (Fig. 4.4 e), *A. breviligulata* initially exceeds K_B but experiences competition from *A. arenaria*, which decreases its abundance around K_B, while *A. arenaria* is negatively affected by direct and indirect competition from *A. breviligulata* (Fig. 4.4 e). These interactions result in an overall dominance of *A. breviligulata*, but at an abundance near K_B due to the reduction of facilitation from the decline in *A. arenaria* (which results from direct competition against *A. arenaria*) (Fig. 4.3).

Sensitivity results for 3- species communities at equilibrium.

When we consider the 3-species community equilibrium solutions, we again see that sand supply rate alters the strength and direction of species interactions, and that both facilitation and competition are present in a 3-species community (Fig. 4.3).

At low sand supply, the interspecific interactions are small in magnitude, so the abundance of each species is most sensitive to its own carrying capacity (Appendix L.2 a,d,g). *A. breviligulata* slightly facilitates *A. arenaria* whose abundance is slightly positively affected by a magnitude increase in α_{AB} or K_B, but mostly affected by an increase in K_A (Appendix L.2 a). Here, *E. mollis* weakly competes with *A. arenaria* such that increasing the magnitude of α_{AM} or K_M will only slightly decrease *A. arenaria* (Appendix L.2 a). We also see that *A. arenaria* facilitates *A. breviligulata*

such that the abundance of *A. breviligulata* is somewhat sensitive to increasing the magnitude of α_{BA} or K_A but most sensitive to K_B (Appendix L.2 d). *E. mollis* (M) is not facilitated much by either non-native species, so its abundance is only slightly sensitive to increasing the magnitude of α_{MA} or α_{MB} (and thus K_A, K_B) and is more sensitive to its own carrying capacity (K_M) (Appendix L.2g).

In summary for the 3-species community at low sand supply, each species is most sensitive to its own carrying capacity (Appendix L.2 a,d,g), and the interspecific interactions are not strong enough to increase or decrease the abundance of each species away from its respective carrying capacity (Fig. 4.4). Therefore, all three species achieve their carrying capacity and maintain it as their equilibrium abundance such that *A. breviligulata* dominates, followed by *A. arenaria*, and *E. mollis* (Fig. 4.4).

At mid sand supply, most of the 3-species community interspecific interactions increase in magnitude compared to the low sand supply, such that the interactions affecting both *A. breviligulata* and *E. mollis* have an equal or slightly stronger influence on their abundances than their own carrying capacities, though the abundance of *A. arenaria* remains most sensitive to K_A (Appendix L.2 b,e,h). *A. breviligulata* switches from facilitating at low sand supply to slightly competing with *A. arenaria* at mid sand supply such that increasing the magnitude of α_{AB} or K_B will slightly decrease *A. arenaria* (Appendix L.2 b). *E. mollis* also switches interactions compared to low sand supply; at mid sand supply it slightly facilitates *A. arenaria* such that an increase in the magnitude of α_{AM} or K_M will slightly increase *A. arenaria* (Appendix L.2 b). *A. arenaria* and *E. mollis* both facilitate *A. breviligulata* such that increasing the magnitudes of α_{BA} or α_{BM} (and thus K_A, K_M) will have a positive effect on *A. breviligulata* (Appendix L.2 e). *E. mollis* is weakly facilitated by *A. arenaria* and *A. breviligulata* – these effects mean that the abundance of *E. mollis* is slightly sensitive to increasing the magnitude of α_{MA} (and thus K_A) and α_{MB} (and thus K_B) (Appendix L.2 h).

In summary for 3-species community at mid sand supply, *A. breviligulata* far exceeds its carrying capacity, and dominates the community, due to facilitation from the two other species (Fig. 4.4 d, Appendix L.2 f). *A. arenaria* reaches and maintains equilibrium abundances near its carrying capacity because it only receives slight facilitation or competition, thus its own carrying capacity mostly limiting its abundance (Fig. 4.4 f). *E. mollis* experiences positive interactions from both *Ammophila* species, and no inter-specific competition, allowing it to slightly exceed its carrying capacity, but remain the lowest abundance species (Fig. 4.4 f).

In contrast, within the 3-species community at high sand, interspecific interaction strengths are large and often opposing, resulting in complex interactions and feedbacks leading to the highest abundance in *A. breviligulata* followed by *A.*

arenaria and *E. mollis* (Fig. 4.3, 4.4 f, Appendix L.2 c,f,i). *Ammophila arenaria* experiences strong direct and indirect competition and facilitation. Specifically, *A. breviligulata* competes with *A. arenaria* while *E. mollis* strongly facilitates *A. arenaria*, such that increasing the magnitude of α_{AB} or K_B will reduce *A. arenaria*, while increasing the magnitude of α_{AM} or K_M will increase *A. arenaria* (Appendix L.2 c). Increasing the magnitude α_{MA} will increase *A. arenaria* by promoting the abundance of its facilitator (*E. mollis*) (Fig. 4.3, Appendix L.2 c). Conversely, because *A. arenaria* facilitates *A. breviligulata* (Fig. 4.3), increasing the magnitude of α_{BM} will reduce *A. arenaria* by promoting the abundance of its competitor (*A. breviligulata*) (Appendix L.2 c).

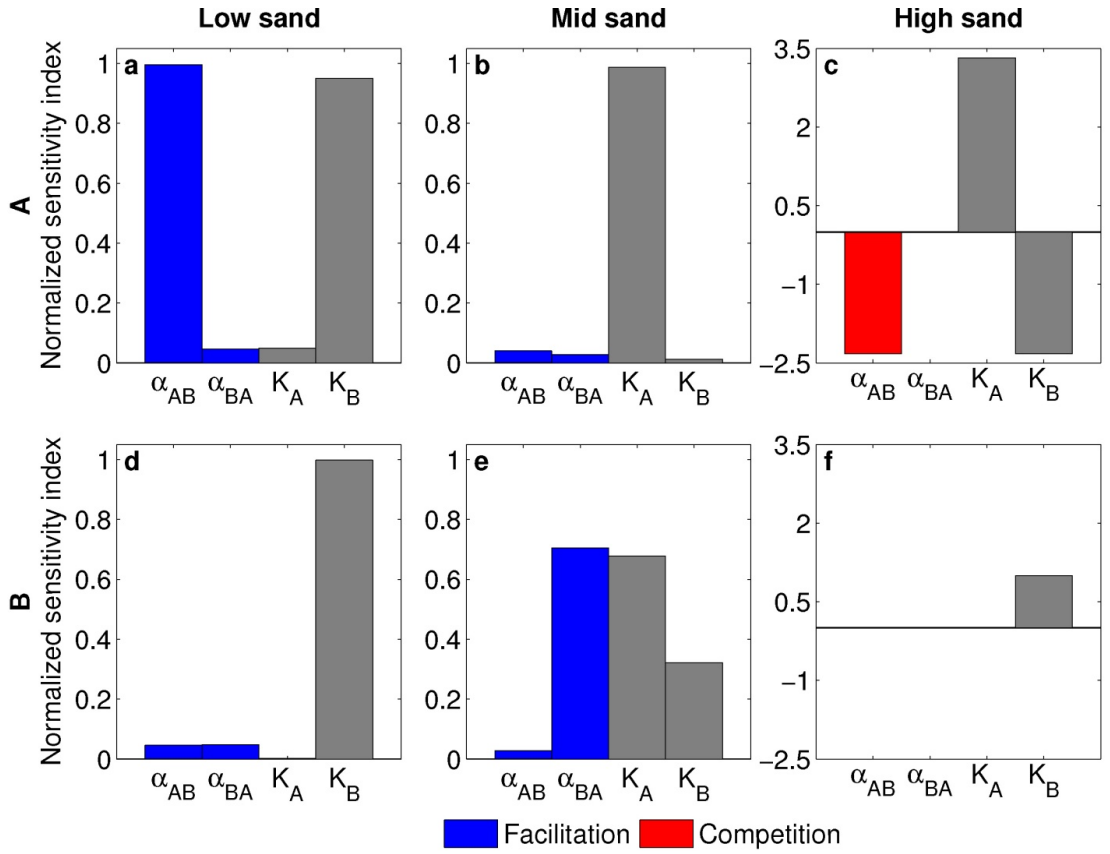
The effects of *E. mollis* and *A. arenaria* on *A. breviligulata* are more complex (Fig. 4.3, Appendix L.2 f). *A. breviligulata* experiences both competitive and facilitative effects that interact to result in overall positive effects and higher equilibrium abundances across all sand levels (Fig. 4.4, Appendix L.2 f). *A. breviligulata* competes with *E. mollis* and the latter facilitates the former, therefore, increasing the magnitude of facilitation of *A. breviligulata* by *E. mollis* (i.e., α_{BM}) will reduce *E. mollis* via competition and thus also reduce *A. breviligulata* (Appendix L.2 f,i). Further, if *A. breviligulata* increases the magnitude of competition against its facilitator, *E. mollis* (α_{MB}, and therefore, K_M), its abundance will decline (Appendix L.2 f). Similarly, because *A. breviligulata* competes with *A. arenaria* and the latter facilitates *E. mollis* which in turn facilitates *A. breviligulata*, increasing the magnitude of α_{AB} or K_B will reduce *A. breviligulata* by indirectly reducing its facilitator (*E. mollis*). *A. arenaria* and *E. mollis* both facilitate each other, and both facilitate *A. breviligulata*. Therefore, increasing the magnitude of α_{AM} and K_A or α_{MA} and K_M will indirectly increase *A. breviligulata*.

The 3-species community effects on *E. mollis* are also complex (Fig. 4.3, Appendix L.2 i). Here, because *A. arenaria* facilitates *E. mollis* (α_{MA}) and *A. breviligulata* competes with *E. mollis* (α_{MB}) a magnitude increase in α_{MA} or K_A will increase and the abundance of *E. mollis*, while α_{MB} or K_B will cause a decrease (Appendix L.2 i). Further, an increase in the magnitude of *E. mollis* facilitating *A. arenaria* (α_{AM}) (and to a lesser extent K_M) will feed back causing an increase in *E. mollis* since *A. arenaria* facilitates *E. mollis* (Fig. Appendix L.2 i). Any increase in the magnitude of *A. breviligulata* competing with *A. arenaria* (α_{AB}) will indirectly cause a decline in the abundance of *E. mollis* by reducing its facilitator (Fig. Appendix L.2 i). Any increase in the direct competition from *A. breviligulata* against *E. mollis* (α_{MB}, and to a lesser extent, K_B) will cause a decline in the abundance of *E. mollis* (Fig. 4.3, Appendix L.2 i).

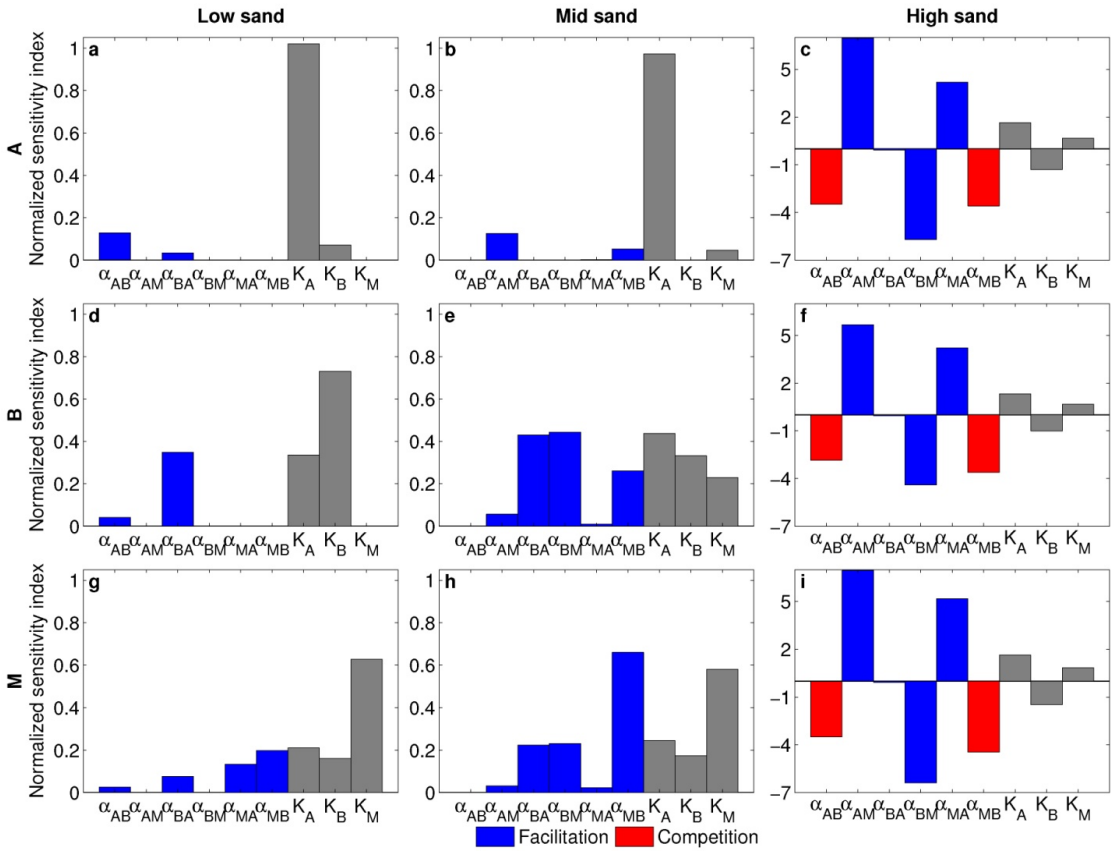
In summary for 3-species high sand supply, *A. breviligulata* outcompetes *A. arenaria* (i.e., $\alpha_{AB}>\alpha_{BA}>0$, Appendix L.2 i, K.1 f) and is facilitated by *E. mollis*,

therefore, *A. breviligulata* reaches equilibrium abundances that are much higher than its carrying capacity and dominates these communities (Fig. 4.4). The strong facilitation between *E. mollis* and *A. arenaria* is larger than the competition by *A. breviligulata* against both *A. arenaria* and *E. mollis* (Appendix K.1 f). This allows both *A. arenaria* and *E. mollis* to exceed their carrying capacities (Fig. 4.4). This 3-species community is mostly regulated by indirect and direct positive interactions that enable each species to exceed its carrying capacity.

Combined, these interactions within the 3-species community all contribute to *A. breviligulata* dominating at low, mid, and high sand, but coexisting with lower abundances of *A. arenaria* and *E. mollis* (Fig. 4.4).



Appendix L.1. Normalized sensitivity indices by sand supply rate for the selected 2-species communities at equilibrium solutions, showing the relative influence of parameters K and α on the equilibrium abundance of species A (*A. arenaria*) and species B (*A. breviligulata*). A positive (negative) normalized sensitivity index means that an increase (decrease) in the magnitude of the parameter will lead to an increase (decrease) in the equilibrium abundance (Chitnis et al. 2008). Here, each α is color-coded to indicate its parameter value sign: $\alpha < 0$ is facilitation (blue), and $\alpha > 0$ is competition (red). The color combined with the index sign (positive or negative) shows the effect of increasing or decreasing the magnitude of each α on the abundance of the given species. For example, in panel (a) a positive effect of α_{AB} on species A and its blue color indicates that increasing facilitation by species B will increase species A. Conversely, in panel (c) a negative effect of α_{AB} on species A and its red color indicates that increasing competition by species B will reduce species A. Note that panels c and f have different scales for the normalized sensitivity index as compared to the other panels.



Appendix L.2. Normalized sensitivity indices by sand supply rate for the selected 2-species communities at equilibrium solutions, showing the relative influence of parameters *K* and *α* on the equilibrium abundance of species A (*A. arenaria*), species B (*A. breviligulata*), and species M (*E. mollis*). See Fig.H.1 legend for a further description of the color coding and sensitivity indices. Note that panels c, f, and i have different scales for the normalized sensitivity index as compared to the other panels.

Appendix M.

Appendix M. Dimensional analysis of the 3-species Lotka-Volterra model.

The basic Lotka-Volterra model describing the dynamics of each species *i* reads:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i N_i \left(1 - \frac{N_i + \alpha_{ij} N_j + \alpha_{ik} N_k}{K_i}\right) = \frac{r_i N_i}{K_i}\left(K_i - N_i - \alpha_{ij} N_j - \alpha_{ik} N_k\right) \qquad \text{eq. 1}$$

For the model to make sense, each term in the differential equation (eq. 1) must have the same units (i.e., focal species density per time). By convention, the units of a given parameter U are denoted as [U]. For the Lotka-Volterra model above, the units are:

$$\left[\frac{\mathrm{d}N_i}{\mathrm{d}t}\right] = \text{density/time} = \text{biomass/area/year}$$

This is the per population growth of each species *i* measured in density/time or biomass/area/month in this study. To confirm that each part of the right hand side (RHS) of eq. 1 has matching units, we present the units of each parameter below.

$$\left[N_i\right] = \text{density} = \text{biomass/area}; \ \left[K_i\right] = \text{density} = \text{biomass/area}; \ \left[r_i\right] = 1/\text{time} = 1/\text{month}$$

Density is measured in biomass/area, with area being constant for all species and times, and the units of the carrying capacity are the same as the density. Because the intrinsic rate of growth is multiplied by the density N_i whose units are biomass/area and divided by carrying capacity K_i whose units are also biomass/area, the former must have units of 1/month.

This means that the first part of the right hand side of eq. 1 has units of 1/month. Hence, the second part of the RHS of eq. 1 must have units of biomass/area since multiplying units of 1/time by units of biomass/area gives units of biomass/area/time, which match the units of the per population growth $\frac{\mathrm{d}N_i}{\mathrm{d}t}$.

Each part of the RHS of eq. 1 must have the same units (focal species density):

$$\left[K_i - N_i - \alpha_{ij}N_j - \alpha_{ik}N_k\right] = \left[K_i\right] - \left[N_i\right] - \left[\alpha_{ij}N_j\right] - \left[\alpha_{ik}N_k\right] \qquad \text{eq. 2}$$

K_i and N_i have units of biomass/area, therefore, all other parts of eq. 2 (namely $\left[\alpha_{ij}N_j\right]$ and $\left[\alpha_{ik}N_k\right]$) must have the same units. Hence, the units of the interaction coefficients must be:

$$\left[\alpha_{ij}\right] = \frac{\text{density of species i}}{\text{density of species j}} = \frac{\text{biomass of species i/area}}{\text{biomass of species j/area}}$$

With these units, multiplying the interaction coefficients by the densities of the non-focal species *j* and *k* will yield units of densities of focal species *i* for each part of eq. 2. Multiplying the second term of the RHS of eq. 1 (i.e., eq. 2) by the first term of the RHS of eq. 1 (i.e., $\frac{r_i N_i}{K_i}$) yields units of biomass/area/time. Hence, the model makes sense as long as it is parameterized with data bearing the proper units.

Appendix N.

Appendix N. Local stability analysis of the –species Lotka-Volterra model.

In this appendix, we perform a local stability analysis on the Lotka-Volterra model presented in the main text. In monocultures, each species *i* increases according to its intrinsic rate of growth r_i until it reaches its carrying capacity K_i. In mixed communities, species interact with one another according to coefficients α_{ij} that describe the effect of species *j* on species *i*. Positive (negative) coefficients denote competition (facilitation). The dynamics of this system is described by the following set of ordinary differential equations:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = \frac{r_1 N_1}{K_1}\left(K_1 - N_1 - \alpha_{12}N_2 - \alpha_{13}N_3\right)$$
$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = \frac{r_2 N_2}{K_2}\left(K_2 - N_2 - \alpha_{21}N_1 - \alpha_{23}N_3\right) \qquad \text{(eq. I.1, eq. I.2, eq. I.3)}$$
$$\frac{\mathrm{d}N_3}{\mathrm{d}t} = \frac{r_3 N_3}{K_3}\left(K_3 - N_3 - \alpha_{31}N_1 - \alpha_{32}N_2\right)$$

The local stability analysis was performed by evaluating the following Jacobian matrix at each equilibrium solution and finding the eigenvalues λ:

$$J = \begin{pmatrix} \frac{r_1\left(K_1 - 2N_1 + \alpha_{12}N_2 + \alpha_{13}N_3\right)}{K_1} & \frac{\alpha_{12}r_1N_1}{K_1} & \frac{\alpha_{13}r_1N_1}{K_1} \\ \frac{\alpha_{21}r_2N_2}{K_2} & \frac{r_2\left(K_2 - 2N_2 + \alpha_{21}N_1 + \alpha_{23}N_3\right)}{K_2} & \frac{\alpha_{23}r_2N_2}{K_2} \\ \frac{\alpha_{31}r_3N_2}{K_3} & \frac{\alpha_{31}r_3N_3}{K_3} & \frac{r_3\left(K_3 - 2N_3 + \alpha_{31}N_1 + \alpha_{32}N_2\right)}{K_3} \end{pmatrix}$$

If the real part of the eigenvalues is negative then the equilibrium solution is locally stable. The model has eight biologically-relevant (i.e., nonnegative and real) equilibrium solutions: (1) the extinction solution where the abundance of all species is zero, (2-4) three single species solutions where each species persists alone, (5-7) three two-species solutions where each pair of species persists alone and (8) the interior equilibrium solution where all three species persist.

The extinction equilibrium solution ($\hat{N}_i = 0$ for all *i*) is locally unstable as long as any species' intrinsic rate of growth is strictly positive (i.e., $r_i > 0$ for any *i*). Next, to determine the stability of the single species equilibrium solutions, we must assess the conditions under which a second species can invade a 1-species system. Species *j* can invade a system consisting of a single resident species *i* at its carrying capacity K_i if the former can grow when rare: $g_j(2) = K_j - \alpha_{ji}K_i > 0$. Hence, the single species equilibrium solution $\left(\hat{N}_i = K_i,\ \hat{N}_j = \hat{N}_k = 0\right)$ for each species *i*={1, 2, 3} will be stable as long as the intrinsic rate of growth of resident species *i* is strictly positive ($r_i > 0$) and each other species *j* is unable to invade: $g_j(2) = K_j - \alpha_{ji}K_i < 0$ for *j*={1, 2, 3} and $i \neq j$.

To determine the stability of the two-species equilibrium solutions, we must assess the conditions under which a third species can invade a two-species system. Species *k* can invade a system consisting of resident species *i* and *j* at their equilibrium

abundance $\left(\hat{N}_i = \frac{K_i - \alpha_{ij}K_j}{1-\alpha_{ij}\alpha_{ji}},\ \hat{N}_j = \frac{K_j - \alpha_{ji}K_i}{1-\alpha_{ij}\alpha_{ji}},\ \hat{N}_k = 0 \right)$ if

$g_k(3) = K_k - \alpha_{ki}\frac{K_i - \alpha_{ij}K_j}{1-\alpha_{ij}\alpha_{ji}} - \alpha_{kj}\frac{K_j - \alpha_{ji}K_i}{1-\alpha_{ij}\alpha_{ji}} > 0$. Hence, the two-species equilibrium solution for resident species $i=\{1, 2, 3\}$, $j=\{1, 2, 3\}$ and $i \neq j$ is stable as long as species *i* and *j* can mutually invade when the other species is at its carrying capacity (i.e., $g_i(2) = K_i - \alpha_{ij}K_j > 0$ and $g_j(2) = K_j - \alpha_{ji}K_i > 0$) and species *k* is unable to invade: $g_k(3) = K_k - \alpha_{ki}\frac{K_i - \alpha_{ij}K_j}{1-\alpha_{ij}\alpha_{ji}} - \alpha_{kj}\frac{K_j - \alpha_{ji}K_i}{1-\alpha_{ij}\alpha_{ji}} < 0$ for $k=\{1, 2, 3\}$ and $i \neq j \neq k$.

The first condition required for coexistence (i.e., $g_i(2) > 0$ and $g_j(2) > 0$) has important ecological implications. Indeed, the two-species equilibrium abundances can be rewritten as: $\hat{N}_i = \frac{K_i - \alpha_{ij}K_j}{1-\alpha_{ij}\alpha_{ji}} = \frac{g_i(2)}{1-\alpha_{ij}\alpha_{ji}}$ and $\hat{N}_j = \frac{K_j - \alpha_{ji}K_i}{1-\alpha_{ij}\alpha_{ji}} = \frac{g_j(2)}{1-\alpha_{ij}\alpha_{ji}}$.

Because $g_i(2) > 0$, $g_j(2) > 0$, $\hat{N}_i > 0$ and $\hat{N}_j > 0$ are required for the two-species equilibrium to exist, we must have $1 - \alpha_{ij}\alpha_{ji} > 0$. Because the intraspecific competition coefficients α_{ii} and α_{jj} are both equal to 1, this inequality can be rewritten as $\alpha_{ii}\alpha_{jj} > \alpha_{ij}\alpha_{ji}$. Hence, each two-species equilibrium solution requires that intraspecific competition $\left(\alpha_{ii}\alpha_{jj}\right)$ be greater than interspecific competition $\left(\alpha_{ij}\alpha_{ji}\right)$.

The three-species interior equilibrium solution:

$$\left(\hat{N}_1 = \frac{K_1\left(1-\alpha_{23}\alpha_{32}\right)-K_2\left(\alpha_{12}-\alpha_{13}\alpha_{32}\right)-K_3\left(\alpha_{13}-\alpha_{12}\alpha_{23}\right)}{\alpha_{32}\left(\alpha_{13}\alpha_{21}-\alpha_{23}\right)+\alpha_{31}\left(\alpha_{12}\alpha_{23}-\alpha_{13}\right)-\alpha_{12}\alpha_{21}+1}, \right.$$

$$\hat{N}_2 = \frac{K_2\left(1-\alpha_{13}\alpha_{31}\right)-K_1\left(\alpha_{21}-\alpha_{23}\alpha_{31}\right)-K_3\left(\alpha_{23}-\alpha_{13}\alpha_{21}\right)}{\alpha_{32}\left(\alpha_{13}\alpha_{21}-\alpha_{23}\right)+\alpha_{31}\left(\alpha_{12}\alpha_{23}-\alpha_{13}\right)-\alpha_{12}\alpha_{21}+1},$$

$$\left. \hat{N}_3 = \frac{K_3\left(1-\alpha_{12}\alpha_{21}\right)-K_1\left(\alpha_{31}-\alpha_{21}\alpha_{32}\right)-K_2\left(\alpha_{32}-\alpha_{12}\alpha_{31}\right)}{\alpha_{32}\left(\alpha_{13}\alpha_{21}-\alpha_{23}\right)+\alpha_{31}\left(\alpha_{12}\alpha_{23}-\alpha_{13}\right)-\alpha_{12}\alpha_{21}+1} \right)$$ exists if each species *k* can

invade each two-species community consisting of resident species *i* and *j* at their

respective equilibrium abundance $\left(\hat{N}_i = \frac{K_i-\alpha_{ij}K_j}{1-\alpha_{ij}\alpha_{ji}},\ \hat{N}_j = \frac{K_j-\alpha_{ji}K_i}{1-\alpha_{ij}\alpha_{ji}} \right)$. This occurs if

$g_k(3) = K_k - \alpha_{ki}\frac{K_i-\alpha_{ij}K_j}{1-\alpha_{ij}\alpha_{ji}} - \alpha_{kj}\frac{K_j-\alpha_{ji}K_i}{1-\alpha_{ij}\alpha_{ji}} > 0$ for *i*={1, 2, 3}, *j*={1, 2, 3}, *k*={1, 2, 3}

and $i \neq j \neq k$. To determine the stability of the interior equilibrium, we resorted to evaluating the Jacobian numerically for each set of parameter values and determining whether the real part of all of the eigenvalues was negative.

Appendix O.

Appendix O: Latitude and longitude of treatment transects within and control transects outside of 8 plover Habitat Restoration Areas in Oregon and Washington, USA. Sites are listed from north to south. Coordinates represent the location of the start of the transect (i.e., most seaward vegetation near the foredune toe). Elk River is also known as McKenzie Ranch.

Transect ID	Site name	Type	Latitude	Longitude
LBP-R1	Leadbetter Point	treatment	46 ° 38 ' 36.11 "	-124 ° 4 ' 9 "
LBP-R2	Leadbetter Point	treatment	46 ° 38 ' 16.62 "	-124 ° 4 ' 8.05 "
LBP-R3	Leadbetter Point	treatment	46 ° 37 ' 58.58 "	-124 ° 4 ' 7.55 "
LBP-R4	Leadbetter Point	treatment	46 ° 37 ' 41.5 "	-124 ° 4 ' 7.41 "
LBP-NR6	Leadbetter Point	control	46 ° 37 ' 22.89 "	-124 ° 4 ' 12.92 "
LBP-NR5	Leadbetter Point	control	46 ° 37 ' 12.37 "	-124 ° 4 ' 11.58 "
LBP-NR7	Leadbetter Point	control	46 ° 36 ' 47.52 "	-124 ° 4 ' 8.79 "
LBP-NR8	Leadbetter Point	control	46 ° 36 ' 31.31 "	-124 ° 4 ' 6.17 "
DO-NR5	Dunes Overlook	control	43 ° 50 ' 52.01 "	-124 ° 9 ' 40.54 "
DO-NR6	Dunes Overlook	control	43 ° 50 ' 46.13 "	-124 ° 9 ' 41.86 "
DO-R3	Dunes Overlook	treatment	43 ° 50 ' 35.49 "	-124 ° 9 ' 43.4 "
DO-R2	Dunes Overlook	treatment	43 ° 50 ' 28.18 "	-124 ° 9 ' 44.6 "
DO-R1	Dunes Overlook	treatment	43 ° 50 ' 22.86 "	-124 ° 9 ' 45.48 "
DO-NR4	Dunes Overlook	control	43 ° 50 ' 8.79 "	-124 ° 9 ' 48.21 "
TK-NR6	Tahkenitch Creek	control	43 ° 48 ' 54.45 "	-124 ° 10 ' 2.7 "
TK-NR5	Tahkenitch Creek	control	43 ° 48 ' 37.66 "	-124 ° 10 ' 6.27 "
TK-NR4	Tahkenitch Creek	control	43 ° 48 ' 24.08 "	-124 ° 10 ' 8.6 "
TK-R3	Tahkenitch Creek	treatment	43 ° 48 ' 18.38 "	-124 ° 10 ' 9.07 "
TK-R2	Tahkenitch Creek	treatment	43 ° 48 ' 7.54 "	-124 ° 10 ' 10.38 "
TK-R1	Tahkenitch Creek	treatment	43 ° 47 ' 53.76 "	-124 ° 10 ' 13.56 "
TM-NR6	Tenmile Creek	control	43 ° 38 ' 46.04 "	-124 ° 12 ' 38.55 "
TM-NR5	Tenmile Creek	control	43 ° 36 ' 27.27 "	-124 ° 13 ' 6.91 "
TM-NR4	Tenmile Creek	control	43 ° 34 ' 56.65 "	-124 ° 13 ' 32.86 "
TM-R3	Tenmile Creek	treatment	43 ° 34 ' 29.47 "	-124 ° 13 ' 39.93 "
TM-R2	Tenmile Creek	treatment	43 ° 34 ' 24.6 "	-124 ° 13 ' 41.21 "
TM-R1	Tenmile Creek	treatment	43 ° 34 ' 22.46 "	-124 ° 13 ' 41.35 "
CNS-NR4	Coos Bay North Spit	control	43 ° 22 ' 7.29 "	-124 ° 19 ' 42.97 "
CNS-NR5	Coos Bay North Spit	control	43 ° 22 ' 3.13 "	-124 ° 19 ' 46.17 "
CNS-R3	Coos Bay North Spit	treatment	43 ° 21' 59.8 "	-124 ° 19 ' 31.83 "
CNS-NR6	Coos Bay North Spit	control	43 ° 21 ' 54.94 "	-124 ° 19 ' 51.41 "

Appendix O. Continued.

Transect ID	Site name	Type	Latitude	Longitude
CNS-R2	Coos Bay North Spit	treatment	43 ° 21 ' 54.33 "	-124 ° 19 ' 30.6 "
CNS-R1	Coos Bay North Spit	treatment	43 ° 21 ' 50.95 "	-124 ° 19 ' 31.99 "
BAN-NR3	Bandon	control	43 ° 3 ' 52.67 "	-124 ° 26 ' 17.64 "
BAN-NR2	Bandon	control	43 ° 3 ' 30.23 "	-124 ° 26 ' 23.44 "
BAN-R6	Bandon	treatment	43 ° 3 ' 17.45 "	-124 ° 26 ' 26.5 "
BAN-R5	Bandon	treatment	43 ° 3 ' 13.93 "	-124 ° 26 ' 27.7 "
BAN-R4	Bandon	treatment	43 ° 3 ' 10.75 "	-124 ° 26 ' 28.29 "
BAN-NR1	Bandon	control	43 ° 2 ' 39.85 "	-124 ° 26 ' 35.87 "
NR-NR1	New River	control	43 ° 0 ' 17.14 "	-124 ° 27 ' 25.49 "
NR-NR2	New River	control	43 ° 0 ' 9.26 "	-124 ° 27 ' 28.49 "
NR-NR3	New River	control	43 ° 0 ' 1.83 "	-124 ° 27 ' 31.05 "
NR-R1	New River	treatment	42 ° 59 ' 52.19 "	-124 ° 27 ' 35.06 "
NR-R2	New River	treatment	42 ° 59 ' 44.59 "	-124 ° 27 ' 38.06 "
NR-R3	New River	treatment	42 ° 59 ' 28.23 "	-124 ° 27 ' 45.44 "
MCK-NR1	Elk River	control	42 ° 48 ' 14.67 "	-124 ° 31 ' 51.02 "
MCK-NR2	Elk River	control	42 ° 48 ' 1.86 "	-124 ° 31 ' 44.28 "
MCK-NR3	Elk River	control	42 ° 47 ' 52.09 "	-124 ° 31 ' 40.34 "
MCK-R1	Elk River	treatment	42 ° 47 ' 45.24 "	-124 ° 31 ' 38.36 "
MCK-R2	Elk River	treatment	42 ° 47 ' 36.36 "	-124 ° 31 ' 33.26 "
MCK-R3	Elk River	treatment	42 ° 47 ' 20.39 "	-124 ° 31 ' 27.98 "

Appendix P

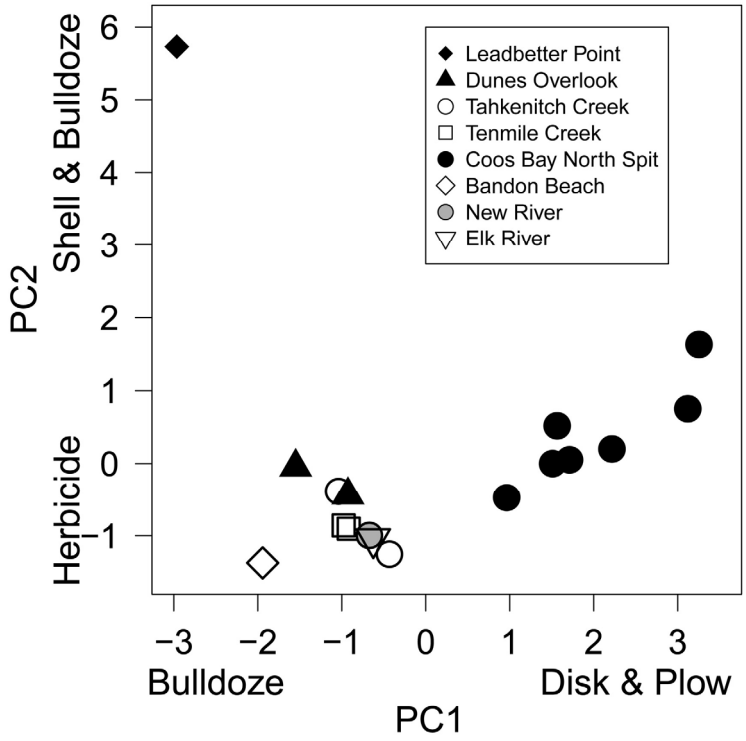
Appendix P: Response and explanatory variables used in Chapter 5 analyses. Abbreviations: trt(s) = treatment(s), ha. = hectares.

Variable	Variable description
Response variables	
Plovers	
Fledglings per male	Number of fledglings (young that reach flying age) per male (males are brooders)
Number of adults	Total number of adults
Number of nests	Total number of observed nests
Exclosed nest success	# of successful exclosed nests/total # exclosed nests (excluding infertile or failed nests)
Unexclosed nest success	# of successful unexclosed nests/total # unexclosed nests (excluding infertile or failed nests)
Egg hatch rate	# of eggs hatched / the number of eggs laid in a nest
Plant relative abundance	See Appendix D for species list
Ammophila spp.	Cover of *Ammophila* given other cover types (including bare ground) in the same quadrat
Non-native plants	Cover of non-native plants given other cover types (including bare ground) in the same quadrat
PNW native plants	Cover of PNW native plants given other cover types (including bare ground) in the same quadrat
PNW endemic dune plants	Cover of PNW endemic dune plants given other cover types (including bare ground) in the same quadrat
Plant richness, evenness	See Appendix D for species list
Non-native plants	Richness, evenness of non-native plants across transect
PNW native plants	Richness, evenness of PNW native plants across transect
PNW endemic dune plants	Richness, evenness of PNW endemic dune plants across transect

Appendix P. Continued

Variable	Variable description
Response variables	
Dune morphology	
Bare ground	Relative cover of bare ground, given vegetation in the same quadrat
Max dune height	The foredune crest: maximum height (m) of the foredune
Dune length	The longest overland distance from foredune toe to foredune crest
Explanatory variables	
Plover management	
Number of human patrols	Number of people patrolling on beach at one time
Predator control (y/n)	Whether predators (e.g., foxes, corvids, skunk, coyotes) were removed or not
Ammophila removal treatment	
Type of treatment	Bulldoze, excavate, plow, disk, rip, handpull, saltwater, burn, herbicide, oyster shells
Cumulative sum: each trt./site	Cumulative sum of each treatment per site
# treatments/yr when treated	Cumulative treatments per year only when treatment occurred
# treatments/yr (cumulative)	Cumulative treatments per year including no treatments in a year
Mean # trts./yr post-start trt.	The mean number of treatments per year, after initial treatment
Mean # trts./ ha/yr post-start trt.	The mean number of treatments per ha. per year, after initial treatment
# treatments/ha/yr post-start trt.	The number of treatments per ha. per year, after initial treatment
Treatment intensity/ha/yr	The intensity of treatments per ha. per year; treatments were rated on a scale of 0 (low) to 10 (high) for the degree of mechanical disruption to ecosystem.
Sum of human treatments	The total sum of human-performed treatments per year (used for yr 2007)
Sum of treatment intensity	The total sum of treatment intensity per year (used for yr 2007)
Treatment proportion	Proportion of HRA habitat which was treated (used for yr 2007)
Natural habitat ha	HRA habitat (in ha.) that is naturally suitable for plover and untreated (used for yr 2007)
Natural habitat proportion	HRA habitat proportion that is naturally suitable for plover and untreated (used for yr 2007)
Treated hectares	Hectares treated per year (used for yr 2007)

Appendix Q.



Appendix Q. Principle components analysis axis 1 (PC1) and axis 2 (PC2) for cumulative treatments of *Ammophila* per hectare by site. In some cases, treatments were performed differently within HRA sections (e.g., Coos Bay North Spit) but generally clump by types of treatments.

Appendix R

Appendix R: List of all plant species found in and near study area treatment and control quadrats, by plant categories. "+" indicates presence, and blank indicates no occurrence within or near quadrats.

Species	Control	Treatment
Non-native plants		
Aira caryophyllea	+	+
Aira praecox	+	+
Ammophila arenaria	+	+
Ammophila breviligulata	+	+
Anthoxanthum odoratum	+	
Cakile edentula	+	+
Cakile maritima	+	+
Cirsium arvense	+	
Cytisus scoparius	+	
Erechtites minima	+	
Hypochaeris radicata	+	+
Rumex acetosella	+	+
Senecio sylvaticus	+	+
Sisymbrium officinale	+	
Sonchus asper		+
Stellaria media	+	
Ulex europaeus	+	
PNW native plants		
Achillea millefolium	+	
Anaphalis margaritacea	+	+
Arctostaphylos uva-ursi	+	
Festuca occidentalis	+	
Fragaria chiloensis	+	+
Gaultheria shallon	+	
Gnaphalium purpureum	+	
Lonicera involucrata	+	
Lupinus littoralis	+	+
Moss	+	
Picea sitchensis	+	
Pinus contorta	+	
Polystichum munitum	+	

Appendix R. Continued.

Species	Control	Treatment
Pteridium aquilinum	+	
Rumex salicifolius		+
Symphyotrichum subspicatum	+	
Vaccinium ovatum	+	
PNW endemic dune plants		
Abronia latifolia	+	+
Abronia umbellata ssp. *breviflora*†		+
Ambrosia chamissonis	+	+
Astragalus sp.‡	+	
Calystegia soldanella	+	
Camissonia cheiranthifolia	+	+
Elymus mollis	+	+
Lathyrus japonicus	+	+
Polygonum paronychia	+	
Tanacetum camphoratum§		+

Notes:

† Manually seeded or planted in treatment sites: Bandon, Coos Bay North Spit, Dunes Overlook, New River, Leadbetter Point

‡ Only 1 plant found.

§ Only 2 plants found at treatment sites, and each at different sites.