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Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact

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Comparisons of congeneric species have provided unique insights into invasion ecology. Most often, non-native species are compared to native ones to look for traits predicting invasion success. In this study, we examine a different facet of congeneric comparisons in which both species are non-native. Ecological variability among non-native congeners might 1) lead to the inhibition or facilitation of either species' ability to colonize and spread, 2) result in larger cumulative impacts due to synergies between species, and 3) depend on the physical context of the invaded habitat. To explore these possibilities, we studied the distribution and abundance of two non-native beach grasses: European beach grass *Ammophila arenaria* and American beach grass *Ammophila breviligulata*, their interaction with one another, and their biotic and physical impacts on dune ecosystems of the Pacific coast of North America. We found that over a two-decade period, *A. breviligulata* has increased its dominance over *A. arenaria* on dunes where it was originally planted in 1935 and has actively spread to new sites formerly dominated by *A. arenaria*. Our results also show that dune plant species richness was lower at *A. breviligulata* sites, although there was an increase in the native beach grass *Elymus mollis*. More significantly, we found that the two grass species are associated with significantly different foredune shapes that are likely controlled by a combination of variability in sand supply along the coast and subtle differences in the congeners' morphology and growth form. These differences have significant implications for the coastal protection services of dunes to humans and the conservation of native species. They provide a cautionary tale on the impacts of introducing novel species based purely on analogy with closely related species.

Comparisons of congeneric species can provide unique opportunities to understand the mechanisms important to invasion ecology (Mack 1996, Daehler 2003, Strauss et al. 2006, Pysek and Richardson 2007, Diez et al. 2008, Mitchell et al. 2008). Most often, non-native congeneric species are compared to native ones to explore whether autecological similarities may allow non-native species to invade or 'naturalize' in novel habitats. Comparisons are also used to understand whether congeneric species share biological interactions with competitors, enemies, or facilitators, which might influence the population size of either one of the species (e.g. Darwin's naturalization hypothesis, Darwin 1859). For example, research on biotic resistance to invasion often involves understanding how congeneric native species hinder or facilitate the invasion of non-native species either through direct interactions or indirectly through shared enemies or mutualists (Maron and Vila 2001, Colautti et al. 2004, Levine et al. 2004, Agrawal et al. 2005, Mitchell et al. 2008, Brandt et al. 2009).

Although much less common, comparisons of non-native congeners can provide important insights into the mechanisms of invasion dynamics by assessing differences among phylogenetically similar non-native species (Rice and Nagi 2000, Lambrinos 2001, 2002, Muth and Pigliucci 2006). As Muth and Pigliucci (2006) argue, it may be more informative to compare non-native species that share phylogeny, but may differ in key characteristics that contribute to their invasiveness. For example, if non-native congeners have different invasion success in their new habitat then characters arising from shared functional traits or provenance may be less important than more subtle species-specific differences.

Differences in invasion rates can arise from traits such as growth form, reproductive mode, or survival (Pysek and Richardson 2007), which ultimately determine how congeners establish themselves and spread (colonization), how they interact with one another (species interactions), and how they affect community structure (community impact). Lambrinos (2001, 2002) provides an example of differential invasion success between two non-native species of pampas grass in the genus *Cortaderia* that co-occur in California. Although morphologically similar, the congeners differ in sexual reproduction, physiological tolerance, and herbivore

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pressure resulting in one species (*C. selloana*) having an expansion rate twice that of the other (*C. jubata*). Thus, several unique differences produced strong and divergent patterns of invasion.

Non-native congeners can also be used to explore the influence of species interactions on invasion success. Congeners with large resource overlap may compete for limited resources and reduce their co-invasion. Alternatively, differences among congeneric species could result in facilitation, producing positive effects. Facilitation can explain why invasion 'meltdowns' occur in communities exposed to multiple non-native species (Simberloff 2006).

The distinctiveness of congeners may also determine whether their combined impacts on the community are additive, sub-additive, or super-additive. When congeners share characteristics that produce similar community impacts, then their joint invasion will be additive. In contrast, differences among congeners may neutralize impacts (e.g. if they have competitive or trophic interactions) or expand them through interactive means (i.e. synergistic effects). Yet another prediction is that differences among congeners will interact with the environment resulting in a widening of the impacts across the range of the invasion (Hacker and Dethier 2009).

Here we examine a particularly dramatic case of a congeneric invasion, where the European beach grass, *Ammophila arenaria* (originally from Europe) and the American beach grass, *Ammophila breviligulata* (originally from eastern North America and the Great Lakes) have invaded dune communities along the Oregon and Washington coasts over the last 100 years. To the casual observer, the two species appear virtually identical and have not historically been recognized as separate species in the field (Baye 1990, Seabloom and Wiedemann 1994). However, the two species differ in morphology and growth form (Baye 1990), their abundance and distribution on the Pacific coast, and their potential to impact dune shape and community structure (Supplementary material Appendix A1, Seabloom and Wiedemann 1994). Motivated by these distinct differences in invasion patterns, we used data collected at large regional spatial scales to 1) assess the distribution and abundance of the two non-native beach grasses over two decades to gain comparative insights into how species-specific characteristics and interactions have affected their spread, 2) measure the impact of both species on biotic and geomorphic characteristics of the dunes, and 3) analyze the relative effect of sand supply versus species identity on differences in dune shape. Below we describe these objectives in more detail. Comparing the invasion dynamics of these two congeners not only informs basic invasion ecology but also has practical implications for the coastal protection and conservation of dune communities.

The study system

Coastal dunes comprise approximately 40% of the Oregon and Washington coasts. One dune sheet in particular, the Coos Bay Dune Sheet, is the largest in North America (Cooper 1958). Sand dunes are ecologically unique and dynamic ecosystems that are subject to high sand movement, low nutrients, and extremes in moisture (Martinez and Psuty 2004, Maun 2009). Along the Pacific coast, dunes have historically been managed to reduce sand movement and increase coastal protection from wave-induced erosion and flooding. Coastal protection is an important ecosystem service (Barbier et al. 2008, 2011, Everard et al. 2010), particularly on the Pacific coast where the most intense wave conditions in the world occur and tsunami risk is high (Allan and Komar 2006).

Stabilization of west coast dunes was achieved primarily through the systematic planting of *Ammophila arenaria* starting in 1868, which by the 1950s dominated dunes from Mexico to Canada (Wiedemann and Pickart 2004). In 1935, a congener, the American beach grass *A. breviligulata*, also was planted on dunes near the Columbia River at Warrenton, Oregon (McLaughlin 1939) (Fig. 1). The status of *A. breviligulata* was largely unknown for 53 years until Seabloom and Wiedemann (1994) surveyed the invasion in 1988 and found that it had spread north along the Washington coast and south as far as Cape Lookout, Oregon (Fig. 1). Our recent surveys show that *A. breviligulata* has spread 10 km farther south to Cape Kiwanda (Fig. 1), and is also present

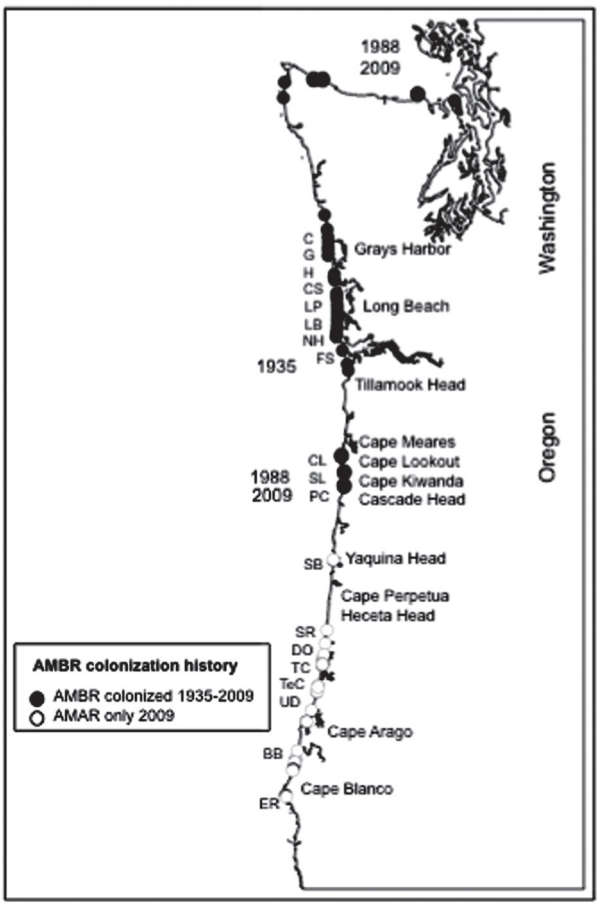

Figure 1. The colonization history and biogeographic distribution of two non-native beach grasses, *A. arenaria* (AMAR, open circles) and *A. breviligulata* (AMBR, black circles) along the coast of Oregon and Washington, USA, between 1935 (first introduction), 1988 and 2009 (see Supplementary material Appendix A2 for exact site locations). Abbreviations indicate sites used for abundance measurements in Fig. 2 (see Supplementary material Appendix A3 for exact site locations).

in small patches further south in Coos County, Oregon, and Orange County, California (Hickman 1993), where it may have been inadvertently introduced in stabilization projects.

Grasses in the genus *Ammophila* highly modify their habitat by creating foredunes, tall ridges of sand parallel to the shoreline, which intercept wind-driven sand delivery to the backdune (Hesp 1989, Gutierrez et al. in press). Prior to the introduction of *Ammophila*, dunes consisted of small hillocks of sand that were sparsely colonized by native plants including the native beach grass, *Elymus mollis* (Cooper 1958, Weidemann and Pickart 2004). Today, *Ammophila* and the foredunes they create, have dramatically changed sand dune ecosystems and human development patterns along the coast. Foredunes, which can be as tall as 15 m, serve as barriers to wind, waves, and sand, thus increasing the coastal protection services for humans (Ruggiero et al. 2001, Barbier et al. 2008, 2011). By decreasing disturbance to the backdune, foredunes have initiated rapid plant succession that has led to the formation of extensive wetlands and coastal scrub habitat, essentially 'stabilizing' these areas (Wiedemann and Pickart 2004). *Ammophila* also is implicated in the decline of six federally listed endangered plant species and the federally listed threatened Western snowy plover. Eventually, the invasive grasses could lead to a loss of the dramatic dune system once unique to the Pacific coast.

Previous research focused on the southern Washington coast (Fig. 1) has shown that there are at least two differences between foredunes dominated by *A. breviligulata* compared to those with *A. arenaria* (Seabloom and Wiedemann 1994). First, plant species richness is lower where *A. breviligulata* dominates suggesting that it may be a superior competitor in the foredune environment. Second, foredune heights are lower where *A. breviligulata* dominates suggesting that it may accrete less sand than *A. arenaria* (Supplementary material Appendix A1). However, dune height is strongly controlled by sand supply (Psuty 1986), which varies considerably along the coast and is highest in areas dominated by *A. breviligulata* (this paper), thus it remains unclear whether the observed differences in dune shape reported by Seabloom and Wiedemann (1994) are attributable to differences in the bioengineering effects of the two congeners or sand deposition rates within their current range. For this reason, we were particularly interested in the relative role of sand supply versus species identity in shaping the invasion dynamics in this system.

Methods

Beach grass colonization, spread and dominance

To document the colonization, spread, and dominance of the two congeners through time, we re-surveyed sites previously surveyed 19 years ago (Seabloom and Wiedemann 1994). In August 2007, we measured the abundance of the two non-native *Ammophila* grasses and the native grass, *Elymus mollis*, at the same 57 sites, and in the same manner, as those in 1988 (Fig. 1, Supplementary material Appendix A2). We visually estimated the overall relative abundance of each species at the site using the following cover classes: 0 = absent, 1 = 1 to 25% cover, 2 = >25 to 50% cover, or 3 = >50 to 100% cover. In addition, at a subset of 34 sites at Grays Harbor and Long Beach (Fig. 1, Supplementary material Appendix A2), we measured foredune height and width between July–October 2006 as in Seabloom and Wiedemann (1994) and described below.

Foredune community structure, geomorphology and sand supply

To compare the impacts of the two *Ammophila* congeners on dune community structure and shape, we conducted more detailed surveys of the foredunes from July–October 2006 at 19 sites from Grays Harbor, Washington, to Cape Blanco, Oregon (Fig. 1, Supplementary material Appendix A3). The sites fall within distinct littoral cells–areas along the coast with different sediment sources and sinks (see Supplementary material Appendix A3 for locations and descriptions) – thus they have variable amounts of sand supply.

At each of the sites, we established 3–10 transects (Supplementary material Appendix A3), separated by distances ranging from 1–10 km, by placing a transect line across the foredune perpendicular to the shoreline, starting at approximately the mean higher high water (MHHW) tide mark (determined by the highest tidally created wet sand zone on the beach), running over the dune crest, and ending at the lowest point on the back of the dune. We used a GPS to determine the latitude and longitude values for each transect (Supplementary material Appendix A3).

At the MHHW tide mark and every 5 m along the transect starting at the location of first vegetation, we measured foredune height and plant community structure. Foredune height was determined using a surveying rod and hand level to record the elevation profile of the foredune, including the maximum foredune height relative to MHHW and the maximum width as measured from the dune toe to the first elevation minimum backshore of the dune crest. The relative accuracy of the survey equipment was approximately 0.05 m in the vertical but, because we interpreted the location of the MHHW datum using visual proxies, the absolute accuracy of our dune height measurements is approximately 0.2–1.0 m (Ruggiero and List 2009). We visually estimated the percent cover of all plant species that fell within quadrats (0.20×0.50 m^2) placed along the transect lines at the same location as each survey point.

We measured sand deposition and shoreline change rates across the biogeographic range of the foredune transects. Sand deposition was measured directly by using 10 PVC stakes placed at the base of the transect locations (without vegetation) at four sites in the north (Grayland, Leadbetter Point, Long Beach and North Beach) and four sites in the south (Cape Lookout, South Beach, Dunes Overlook and Umpqua Dunes). In February 2006, we pounded a 1.5 m stake into the toe of the foredunes to 0.75 m depth, marked the surface of the sand on the stake using permanent ink, and marked the new sand surface roughly six months later (August) to measure sand deposition. We also calculated shoreline change, which is an integrated measure of the gain or loss of beach sediment over time, for each transect at all 19 sites. We compared aerial photographic-derived shoreline positions from the 1950–60s to lidar-derived shoreline positions in 2002 to compute end-point shoreline change rates at a decadal scale.

Beach grass morphology and growth form

We measured the morphology of the three beach grass species collected (where present) at all 19 sites on the transects. We collected grasses in two ways. First, we placed a quadrat (0.25×0.25 m^2) on the upper face of the foredune next to the transect in monocultures of each species (where present) and dug up all the plants including as much as 50 cm of the belowground stem or rhizome. We counted individual plants (defined as one or more tillers attached to a single proximal rhizome) within each quadrat. Second, we extracted individual plants of each species (where present), including at least 50 cm of the rhizome, on the upper face of the foredune along the transect. We dried the plants to a constant mass at 60°C and measured tiller density (tillers per rhizome), tiller height (cm), tiller weight (g), length of primary rhizome internodes and lateral (approx. 90° orientation to the primary rhizome) versus vertical (less than approx. 90° orientation to the primary rhizome) secondary rhizomes produced at the nodes and terminating in tillers.

Statistical analyses

We analyzed the abundance of each grass species (proportional cover for each transect per site) for the effect of site with one factor ANOVAs. We analyzed the proportional change in species dominance from 1988–2007 using a one factor ANOVA and that of foredune height and foredune width, for the same period, using unpaired student's t-tests. We analyzed foredune community structure (non-native grass cover, native grass cover, native plant species richness and the proportion non-native plant species richness) and physical conditions (maximum foredune height, width, slope and sand deposition and shoreline change) for sites dominated by *A. breviligulata* (including, and north of, Fort Stevens that had >50% proportional cover of *A. breviligulata*) and *A. arenaria* (including, and south of, Cape Lookout that had >50% proportional cover *A. arenaria*) using unpaired student's t-tests. We calculated an exponential regression between dune height and shoreline change for transects dominated by *A. breviligulata* and *A. arenaria*. In addition, for a subset of foredune transects that had statistically similar shoreline change values of ±2 m or less, we compared beach grass cover, foredune height, width, and slope using unpaired student's t-tests. We analyzed beach grass morphology (plant number, tiller density, lateral to vertical secondary rhizomes, primary rhizome internode length, tiller weight and tiller height) for the three species using one factor ANOVAs. Bonferroni-Dunn post hoc tests were conducted to determine significant treatment effects. We performed all analyses using JMP 7.0 (SAS 2007).

Results

Beach grass colonization, spread, and dominance

The transect data show that the two *Ammophila* species overlapped at 9 of the 19 sites surveyed (Fig. 2). *A. breviligulata* had a higher proportional cover at sites north of Fort Stevens compared to Fort Stevens or Cape Lookout, which did not differ, and it was absent south of Cape Lookout (although we have found it at very low density outside the transects at Sand Lake and Pacific City) (Fig. 1, 2). *Ammophila arenaria* was present at all sites and had higher proportional cover at Cape Lookout and south where *A. breviligulata* was absent (Fig. 1, 2). The native *Elymus mollis* was present at low to moderate proportional cover at all sites but varied among sites (Fig. 2). It was most abundant at the central Oregon sites (South Beach, Siltcoos, Dunes Overlook and Tahkenitch) and least abundant at northern and southern sites (Fig. 2). The northern and southern sites did not differ (Fig. 2).

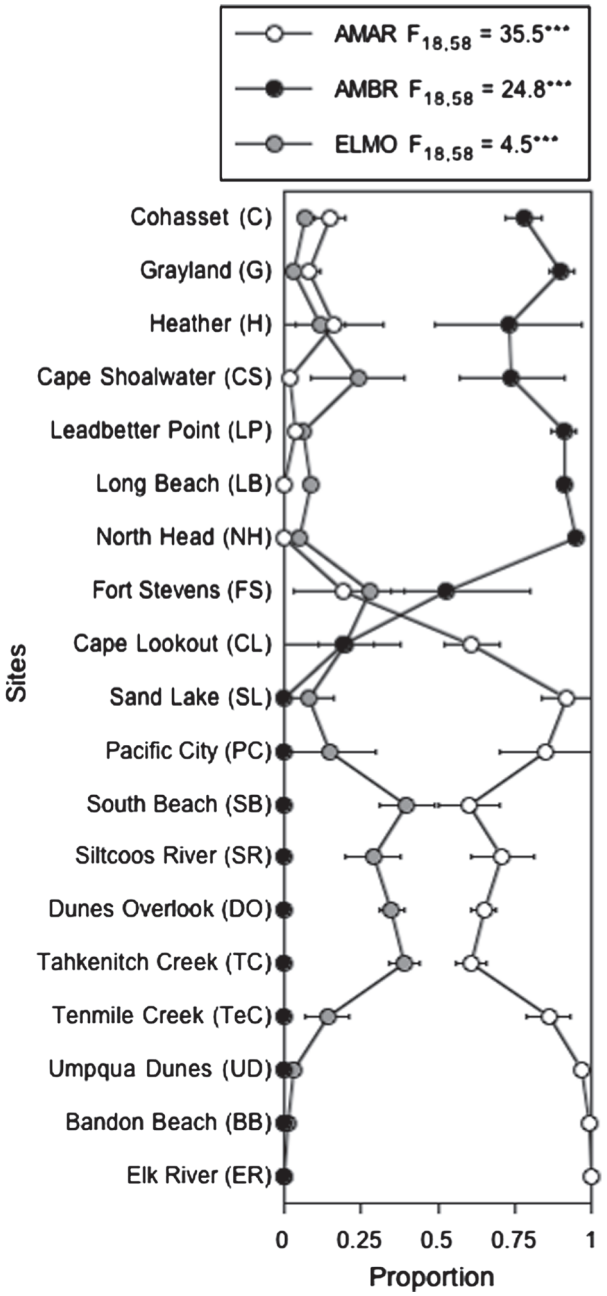

Figure 2. Mean (±SE) proportional abundance for two non-native (*A. arenaria* = AMAR and *A. breviligulata* = AMBR) and one native (*E. mollis* = ELMO) beach grass species at 19 sites, from north (top) to south (bottom), along the Washington and Oregon coasts, USA (see Fig. 1 and Supplementary material Appendix A3 for site locations). One factor ANOVA results for the effect of site on the three dune grass species are given in legend (***$p < 0.0001$).

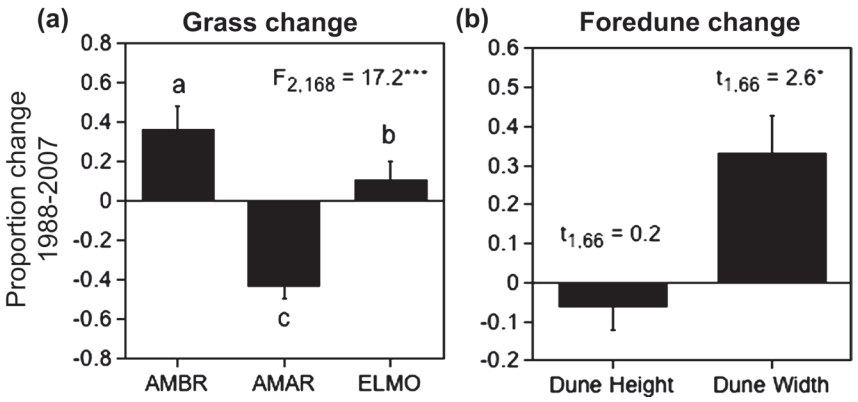

Figure 3. Mean (±SE) proportional change over 19 years (1998–2007) in (a) beach grass cover (*A. breviligulata* = AMBR, *A. arenaria* = AMAR and *E. mollis* = ELMO) at 57 sites, and (b) maximum foredune height and width at 34 sites (see Supplementary material Appendix A2 for site locations). One factor ANOVA results for the change in the three beach grass species are given in plot a (***$p < 0.0001$). Bars that do not share letters are significantly different (Bonferroni Dunn $p < 0.05$). Student t-test results for the change in dune height (not significant) and dune width (*$p < 0.05$).

At the 57 sites where all three species co-occurred (Fig. 1), we found that *A. breviligulata* increased in abundance by 36%, *A. arenaria* decreased by 43%, and *E. mollis* increased by 11% over the past 19 years (Fig. 3a). Over the same period, there was no change in foredune height (Fig. 3b) and a significant 32% increase in foredune width (Fig. 3b). In addition to its dominance, *A. breviligulata* colonized an additional 10 km of coast to the south (Fig. 1).

Foredune community structure, geomorphology and sand supply

Grass cover did not differ on foredunes dominated by *A. breviligulata* or *A. arenaria* (Fig. 4a) although the native grass, *E. mollis*, was more abundant at *A. arenaria* sites (Fig. 4b). In addition, plant species richness was lower on foredunes dominated by *A. breviligulata* compared to *A. arenaria* (Fig. 4c). Although the number of non-native plant species (ignoring the grasses themselves) was lower for foredunes dominated by *A. breviligulata*, they did not differ by proportion (17.0 ± 4.4% and 19.6 ± 4.2% for *A. breviligulata* and *A. arenaria* sites, respectively; $t_{1,17} = 0.4$; $p = 0.69$).

Foredunes dominated by *A. breviligulata* were almost half the height, nearly twice the width, and half as steep as those dominated by *A. arenaria* (Fig. 4d–f). They also had higher sand deposition and greater shoreline change rates than those dominated by *A. arenaria* (Fig. 4g–h).

We found a negative exponential correlation between shoreline change rate and foredune height across all transects (Fig. 5). Transects with highly positive or negative shoreline change rates had shorter foredunes compared to those with rates near zero, and were dominated by *A. breviligulata* (Fig. 5). A second analysis, which removed the confounding effect of shoreline change, showed that within a restricted range of shoreline change rates of ± 2 m or less, *A. arenaria* foredunes were taller, narrower, and steeper than those with *A. breviligulata* even though the grass cover did not differ (Table 1).

Beach grass morphology and growth form

For a given area, *E. mollis* had the lowest density of plants compared to *A. arenaria* and *A. breviligulata*, which did not differ (Fig. 6a). For a given plant, tiller density was lowest for *E. mollis* compare to *A. arenaria* and *A. breviligulata*, which did not differ (Fig. 6b). In addition, *A. arenaria* plants had significantly fewer lateral compared to vertical rhizomes (Fig. 6c), longer internodes (Fig. 6d), and lighter tillers (Fig. 6e) compared to *A. breviligulata* or *E. mollis* plants. *E. mollis* had the heaviest but also the tallest tillers compared to the two *Ammophila* species, which did not differ in height (Fig. 6f).

Discussion

We found that two closely related and superficially similar beach grass species differ substantially in their success as invaders and their impacts on Pacific coast dune ecosystems. Over the last 19 years, *A. breviligulata*, a congener species that was introduced to the west coast of North America after *A. arenaria*, has colonized new sites and increased in abundance at sites previously dominated by the European species (Fig. 1, 3a). There has been a concomitant decline in *A. arenaria*, which has shown long-term declines since 1941 at sites where it co-occurs with *A. breviligulata* (Seabloom and Wiedemann 1994). We attribute this displacement to morphological and growth habit differences between the species and how they interact with large-scale variability in sand supply to the coast.

We found that *A. breviligulata* produces more lateral rhizomes with larger tillers compared to the tussock-like growth form of *A. arenaria* (Fig. 6). In the only common garden study of both species, Baye (1990) found that *A. breviligulata* is better at spreading over a wider area, thus producing a 'guerilla' type growth pattern compared to the 'phalanx' type of spread of *A. arenaria* (Fig. 7). The lateral dispersion pattern of *A. breviligulata*, along with its larger tiller size, could give it a competitive advantage over *A. arenaria*, and is a likely reason for its increasing dominance (Fig. 3a).

Moreover, we suspect a critical contributing factor for this dominance is the sand supply regime on the coast. We show that at sites where *A. breviligulata* dominates (Fig. 2), shoreline change and sand deposition are significantly higher than those where *A. arenaria* dominates (Fig. 2, 4g–h). Positive shoreline change rates create wider, shorter foredunes with

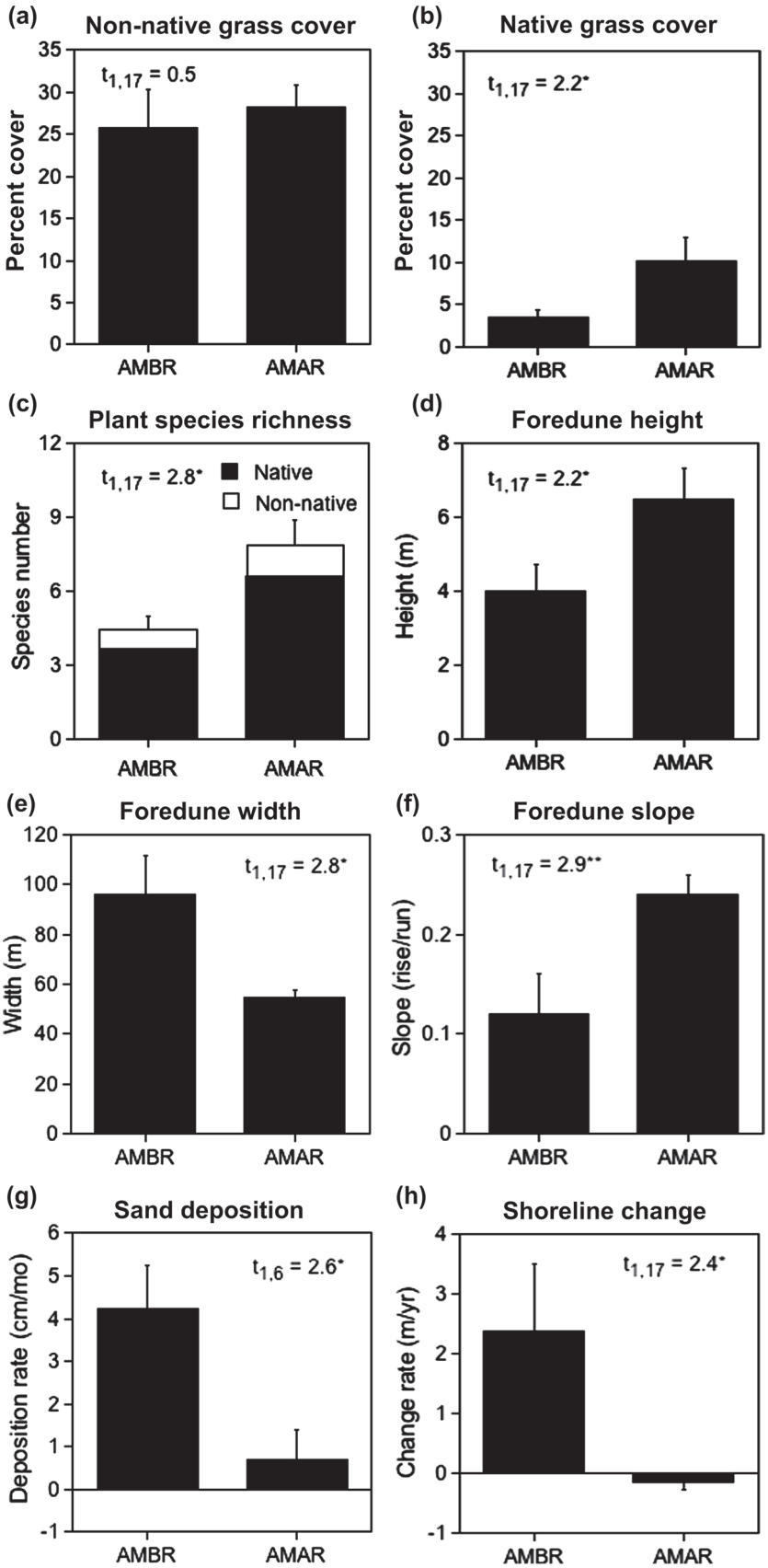

Figure 4. Comparisons of mean (±SE) plant community characteristics, geomorphology, and sand supply of foredunes, including (a) non-native grass cover, (b) native grass cover, (c) native and non-native plant species richness, (d) maximum foredune height, (e) maximum foredune width, (f) maximum foredune slope (height/0.5 width), (g) sand deposition, and (h) shoreline change rate at sites dominated either by *A. breviligulata* (AMBR, n = 9 sites) or *A. arenaria* (AMAR, n = 10 sites) (except sand deposition AMBR n = 4, AMAR n = 4). See Supplementary material Appendix A1 for photos of both species. Student t-test results are given in the plots ($^{*}p < 0.05$, $^{**}p < 0.001$).

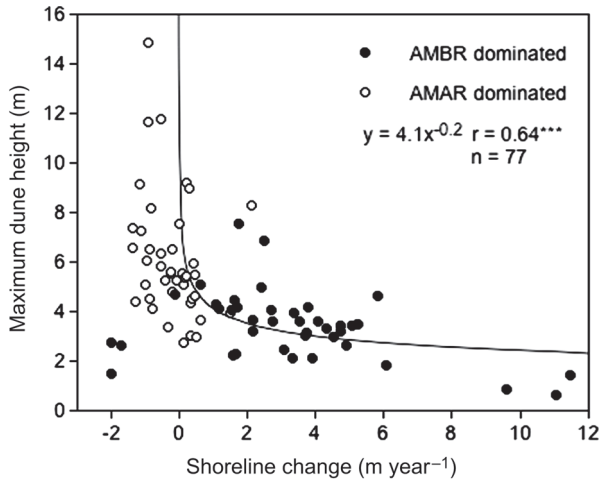

Figure 5. Relationship between maximum foredune height and shoreline change rate for transects dominated by *A. breviligulata* (AMBR, dark circles) and *A. arenaria* (AMAR, open circles). The line represents a negative exponential relationship for all transects combined (***$p < 0.0001$).

open areas of sand in which to colonize (Fig. 4, 5, Supplementary material Appendix A1). The horizontal growth of *A. breviligulata* would likely be favored over that of *A. arenaria*, allowing it to more easily colonize this newly created habitat. However, given the observational nature of our data, experimental studies will be critical in resolving the relationships between sand deposition and species interactions.

We also found much lower plant species richness where *A. breviligulata* dominates relative to *A. arenaria* (Fig. 4c). It may be that different community impacts arise from differences in the grasses growth form and morphology because overall cover was nearly identical between the two species (Fig. 4a). Or the differences may be controlled by sand supply. Whether the spread of *A. breviligulata* could cause a decline in plant species richness is unknown. However, a study on the eastern coast of the US by Cheplick (2005) shows *A. breviligulata* to have negative effects on the density and reproduction of two of the three most common annual plants in these dunes.

Interestingly, the native beach grass, *Elymus mollis*, which has the most robust tillers of all the grasses, has also increased in abundance during this time (Fig. 4b). Again, a reason for this may be its morphology and growth form, which is characterized by more lateral rhizomes but low tiller density relative to the two *Ammophila* species (Fig. 6). These results are concordant with the only other study comparing these species (Pavlik 1983). While we lack quantitative data, Wiedemann and Pickart (2004) provide anecdotal evidence that the native grass was never abundant along the coast where foredunes now currently exist. Despite the modest increase we document for *E. mollis* on foredunes with *A. breviligulata* (Fig. 3a), it is actually more abundant on the taller and steeper foredunes of *A. arenaria* (Fig. 4b, d). Thus, it is possible that the *A. arenaria* created foredunes could benefit some native species by decreasing wind and sand scouring stress. More generally, we suggest that there are important relationships between competition, facilitation, and growth form for the three species under different sand supply contexts that could control their co-existence and will require experiments to resolve.

Although *A. breviligulata* has spread fastest in the northern part of its invasive range, it continues to move steadily south into *A. arenaria* dominated areas (Fig. 1). *Ammophila breviligulata* can grow in southern California (Hickman 1993) suggesting that its current restricted range likely results from dispersal limitation rather than environmental limits. While both species of *Ammophila* have the potential to survive long distance dispersal via ocean currents (Baye 1990), this movement is likely restricted along the coast for two reasons. First, prevailing currents and winds move to the north in the winter when sand erosion and dispersal potential is highest (Komar 1997). Second, the Oregon coastline is composed of several discrete littoral cells bracketed by large headlands that will slow dispersal between adjacent littoral cells.

Beach grass impact on dune geomorphology

In addition to beach grass colonization and species interactions, the congeners differ in their impact on dune geomorphology and ultimately the coastal protection services they provide. The impact of the grasses, though, appears to be dependent on sand supply, suggesting that beach grass invasions could be context dependent. Foredunes in the northern sites where *A. breviligulata* dominates are shorter, wider, and have a shallower slope compared to sites in the south where *A. arenaria* dominates (Fig. 4, 5, Supplementary material Appendix A1). Many of the beaches in the northern region are prograding (building seaward), primarily due to massive offshore sand remobilization following the construction of jetties at the mouths of the Columbia River and Grays Harbor (Kaminsky et al. 2010). In contrast, the shoreline change rate is lower at the southern sites where *A. arenaria* dominates resulting in foredunes that are taller, thinner, and steeper (Fig. 4, 5, Supplementary material Appendix A1).

Table 1. Means (± SE) and results of Student t-test comparisons of shoreline change rate, total beach grass cover, maximum foredune height, width, and slope between *A. breviligulata* (AMBR) and *A. arenaria* (AMAR) dominated foredunes with ± 2 m or less shoreline change rates in Washington and Oregon, USA (AMBR n = 13, AMAR n = 36; all DF = 1, 47; ***$p < 0.0001$).

Variable	AMBR dominated mean ± SE	AMAR dominated mean ± SE	t
Shoreline change rate (m year^{-1})	0.36 ± 0.49	–0.27 ± 0.11	1.9
Total beach grass cover (%)	29.2 ± 3.5	28.8 ± 1.5	0.1
Maximum foredune height (m)	3.8 ± 0.4	6.4 ± 0.4	3.6***
Maximum foredune width (m)	109.2 ± 13.5	53.5 ± 2.3	6.3***
Maximum foredune slope (height/0.5 width)	0.09 ± 0.02	0.24 ± 0.01	6.1***

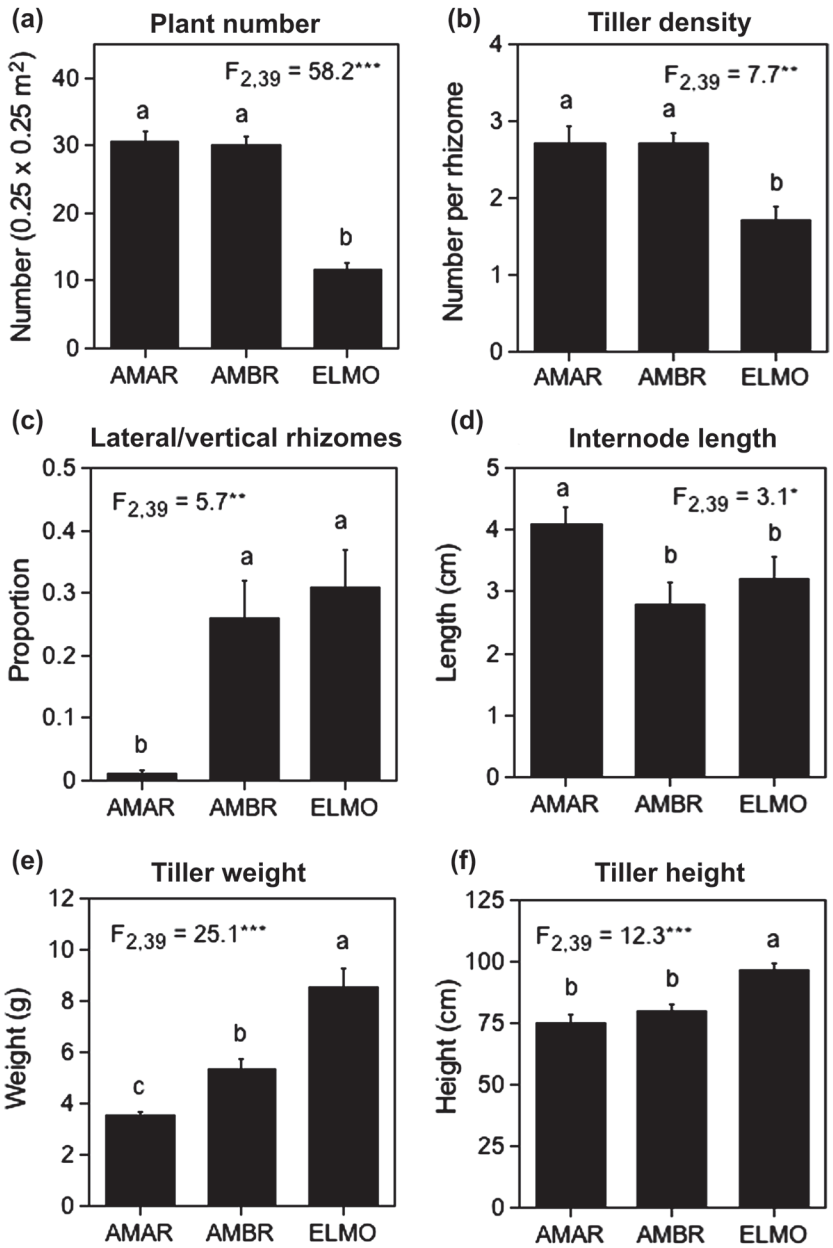

Figure 6. Comparisons of mean (±SE) morphological characteristics (plant number, tiller density, proportion lateral to vertical secondary rhizomes, primary rhizome internode length, tiller weight, and tiller height) for beach grasses (*A. breviligulata* = AMBR, n = 9 sites, *A. arenaria* = AMAR, n = 16 sites, *E. mollis* = ELMO, n = 17 sites) on the foredune face at sites where they occurred. One factor ANOVA results are given in plots ($^{*}p < 0.01$, $^{**}p < 0.001$, $^{***}p < 0.0001$). Bars that do not share letters are significantly different (Bonferroni Dunn $p < 0.05$).

In part, the difference in foredune shape can be explained purely through geomorphological models that predict foredune development based on the amount of sand blown inland from the beach (Psuty 1986). When sand delivery rates are high, the foredune becomes wider rather than taller because sand deposition is spread out over an ever-expanding area, creating a series of long, low foredune ridges. In contrast, when sand supply to the beach is negligible (slightly positive or negative), the sand traveling from the beach to foredune will be deposited over a smaller area thus causing the dune to become taller rather than wider. Likewise, if sand supply is negative, beach erosion and scarping will create shorter and narrower foredunes with a greater chance of overwash by waves. Despite these physical explanations, we still found biologically driven differences in foredune shape if we accounted for sand supply rates. At sites with shoreline change rates of ±2 m or less per year, *A. arenaria* foredunes were taller, narrower, and steeper than *A. breviligulata* foredunes (Table 1, Fig. 5). This was true despite statistically similar grass cover values for each species (Table 1).

We hypothesize that the differences in dune geomorphology produced by each species is a consequence of beach grass growth form and the amount of sand making its way to the foredune. The growth of *A. arenaria*, with its longer, more vertical rhizomes and clumped, more erect tillers, should be better at building tall foredunes, especially under con-

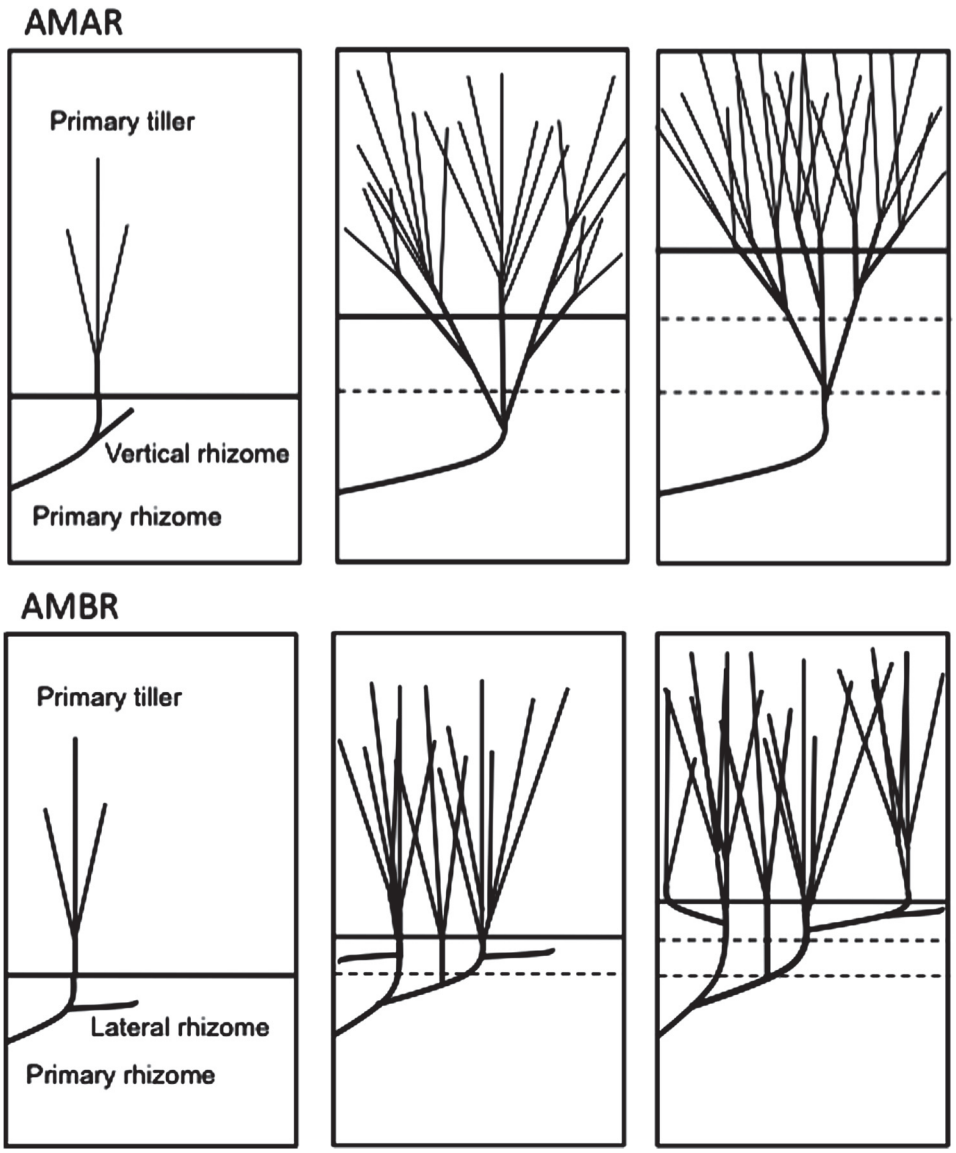

Figure 7. Illustration of differences in beach grass growth forms and sand deposition (delimited by solid and dashed horizontal lines) assuming similar sand supply for *A. arenaria* (AMAR; top panels) and *A. breviligulata* (AMBR; bottom panels). With sand deposition (panel progression from left to right), the growth pattern of AMAR involves more, longer vertical rhizomes with multiple tillers, resulting in clumped tussocks that capture more sand in the vertical plane. For AMBR, the growth pattern involves more lateral rhizome production with shorter vertical internodes, resulting in evenly distributed tillers that capture more sand in the horizontal plane. Modified from Baye (1990).

ditions of little or no shoreline change (Fig. 7). Here the foredunes rise vertically because sand deposition is occurring over a smaller area. Grasses with the ability to keep pace with this deposition should enhance the elevation of the foredune by participating in a positive feedback between their own growth and continued sand deposition (Baye 1990, Maun 1998, Fig. 7, Table 1). In contrast, under similar sand deposition conditions, the horizontal spread of *A. breviligulata*, and even that of the native *E. mollis*, is likely to result in shorter and wider foredunes with shallower slopes (Fig. 7, Table 1). Thus, it appears that the existence of tall foredunes, some of which are 10–15 m high and have important knock-on effects for plant succession and coastal protection, are the result of both slow shoreline change rates and the dominance of one congener, *A. arenaria*.

Although the differential impact of the two congeners on foredune geomorphology makes sense when sand deposition is negligible, it is harder to know whether these growth form differences are a factor where shoreline change rates are more extreme. No sites exist in our current survey in which high shoreline change rates coincide with the dominance of *A. arenaria* (Fig. 5). Instead, the newly created foredunes produced under high shoreline change rates seem to be preferentially colonized and stabilized by the faster spreading *A. breviligulata* (Fig. 2, 4, 5). Thus it remains unknown whether foredunes experiencing more extreme sand deposition regimes remain shorter and wider because 1) *A. breviligulata* maintains them that way through sand stabilization, 2) *A. arenaria* is so sparse that it has no impact, and/or 3) sand supply swamps any effects of the grasses regardless of their growth form or morphology. It is interesting to note, though, that over roughly two decades as *A. breviligulata* has become more abundant and *A. arenaria* has declined, there has been a concomitant change in

dune shape (Fig. 3). This change in abundance fits a pattern in which the loss of *A. arenaria*, either due to competition with *A. breviligulata* or decreased vigor due to, for example, the extreme sand deposition conditions, results in shorter and wider foredunes.

Implication of congener invasions to ecosystem functions and services

In this system, the co-invasion of congeneric species has important implications for ecosystem functions and services. Because dune height controls wave attenuation and thus the protective function of the foredune (Ruggiero et al. 2001, Barbier et al. 2008), we predict that the interaction between sand deposition along the coast and the dominant beach grass species at a particular location will largely determine the protective services of those dunes. For example, if *A. breviligulata* continues its invasion to the south (Fig. 1), we might expect an eventual decrease in foredune elevation and thus a decline in their coastal protection value. The implications are considerable given the amount of human development along the coast and the dependence on the protective services of these structures from storms and tsunamis (Komar 1997).

It may be that where shoreline change is high, the coastal services provided by either grass species is likely negligible when compared to the overwhelming effects of sand supply. Under these conditions, the influence of beach grasses on coastal protection may be purely one of 'battening down' newly deposited sand and maintaining the shorter dune geomorphology set by the greater oceanographic context of sand deposition. Nonetheless, the strong dynamic between beach grass invasion and coastal processes implies that changes in sand exchange, sea level, and wave heights due to climate change could have critical effects on dune height, foredune erosion, and ultimately coastal protection. The interplay between the co-invasion of the two congeners and changes in beach processes from climate is an understudied but potentially critical avenue of research for these systems in the future.

In this study we found that two congeneric invaders, which on first impression are ecologically and morphologically similar, display differences in invasion success and impact. Clearly, these differences make decisions about the management of both beach grass species more complex and thus more uncertain. However, if we ignore subtle differences in congeneric species and categorize them as functional equivalents, or overlook the variability in the habitats or contexts in which they invade, we underestimate the possible synergistic impacts they may have and we risk applying management decisions that are inappropriate for either species. More generally, this case study serves as an important caveat to the growing literature on the use of functional groups to predict species impacts or fate. As is true in so many cases in ecology, the details matter. We are unlikely to be able to make strong predictions about the impacts of introducing novel species based purely on analogy with closely related species.

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References

Agrawal, A. A. et al. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. – Ecology 86: 2979–2989.

Allan, J. C. and Komar, P. D. 2006. Climate controls on US West Coast erosion processes. – J. Coast. Res. 22: 511–529.

Barbier, E. B. et al. 2008. Coastal ecosystem-based management with non-linear ecological functions and values. – Science 319: 321–323.

Barbier, E. B. et al. 2011. The value of estuarine and coastal ecosystem services. – Ecol. Monogr. 82:00–00.

Baye, P. R. 1990. Comparative growth responses and population ecology of European and American beachgrasses (*Ammophila* spp.) in relation to sand accretion and salinity. – PhD thesis. The Univ. of Western Ontario.

Brandt, A. J. et al. 2009. Phylogeny and provenance affect plant–-soil feedbacks in invaded California grasslands. – Ecology 90: 1063–1072.

Cheplick, G. P. 2005. Patterns in the distribution of American beachrass (*Ammophila breviligulata*) and the density and reproduction of annual plants on a coastal beach. – Plant Ecol. 180: 57–67.

Colautti, R. I. et al. 2004. Is invasion success explained by the natural enemies release hypothesis? – Ecol. Lett. 7: 721–733.

Cooper, W. S. 1958. Coastal sand dunes of Oregon and Washington. – Memoir 72. Geol. Soc. Am.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. – Annu. Rev. Ecol. Syst. 34: 183–211.

Darwin, C. 1859. On the origin of species. – Murray.

Diez, J. M. et al. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. – Ecol. Lett. 11: 674–681.

Everard, M. et al. 2010. Have we neglected the societal importance of sand dunes? An ecosystem services prospective. – Aquat. Conserv. 20: 476–487.

Gutierrez, J. L. et al. in press. Physical ecosystem engineers and the functioning of estuaries and coasts. – In: Heip, C. H. R. et al. (eds), Vol. 7. Functioning of estuaries and coastal ecosystems. – In: Wolanski, E. and McLusky, D. (series eds), The treatise on estuarine and coastal science, Elsevier, pp. xx-xx.

Hacker, S. D. and Dethier, M. N. 2009. Differing consequences of removing ecosystem–modifying invaders: significance of impact and community context to restoration potential. – In: Rilov, G. and Crooks, J. (eds), Marine bioinvasions: ecology, conservation and management perspectives. Springer, pp. 375–385.

Hesp, P. A. 1989. A review of biological and geomorphological processes involved in the initiation and development of incipient foredunes. – Proc. R. Soc. Edinburgh 98B: 181–201.

Hickman, J. C. 1993. The Jepson manual: higher plants of California. – Univ. of California Press.

Kaminsky, G. K. et al. 2010. Historical evolution of the Columbia River littoral cell. – Mar. Geol. 273: 96–126.

Komar, P. D. 1997. The Pacific Northwest coast: living with the shores of Oregon and Washington. – Duke Univ. Press.

Lambrinos, J. G. 2001. The expansion history of a sexual and asexual species of *Cortaderia* in California, USA. – J. Ecol. 89: 88–98.

Lambrinos, J. G. 2002. The variable invasive success of *Cortaderia* species in a complex landscape. – Ecology 83: 518–529.
Levine, J. M. et al. 2004. A meta-analysis of biotic resistance to exotic plant invasions. – Ecol. Lett. 7: 975–989.
Mack, R. N. 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. – Biol. Conserv. 78: 107–121.
Maron, J. L. and Vila, M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies hypotheses. – Oikos 95: 361–373.
Martinez, M. L. and Psuty, N. P. 2004. Coastal dunes: ecology and conservation. – Springer.
Maun, M. A. 1998. Adaptations of plants to burial in coastal sand dunes. – Can. J. Bot. 76: 713–738.
Maun, M. A. 2009. The biology of coastal sand dunes. – Oxford Univ. Press.
McLaughlin, W. T. 1939. Planting for topographic control on the Warrenton, Oregon coastal dune area. – Northwest Sci. 13: 26–32.
Mitchell, C. E. et al. 2008. Biotic interactions and plant invasions. – Ecol. Lett. 9: 726–740.
Muth, N. Z. and Pigliucci, M. 2006. Traits of invasives reconsidered: phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. – Am. J. Bot. 93: 188–196.
Pavlik, B. M. 1983. Nutrient and productivity relations of the dune grasses, *Ammophila arenaria* and *Elymus mollis*. III. Spatial aspects of clonal expansion with reference to rhizome growth and the dispersal of buds. – Bull. Torr. Bot. Club 110: 271–279.
Psuty, N. P. 1986. A dune/beach interaction model and dune management. – Thalassas 4: 11–15.
Pysek, P. and Richardson, D. M. 2007. Traits associated with invasiveness in alien plants: where do we stand? – In: Nentwig, N. (ed.), Biological invasions, Springer, pp. 97–125.
Rice, K. J. and Nagi, E. S. 2000. Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. – Am. J. Bot. 87: 1699–1706.
Ruggiero, P. and List, J. H. 2009. Improving accuracy and statistical reliability of shoreline position and change rate estimates. – J. Coast. Res. 25: 1069–1081.
Ruggiero, P. et al. 2001. Wave runup, extreme water levels, and the erosion of properties of backing beaches. – J. Coast. Res. 17: 407–419.
Seabloom, E. W. and Wiedemann, A. M. 1994. Distribution and effects of *Ammophila breviligulata* Fern. (American beachgrass) on the foredunes of the Washington coast. – J. Coast. Res. 10: 178–188.
Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? – Ecol. Lett. 9: 912–919.
Strauss, S. Y. et al. 2006. Exotic taxa less related to native species are more invasive. – Proc. Natl Acad. Sci. 103: 5841–5845.
Wiedemann, A. M. and Pickart, A. J. 2004. Temperate zone coastal dunes. – In: Martinez, M. and Psuty, N. (eds), Coastal dunes: ecology and conservation, Springer, pp. 53–65.

Supplementary material (available online as Appendix o18887 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A3.