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Review

Ammophila Invasion Ecology and Dune Restoration on the West Coast of North America

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Abstract: The invasive ecosystem engineer *Ammophila arenaria*, native to Europe, was first introduced to California (USA) in 1896. More than a century later, it has come to dominate coastal foredune vegetation on the west coast of North America to the near exclusion of native species. *A. arenaria* builds a narrow, steep, peaked, and densely vegetated foredune, in contrast to the broad, more sparsely vegetated foredunes built by the native *Elymus mollis*. As such, it has modified dune processes by fixing the foredune and disrupting exchange of sediment between the beach, foredune, and dunefield. In the 1930s the congener *A. breviligulata*, native to the east coast and Great Lakes USA, was first introduced to Oregon, and has been displacing *A. arenaria* in southern Washington. *Ammophila* spp. have drastically reduced biodiversity, outcompeting native plant species, and displacing both invertebrate and vertebrate species. Restoration of west coast dunes through the removal of *Ammophila* began in the 1990s. Methods usually consist of one or a combination of manual digging, burning/herbicides, or excavation with heavy equipment. There are benefits and disadvantages to each method. Manual removal has proven most effective at restoring foredune form and process but is expensive. Excavation and herbicides may result in the loss of foredune morphology. Managers must articulate goals carefully before selecting restoration methods.

Keywords: *Ammophila arenaria*; *Ammophila breviligulata*; dunes; invasive species; ecosystem engineer; dune restoration

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1. Introduction

An important ecosystem service of coastal dunes is their ability to ameliorate storm-induced erosion through dissipation of wave energy and protection from flooding, thus protecting human infrastructure and natural resources [1,2]. In the context of climate change, dunes provide the potential for adaptation to sea level rise and increased storm frequency and severity, with the ability to maintain shoreline position or translate inland and upward while retaining the beach-foredune morphology, depending on available sediment budgets [3,4]. Coastal dunes line much of the Pacific Coast of North America, from the Mexican border to British Columbia, comprising 42% of the California, Oregon, and Washington coastline [5,6] but only 10% of the British Columbia coastline [7]. West coast dunes have, in many places, been replaced or degraded by residential, commercial, and industrial development and recreational vehicle use [7,8].

The vegetation native to west coast dune systems includes the foredune community *Elymus mollis* herbaceous alliance dominated by the dune builder *Elymus mollis* Trin. subsp. *mollis* (American dune grass) (Figure 1), as well as the *Abronia latifolia-Ambrosia chamissonis* herbaceous alliance (dune mat), a diverse, suffrutescent community characterized by variable but often moderate to low cover [9,10] (Figure 2). *Elymus*, once present from Alaska to southern California [11], has undergone large-scale replacement by the invasive grasses *Ammophila arenaria* (L.) Link (synonym *Calamagrostis arenaria* (L.) Roth), (marram grass), native to the Atlantic coast of Europe, and to a lesser extent, *A. breviligulata* (also *Calamagrostis breviligulata* (Fernald) Saarela) or American beach grass, originating on the East coast and Great Lakes (USA). *A. arenaria* is a worldwide invader, colonizing dunes between 32° and 60° on both sides of the equator [12].

Figure 1. Broad foredune with *Elymus mollis* dominant.

Ammophila spp. are ecosystem engineers [13,14] that have had a profound impact on west coast dunes, including changes to morphodynamics of the dunes themselves, and the near extirpation of native dune plant communities. Eradication of these (and other) dune invaders, and the re-establishment of native communities, has been carried out on the west coast of North America (west coast) since the 1990s and has been shown to restore ecosystem diversity, complexity, and underlying dune processes [15–17]. This paper reviews the introduction history, biological characteristics, invasion ecology, and restoration ecology of these two ecosystem engineers with the purpose of encouraging more and larger sea level rise adaptation projects through dune restoration.

Figure 2. Dune mat community on foredune.

2. Biology, Introduction, and Spread

2.1. Ammophila arenaria

Ammophila arenaria is an obligate psammophyte, dune-building grass native to the west coast of Europe and the north shore of the Mediterranean and Black Seas, stretching from 63° to 32° N [18]. It was introduced to the west coast at Golden Gate Park, San Francisco, California as a stabilizer in 1869 [6,19], and to Oregon in 1910 [20]. From the time of its introduction to North America it took only 75 years to spread by tidal dispersal and intentional introduction to its present-day distribution from 34° N at Los Angeles to 54° N on Haida Gwaii (formerly Queen Charlotte Islands) [21,22].

Ammophila arenaria is a perennial, tussock-forming grass up to 120 cm high that tolerates up to 1 m of sand burial per year [18]. Tightly inrolled leaves bear stomata only on the furrows between ribs on the adaxial surface, while ribs have short hairs, both of which are adaptations for water retention. [18,23]. *A. arenaria* generates both horizontal and vertical rhizomes, and produces a dense, sand-binding network of rhizomes and adventitious roots [24]. Active sand burial stimulates the production of new shoots from vertical rhizomes [25,26]. Feedbacks between the environment and the spatial arrangement of vegetation determine foredune morphology [27]. In the absence of sand accumulation *A. arenaria* declines in vigor, a phenomenon much discussed in the European literature and deemed "The *Ammophila* Problem" [28,29]. Suggested causes have included physiological ageing expressed as reduced root production [30], competition [18], and lack of mineralization of organic nitrogen contained in fresh dune sand [31]. Most recently, agreement on the cause has coalesced around the role of pathogens, and more specifically root-feeding nematodes [32–35]. However, beneficial microorganisms such as AM fungi are also present in the rhizosphere and can mitigate the effect of harmful plant pathogens [36–42]. All three dune-building grasses of the west coast, *A. arenaria, A. breviligulata*, and *Elymus mollis* host endophytic fungi that contribute to their success in the nutrient poor environment of dunes [43]. In addition, nitrogen fixation by rhizosphere microbes contributes to growth [44–46].

A. arenaria's primary mode of spread is vegetative [18], with long distance dispersal via marine transport of dormant rhizomes [47,48]. It produces abundant viable seed, primarily in areas of fresh sand deposition, such as the foredune [9,49]. However, while germination rates can be high, establishment from seed is uncommon [9,49]. Seedlings are more common on the foredune than backdune [9]. However, wind dispersed seeds that reach moist areas represent a mode of relatively long-distance spread [49,50]. In New Zealand, a persistent seedbank has been observed to preserve viable seed for up to 21 years [51]. Anthesis is in July and August, with seed dispersal in September [18]. The active period of growth is spring and summer (April to September), although some growth occurs during senescence in winter [18]. *Ammophila arenaria* was found to exhibit two modes of spread at a barrier located in northern California, a linear, shore-parallel advance along the foredune characterized by exponential growth, and invasion from satellite populations (some planted) in the more inland dunefield [52]. *A. arenaria* is capable of rapid spread, at one site the area occupied was shown to increase 574% in 50 years [52].

2.2. *Ammophila breviligulata*

Ammophila breviligulata is native to the Atlantic coast of North America, from North Carolina to Newfoundland and the Great Lakes [18], and was first introduced to the west coast during a large scale stabilization project in Oregon in 1935 performed by the Soil Conservation Service [20,53]. It now occurs from British Columbia to California [54,55]. *A. breviligulata* now dominates foredunes in the southern half of Washington where it has displaced *A. arenaria* [53,56]. Researchers in Oregon modeled the spread of *A. breviligulata* and found that its range is restricted southward but not northward [57] although others warn of potential spread southward along the entire California coast [58]. In California, it occurs as a small population at Humboldt Bay, where it was planted in the 1980s [59]. Additional records exist for San Francisco [57,60] and in Orange County [61,62]. Under climate change, differences in physiological tolerances and response to competition between *A. arenaria* and *A. breviligulata* suggests that further southern spread of *A. breviligulata* is unlikely, but *A. arenaria* could extend its northern distribution [57]. *A. breviligulata* shares many of the same traits as *A. arenaria* [53]. It is a rhizomatous species that responds positively to sand burial [63–65], forms tussocks in areas of active sediment deposition [64], and produces viable seeds but spreads primarily vegetatively [66]. Mortality of seeds and seedlings is primarily due to excessive burial and desiccation, but windblown seeds that reach moist slacks provide an opportunity for range extension [49]. *A. breviligulata*, similar to *A. arenaria*, is also subject to "The *Ammophila* Problem" [49,53], exhibiting decreased shoot weight, height, and density when sand accretion ceases [67,68]. Burial alone does not allow escape from parasitic nematodes, but AM fungi and rhizosphere bacteria ameliorate detrimental effects [39]. The ecology of *A. breviligulata* was extensively reviewed by Maun and Baye [29]. *Ammophila breviligulata* hybridizes with *A. arenaria* in Oregon and Washington. The hybrid exceeds both parents in terms of shoot height, which generally correlates with sand deposition [69].

3. Invasion Ecology

3.1. Invasibility

Dunes have several traits that render them susceptible to invasion, including constant disturbance, low cover, and ease of long-distance dispersal by ocean currents [70–74]. Conversely, species diversity, or communities characterized by a diversity of functional groups may be resistant to invasion [75]. In northern California, *A. arenaria* invaded open sand more rapidly than existing stands of dune mat, a diverse community of dune natives [76]. The rapid spread of *A. arenaria* along foredunes compared to vegetated backdune may be due to a combination of disturbance and low vegetation cover on foredunes, and the tendency for *A. arenaria* to senesce without active sand deposition [52,53]. Facilitation can also play an important role in invasions [77] and may increase with the level of the abiotic stress characteristics of dunes [78].

3.2. Plant and Soil Pathogens and Beneficial Microbiota

Plant interactions take place within a complex background of biotic processes [79] For example, plant abundance is strongly controlled by root herbivory and soil pathogens [80,81]. Escape from these adversaries when introduced to a new locale has been proposed as one cause of successful invasion, known as the Enemy Release Hypothesis [82–84]. Species subject to strong enemy effects in their native range, such as *A. arenaria* [85], are hypothesized to escape these enemies in their introduced range [86]. Conversely, the Biotic Resistance Hypothesis posits that introduced species may fail to thrive due to strong biotic interactions with native species, such as plants that fail to invade due to herbivory [83,87]. Soil-borne pathogens (primarily nematodes and fungi) suppress growth of *A. arenaria* in its native range [32,87]. In its introduced range, other native plants were shown to have more nematode taxa than *A. arenaria*, supporting the Enemy Release Hypothesis [35]. Introduced *A. arenaria* was associated with reduced soil nematodes compared with the native *Elymus mollis* in dune systems of Oregon and Washington [88]. Species growing on home soils may be disadvantaged due to a buildup of species-specific soil pathogens [89]. An alternative explanation is that accumulated local pathogens by *A. arenaria* could result in the exclusion of native species [32,90]. There is no consensus on the Enemy Release Hypothesis, which is not a straightforward phenomenon [91,92].

3.3. Competition

Despite the large body of literature on *A. arenaria*, and a history of three decades of control on the west coast of North America, there has been little direct research on the role of competition between *Ammophila* spp. and native species, including *Elymus mollis*. In one such study, when all three foredune grass species occurred together in Oregon, sand supply mediated the outcome of competition, favoring *A. arenaria* in lower sand supply and *A. breviligulata* in higher sand supply regimes; the native dune builder *Elymus mollis* had only a slight negative effect on other species at low levels of sand supply [93]. In addition, a study in northern California mapped cover of *A. arenaria*, bare sand, and native species over seven years at the boundary of an *A. arenaria* invasion. *A. arenaria* cover increased, while bare sand and native plants decreased [94]. Bare sand declined most rapidly, suggesting that *A. arenaria* exploits open space in the dune mat community prior to competing directly with native species. Apparent competition has also been demonstrated for *A. arenaria*, a phenomenon in which invasive species increase pressure of native consumers [95]. At a site in central California, *A. arenaria* provided refuge to a native predator on an endangered plant, resulting in high levels of predispersal seed consumption [95]. Removal of *A. arenaria* resulted in a lasting reduction in seed predation [96].

The majority of research on competition between *A. arenaria* and native dune species has been indirect, documenting a negative correlation between *A. arenaria* and native species along the Pacific Coast [21,22,97]. Similarly, studies in New Zealand infer mechanisms of displacement between *A. arenaria* and a native dune colonizer [98]. Pavlik [99–101] examined morphological and physiological traits that could make *A. arenaria* a superior competitor to *Elymus mollis*. *A. arenaria* was found to allocate nitrogen preferentially to blades, favoring photosynthesis and resulting in greater nitrogen use efficiency than *Elymus mollis*, which directed resources to stress tolerance [102]. *A. arenaria* rolls its leaves more tightly, an inexpensive way of dealing with drought. *A. arenaria* buds are located near the parent ramet on vertical rhizomes, resulting in the dense tussock morphology of *A. arenaria* compared with the more dispersed pattern of *Elymus mollis*. *A. arenaria* also has taller and denser leaves [103].

Several control and restoration projects have demonstrated that native dune mat species return after *A. arenaria* is removed, suggesting a release from competition [15,104]. Relict native plants can persist during *A. arenaria* invasion, and propagule sources may be available in nearby dune mat [9], thus it is difficult to determine the source of returning plants. In a study in northern California, *A. arenaria* was found to preferentially invade open sand areas, which, after control, were colonized by native species [76].

3.4. Wildlife

In addition to observed and inferred displacement of native plant species, *A. arenaria* has impacted other aspects of the dune ecosystem. Julian [105] found a negative correlation between native solitary bees and *A. arenaria* at dune systems in northern California. Doudna and Conor [106] sampled six dune systems in California for terrestrial arthropods and found that species richness and abundance were significantly lower in invaded dunes than in restored and uninvaded native dunes. A similar negative correlation was reported by Slobodchikoff and Doyen [107]. In contrast, the field mouse *Peromyscus maniculatus* has been shown to preferentially use dense *A. arenaria* compared with native dune vegetation [108,109]. This was attributed to shading, moisture, stable substrate for nesting, and dampened temperature oscillations [108]. *Peromyscus* and other rodents were found to leave behind less food when foraging in *A. arenaria* compared with dune mat [109]. Conversely, mesocarnivores were found to be more active in restored dunes than invaded dunes, possibly due to inaccessibility of prey in dense *A. arenaria* [110,111]. Closeness to the dune forest played an important role in mesocarnivore activity and may have confounded results [111].

3.5. Dune Morphodynamics

Arguably the most significant ecological impact of *Ammophila* spp. is their exceptional ability to stabilize dunes, the very characteristic that led to *A. arenaria*'s widespread introduction around the world. In the 1930s, before *A. arenaria* had gained a strong foothold in northern California, foredunes, if present, were either semi-stable continuous ridges or a series of nebkha [112]. Some nebkha later coalesced into a foredune ridge vegetated by a combination of *Elymus mollis* and native, mound-building species [5,6,76]. From Oregon north, a foredune feature was lacking altogether in the 1930s when the earliest air photos are available [5,113]. In a relatively short time, *A. arenaria* had built a steep, high, peaked foredune all along the coast of Oregon and Washington (Figure 3), although some stretches populated by *Elymus* can be found [53,114].

Figure 3. Steep peaked foredune characteristic of *Ammophila*.

The cause of this lack of foredune has been the subject of speculation, and theories include cyclic ruptures along the Cascadia Subduction Zone although the last recorded mega rupture was 1700 [115]. However, lower magnitude disturbances, such as severe scarping, can also remove foredunes [116]. Pickart and Hesp [76] traced the fate of a foredune swamped by sand following a large flooding event. The foredune then recovered through the formation and coalescence of nebkha into a semi-continuous ridge vegetated by native plants over a period of 17+ years, suggesting that foredunes can be ephemeral in this region [76]. In areas where *A. arenaria* was present, steeper, continuous ridges developed. The Lanphere Dunes in northern California are one of very few sites in the Pacific Northwest (Pacific NW) where *Elymus mollis*-built foredunes still exist [76,117]. Other restored native dunes may have a legacy effect from prior *Ammophila* invasion. On the North Spit of Humboldt Bay, California, foredune height is more a function of sediment supply than vegetation [117]. *A. arenaria* foredunes are steeper, narrower, and more peaked but not higher than native and restored foredunes in northern California [118]. Mature foredunes are rarely vegetated solely by *Elymus*, but rather by a mix of *Elymus* and pioneer dune mat species, such as *Lathyrus littoralis* (Nutt.) Endl. ex Walp. and *Abronia latifolia* Eschsch. [9]. Incipient foredunes commonly support pure stands of *Elymus*, but these are subject to removal periodically by winter storms [9].

There is a recent body of research on *A. arenaria*, *A. breviligulata*, and their hybrid, and how they affect the morphodynamics of the foredunes of the Pacific NW, originating from Oregon State University. *A. beviligulata* was observed to be outcompeting *A. arenaria* where both occurred [53]. The more lateral pattern of spread and larger tiller size of *A. breviligulata* was suggested as a reason for its increasing dominance [61]. Where *A. arenaria* had been displaced by *A. breviligulata*, the foredune was lower and broader [61,119]. This was shown to be the result of differential biofeedback by these two subtly different species combined with a difference in sand supply alongshore [56]. The taller and denser *A. arenaria* can keep pace with greater sand deposition leading to a positive feedback on the height of the dune in areas of neutral sand budgets. *A. breviligulata* is more indifferent to levels of sand supply [61].

This ongoing research on the two species and their hybrid highlights the role of the foredune in preventing overtopping during storm events [56,61,119]. However, a shorter, broader, and less vegetated foredune (such as one built by *E. mollis*) may play an important role in resilience to climate change. As Nordstrom [120–122] argues, dynamic dunes are more resistant to erosion, given their ability to gradually migrate landward or seaward under aeolian processes. Mull and Ruggierro [123] modeled dune erosion for the Pacific NW but did not take into account resilience. Foredunes recover from wave scarping events by the formation of a scarp-fill ramp [124] which allows sand to reach the top of the foredune, where it may bypass the foredune and allow for translation in response to sea level rise. However, scarps may last a decade or more [116,124,125], which could prevent recovery before the next scarping event. Davidson-Arnott et al. [126] modeled dune-lined sandy shorelines and predict that under an equilibrium sediment budget, the upper beach and foredune will migrate in tandem with sea level rise. However, in a sea level rise adaptation demonstration site in northern California, the *A. arenaria* foredune scarp, which was vertical and tightly bound by rhizomes, resisted ramp building much longer than the native foredune [127], which quickly underwent slumping that contributed to ramp building. This behavior is consistent with Davidson-Arnott's [3] model of migration of the foredune morphology inland. The taller, steeper foredune of *A. arenaria* in Oregon and Washington may not allow for translation while maintaining a foredune morphology, especially with more frequent storms. However, the coast of Oregon contains much more beachfront infrastructure than northern California, leaving only the foredune as a defense [7]. As Wiedemann [7] points out: "along the Pacific NW coast, well-developed foredunes formed by European beachgrass are prime building sites. This can be readily seen on almost any dune area that is in private ownership." This may justify a focus on resistance rather than resilience in the short term. Ultimately, managed retreat is likely the only viable response to sea level rise in these situations.

4. Restoration of *Ammophila*-Invaded Dunes

The Society for Ecological Restoration defines restoration as " ... the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed ... restoration practitioners do not carry out the actual work of ecosystem recovery. Rather, they create the conditions needed for recovery so the plants, animals, and microorganisms can carry out the work of recovery themselves" [128]. The goals of dune restoration include the recovery of morpho-ecological states, the recovery of sediment dynamics, and the restoration of native vegetation [129]. For the purpose of this paper restoration includes projects that remove *Ammophila* in order to release underlying geomorphic processes needed to maintain ecosystem function and diversity, i.e., sand is able to be transported from the beach to the foredune and landward to the dunefield, supporting biota and biotic processes, including vegetation. The majority of dune restoration projects on the west coast documented here have successfully removed *A. arenaria*. However, the introduction of *Ammophila* to the west coast has been shown to create foredunes where none previously existed [7], and this must be taken into account when setting restoration goals and assessing success. The goal of restoring historic conditions may be subordinate to creating a more resilient system. Unfortunately, most dune restoration projects do not end up in the published literature, making it difficult to assess landscape scale restoration success. Projects are often under-budgeted and land managers choose to spend their limited time "doing" rather than documenting. If reports are written, including monitoring results, they remain a part of the "gray literature." This creates a divide between academia and management. There is, however, excellent informal communication between managers that allows for the flow of information [130].

A special case exists for the restoration of invaded dunes for the express purpose of managing for the threatened species Western Snowy Plover (*Charadrius nivosus nivosus*), which nests on ocean beaches or gravel bars [131]. This type of single-species management/restoration addresses an ecosystem service but is not ecosystem based. Management actions frequently consist of breaching or flattening foredunes, resulting in a tradeoff of ecosystem services [131–134]. While this does allow for sediment transport, it ignores all other aspects of the ecosystem and is not included here.

Because *Ammophila* disrupts foredune morphodynamics through stabilization, the removal of *Ammophila* is prerequisite to dune restoration and is usually the first step in restoration projects. Projects with other goals, such as the stabilization of open, moving sand with native species (revegetation) are not considered here, other than as a later step in ecogeomorphic or "dynamic" restoration [17]. There are three primary methods of *Am-*

mophila removal utilized on the west coast: manual removal (digging), excavation and burial, and herbicides, usually in combination with burning [9,15,135–139]. The most common outcomes of these restorations are (1) a discontinuous (with blowouts) foredune grading into vegetated and unvegetated dunefield morphology, or (2) nebkha fields. Some of these dune systems may have lacked a foredune prior to *Ammophila* removal, so conversion to nebkha fields may be appropriate if the goal is to replicate historic conditions. However, the outcome is at least somewhat dependent on removal methods. Three dune restoration sites utilizing three different methods of *A. arenaria* removal were surveyed in northern California and compared for species richness and cover with reference (uninvaded) sites [15]. At Point Reyes National Seashore, a project that utilized heavy equipment, a significant volume of sand was mobilized and, to date, has resulted in a lowered, near- bare foredune with nebkha in the dunefield. Recovered vegetation at this site, the most recently restored of the three, was lowest, as was species richness (Figure 4). At MacKerricher State Park, burning was followed by herbicide application. Restoration to native vegetation was successful [15] but the previous well-developed *A. arenaria* foredune transitioned into a series of native nebkha (Figure 5). At the Lanphere Dunes, three decades after restoration was initiated, manual removal of *A. arenaria* resulted in a discontinuous foredune interrupted by blowouts, similar to the reference area. This site was the oldest restored (30 years), had the highest species richness, and was the only site to reach equivalence of species richness and cover with control (uninvaded) dunes [15].

Figure 4. Low cover area at Point Reyes restored using heavy equipment.

Mechanical restoration has the greatest impact on ecogeomorphic processes, because invasive species and disturbed soil are buried under several meters of clean sand [136]. In two other excavated dune systems in northern California a similar response occurred, and both systems are now dominated by nebkha [139]. This treatment resets the ecosystem, both in terms of biotic and geomorphic processes. In addition to burial of invasives, beneficial microbes are buried. *Ammophila* has beneficial microbes in the rhizosphere, especially AM fungi [36–42], which are no longer present, and could help native species become established. In addition, the high mobility of the sand slows the establishment of vegetation [137,139]. It is unknown whether nebkha fields will develop into a native foredune. It is possible for nebkha to coalesce into an incipient foredune, and then transition into an established foredune [140]. However, it will be some time, perhaps decades, before this is likely to occur [76].

Figure 5. Foredune at MacKerricher dunes restored using herbicides/burning, showing nebkha.

Herbicides have increased in use as a means of controlling *A. arenaria*. The reluctance of managers to employ this method in the past has been due in part to the legacy of the timber era's use of highly toxic chemicals. Early efforts used Glyphosate, with mixed results [9] and more recently Imazapyr is commonly used. Application is by hand, as the topography and sometimes large wood debris make driving a UTV challenging. Spraying is usually preceded by a prescribed burn, so that thatch is reduced and vigorously growing resprouts can be sprayed. Hyland and Holloran [141] used this method in Monterey County, applying 7% Glyphosate, and had to return for retreatment, but ultimately succeeded in reducing *A. arenaria* cover to less than 1% (no data on native species recovery were available). Spraying *A. arenaria* without burning was used at Point Reyes in a more stable dune scrub area. *A. arenaria* was slow to break down due to legacy effects, including a link between bacterial and fungal soil communities, with heavily invaded sites characterized by a lower abundance of nitrifiers, fermentative bacteria, and fungal parasites [142]. Soil microbiota did not fully dissipate after herbicide treatments. The fact that this was a later successional community, and thatch was not burned may explain why *A. arenaria* successfully degraded in the herbicide treatments at MacKerricher [15].

Manual removal of *A. arenaria* has many benefits but can be prohibitively expensive (37–55,000 USD/ha [9,104] compared with 13–38,000 USD/ha for mechanical removal [136], and 2000 USD/ha for herbicide control, which additionally requires a prescribed burn [141]. Costs can vary greatly depending on the accessibility of the site [9]. Manual removal has been feasible when labor was provided through mitigation funds [104]. An important benefit of manual removal is that it retains foredune morphology because the dead subaerial rhizomes and tillers become exposed and slow wind erosion [9]. The rhizosphere microbiota below digging depth are undisturbed and available to native plants. None of the projects described here used revegetation. However, in the manual removal project there were relict natives mixed in with the *A. arenaria* and potentially a seedbank, accelerating revegetation. This was the case because it was a site in which *A. arenaria* had invaded native foredunes, rather than building the foredunes. In an *A. arenaria* built foredune, restoration requires revegetation to prevent major blowouts or loss of the foredune [104]. The ability of restoration to maintain the morphology of the foredune is influenced by sediment supply as well as restoration method. The restoration of geomorphic processes was qualitatively observed and photo-documented at the Lanphere site, but none of the projects mentioned above used quantitative metrics to evaluate the success of morphodynamic restoration. Dune restoration has generally been plant-centric in terms of monitoring. Eco-geomorphic monitoring of dune restoration has been utilized in British Columbia at the Wickaninnish dunes, where *Ammophila* spp. was removed selectively to test dynamic restoration of geomorphic processes and revegetation with native *Elymus* [17,138]. This type of monitoring requires expertise and expensive equipment, such as Terrestrial LiDAR Scanners, Airborne LiDAR, Unmanned Aerial Systems, Structure from Motion software, and Real Time Kinematic GPS, which are not available to most land managers except through collaboration with academic labs. At the Wickaninnish dunes geomorphic monitoring was able to show the successful return of dune function [17,138]. The project objectives were to re-establish dune process, remove *Ammophila* spp., and create habitat for rare plants. An experiment is underway at the Lanphere Dunes in northern California which encompasses manual and burning/herbicide removal of *A. arenaria,* revegetation with native species, and spatio-temporal eco-geomorphic monitoring [127]. This project is part of a six-year collaboration between a land management agency (U.S. Fish and Wildlife Service) and the University of Arizona/University of California, Santa Barbara. Results to date show a return of foredune morphodynamics and resiliency through restoration of sediment budgets as well as seaward and landward expansion of the foredune when compared with the *A. arenaria* control site [127], fulfilling the Society for Ecological Restoration's definition of restoration.

Dynamic restoration has also increasingly been performed in northwest Europe, where dunes have traditionally been managed for stabilization to provide coastline defense [142]. Methods differ and include the creation of a series of notches in the foredune to deliver sand to the dunefield via the formation of blowouts [143]. The goal of these projects is to rejuvenate dunefields in order to recover biodiversity [143,144]. The paradigm shift from increasingly stabilized dunes (attributed to climate change and nitrogen deposition) to restoring dynamism has also received criticism. Delgado-Fernandez et al. [145] argue that stabilizing dunefields are just one manifestation of natural dune landscapes, and that biodiversity is dependent on the interaction of abiotic and biotic processes and will change over time based on internal evolution and external forcing. It is important to note that restoration on the west coast of North America differs significantly in that an invasive species has altered dune processes. Even so, west coast dune restoration has its detractors among the general public who perceive, erroneously, that the steep and densely vegetated *Ammophila* foredunes provide greater defense against storm erosion [146].

5. Summary

Since its first introduction in 1896 to San Francisco, California, *Ammophila arenaria* has spread to virtually every beach and dune system along the west coast of North America, resulting in profound changes to the morpho-ecological nature of the dunes. It was joined in the 20th century by its congener *Ammophila breviligulata* in the dunes of Oregon and Washington, eliciting further changes to dune morphology. *A. arenaria* is an ecosystem engineer, forming steep, narrow foredunes in contrast with the broad, sloping foredunes formed by the native dune builder *Elymus mollis*. *A. arenaria* reduces sediment transport from the beach to the foredune crest and beyond. Restoration of *Ammophila*-invaded dunes aims to restore dune morphodynamics through the removal of invasive vegetation using manual, mechanical, or chemical means. Although more research is needed, preliminary results indicate that native foredunes have the potential to increase resilience to rising sea levels and more frequent scarp-inducing storms. Scaled up adaptation experiments are needed to determine whether these preliminary results are borne out.

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