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.

Key words: Ammophila arenaria; Ammophila breviligulata; beachgrass; Charadrius alexandrinus nivosus; coastal dune; ecosystem engineer; invasive species; Oregon; restoration; targeted management; threatened species; Washington.

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 (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 and 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 1800s (A. arenaria) and 1935 (A. breviligulata) (Cooper 1958, Seabloom and Wiedemann 1994, Wiedemann and Pickart 2004; Hacker et al., in press). 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
In addition, a number of dune plants endemic to the Pacific Northwest have declined due to the grass invasion (Pavlik 1983, Seabloom and Wiedemann 1994, Wiedemann and Pickart 2004; Hacker et al., in press). 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?

**Methods**

**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, 2007, Jones and Stokes 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).

**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. 1, Appendix A). Depending on the HRA, habitat restoration techniques involved (1) different types of *Ammophila* removal (i.e., bulldozing, plowing, diskng, 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.

Fig. 1. Study region (A) and example inset maps of habitat restoration areas (HRAs), showing plover nesting area and transects (black lines). (B) Leadbetter Point, Washington, HRA; (C) Coos Bay North Spit, Oregon, HRA. See Appendix A for location details.
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 B). 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 B).

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 C).

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 (“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 quadrant level. For relative abundance, we calculated the mean of the quadrant 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.

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 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 Ammophila removal (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 B) 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 generalized linear models with Gaussian distributions and identity link functions (i.e., normal linear regression) 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).

RESULTS
Ammophila removal effects on dune morphology and plant community structure
Dunes in Ammophila removal areas were roughly 3 m shorter (Fig. 2A) and 7 m longer (Fig. 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. 3A, B, Table 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. 3C, D, Table
1, Appendix D) and a decrease in PNW native dune plant species evenness (Fig. 3D, Table 1). \textit{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 2). PNW endemic dune plant relative abundance and richness were positively correlated with cumulative saltwater/ha and cumulative ripping/ha (Table 2).

\textbf{Ammophila removal effects on plovers}

Plovers responded positively to overall habitat treatment over time throughout the region (Fig. 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 \textit{Ammophila} removal treatment (Fig. 5); the change in plover metrics from pre- to post-\textit{Ammophila} removal did not correlate with the proxy for first time change in \textit{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 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 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 2).

**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, $R^2 = -0.975$, $t = -7.575$, df = 3, $p = 0.005$). From these results, plovers, *Ammophila*, and PNW endemic dune

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**Fig. 3.** Comparison of the mean relative abundance ($\pm$ SE) and diversity metrics ($\pm$ 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 D for species list.
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. 4, Table 1) but concurrently reduced native plant species abundance (Fig. 3, Table 1). We found that all removal treatments were effective at reducing *Ammophila* cover and had similar results for plover recovery (Table 2). However, plover recovery was not correlated with the reduction of *Ammophila* cover following the first *Ammophila* removal event (Fig. 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 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

Table 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 = 4.856**    | 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*    | -2.253         |
| Non-native plant cover     | t = -5.834***  | -1.650         |
| PNW endemic dune plant richness (excluding *Abronia umbellata* ssp. *breviflora*) | t = -0.984 | -0.201 |
| PNW native plant richness  | t = -1.750     | -3.416         |
| Non-native plant richness  | t = -2.261     | -0.481         |
| PNW endemic dune plant evenness (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.
exposed to predators was explained by treated hectares and cumulative bulldozing and hand-pulling per hectare (Table 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. 3) are similar to those in preferred plover nesting habitat in California (6–18% vegetation cover (Powell et al. 1995, 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 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. 3, Table 1, Appendix D). Richness of PNW endemic dune plants declined in treated areas as well—when we removed the state listed

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Table 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: 6.053, 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 = 0.533 + 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 1.
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 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. 2). Coastal dunes in the Pacific Northwest were dynamic, transgressive, wind-controlled systems prior to *Ammophila* introduc-
tions (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 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

Fig. 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.
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 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., *in press*). *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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**Table A1.** 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 |
|-------------|----------------------------|----------|----------|-----------|
| BP-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°4'7.35" |
| LBP-R4      | Leadbetter Point treatment | 46°37'41.5" | -124°4'7.41" |
| LBP-NR5     | Leadbetter Point control   | 46°37'22.89" | -124°4'12.92" |
| LBP-NR6     | Leadbetter Point control   | 46°37'12.57" | -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°4'6.67" |
| 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-NR5      | Tahkenitch Creek control   | 43°48'54.45" | -124°10'2.7" |
| TK-NR6      | 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-R2       | Tahkenitch Creek treatment | 43°48'18.38" | -124°10'9.07" |
| TK-R1       | Tahkenitch Creek treatment | 43°47'53.76" | -124°10'13.56" |
| TM-NR6      | Tennmile Creek control     | 43°38'46.04" | -124°12'38.55" |
| TM-NR5      | Tennmile Creek control     | 43°36'27.27" | -124°13'6.91" |
| TM-NR4      | Tennmile Creek control     | 43°34'56.65" | -124°13'32.86" |
| TM-R3       | Tennmile Creek treatment   | 43°34'29.47" | -124°13'39.93" |
| TM-R2       | Tennmile Creek treatment   | 43°34'24.6" | -124°13'41.21" |
| TM-R1       | Tennmile 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°22'1.3" | -124°19'5.17" |
| 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" |
| CNS-R2      | Coos Bay North Spit treatment| 43°21'54.33" | -124°19'50.6" |
| 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-R1       | New River control          | 43°0‘17.14” | -124°27’25.49” |
| NR-NR1      | New River control          | 43°0‘9.26” | -124°27’28.49” |
| NR-R2       | New River control          | 43°0‘1.83” | -124°27’31.05” |
| NR-R3       | New River treatment        | 42°59‘42.19” | -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-R3      | Elk River treatment        | 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” |

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### APPENDIX B

Table B1. Response and explanatory variables used in analyses.

| 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                         | Number of successful exclosed nests/total number of exclosed nests (excluding infertile or failed nests) |
| Unexclosed nest success                       | Number of successful unexclosed nests/total number of unexclosed nests (excluding infertile or failed nests) |
| Egg hatch rate                                | Number 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                          |
| 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                                             |
| Number of treatments/yr when trt. completed   | Cumulative treatments per year only when treatment occurred                           |
| Cumulative treatments per year including no treatments in a year | Cumulative treatments per year, after initial treatment |
| The mean number of treatments per year, after initial treatment | The mean number of treatments per hectare per year, after initial treatment |
| The number of treatments per hectare per year, after initial treatment | The number of treatments per hectare per year, after initial treatment |
| The intensity of treatments per hectare per year; treatments were rated on a scale of 0 (low) to 10 (high) for the degree of mechanical disruption to ecosystem. | The intensity of treatments per hectare per year; treatments were rated on a scale of 0 (low) to 10 (high) for the degree of mechanical disruption to ecosystem. |
| The total sum of human-performed treatments per year (used for yr 2007) | The total sum of human-performed treatments per year (used for yr 2007) |
| The total sum of treatment intensity per year (used for yr 2007) | The total sum of treatment intensity per year (used for yr 2007) |
| HRA habitat proportion                        | Proportion of HRA habitat which was treated (used for yr 2007)                        |
| HRA habitat (in hectares) that is naturally suitable for plover and untreated (used for yr 2007) | HRA habitat (in hectares) that is naturally suitable for plover and untreated (used for yr 2007) |
| HRA habitat proportion that is naturally suitable for plover and untreated (used for yr 2007) | 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)                                          |

*Note:* Abbreviation: trt(s) = treatment(s).
Fig. C1. 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 D

Table D1. 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*      | +       |           |
| *Anthemanthum 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*          | +       |           |
| *Pteridium aquilinum*          | +       |           |
| *Rumex salicifolius*           | +       |           |
| *Symphyotrichum subspicatum*   | +       | +         |
| *Vaccinium ovatum*             | +       |           |
| **PNW endemic dune plants**    |         |           |
| *Abronia latifolia*            | +       | +         |
| *Abronia umbellata ssp. breviflora*† | +       |           |
| *Ambrosia chamissonis*         | +       |           |
| *Astragalus sp.*†               | +       |           |
| *Calystegia soldanella*        | +       |           |
| *Canissoina cheiranthifolia*   | +       |           |
| *Elymus mollis*                | +       | +         |
| *Lathyuris japonicus*          | +       | +         |
| *Polygonum parvifolium*        | +       |           |
| *Tanacetum camphoratum§*       | +       |           |

† 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.