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

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Citation: Biel, R. G., S. D. Hacker, P. Ruggiero, N. Cohn, and E. W. Seabloom. 2017. Coastal protection and conservation on sandy beaches and dunes: context-dependent tradeoffs in ecosystem service supply. Ecosphere 8(4):e01791. 10.1002/ecs2.1791

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

Key words: coastal protection; conservation; ecosystem management; ecosystem services; natural capital; restoration.

Received 7 December 2016; revised 9 March 2017; accepted 10 March 2017. Corresponding Editor: Debra P. C. Peters.

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Introduction

Throughout human history, ecosystems have been manipulated to provide goods and services that enhance human wellbeing. However, a confluence of factors, such as population and economic growth, has created a rising demand for ecosystem services (ESs). In some cases, this demand is unmet because of misallocation of resources, ecosystem mismanagement, and habitat degradation and destruction (MEA 2005). To improve the efficiency of ES management, multiple studies have called for more research on common patterns and relationships among ESs (Bennett et al. 2009, Lester et al. 2013, Needles et al. 2015).

Ecosystems are often managed to maximize individual ESs, most commonly provisioning services such as food, fuel, and timber production (MEA 2005). While these strategies boost target

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

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

In this study, we examined interactions among three ESs within the context of invasive species management and ecosystem restoration in the U.S. Pacific Northwest coastal dune system: coastal protection, conservation of the federally threatened western snowy plover (*Charadrius nivosus nivosus*; hereafter, plover), and conservation of endemic beach and foredune plants (e.g., pink sand verbena, *Abronia umbellata*). Western snowy plovers and endemic dune plants provide cultural and supporting ecosystem goods and services. They support both non-consumptive direct use values (e.g., education, tourism, and recreation) and indirect use value (e.g., maintenance of wildlife, Giles-Johnson and Kaye 2014). Moreover, as threatened species, they have significant existence and bequeath value and are targets of intensive restoration efforts (USFWS 2007, Giles-Johnson and Kaye 2014).

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

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

Given the impacts of beachgrass on foredune geomorphology and community structure, we assessed the effects of U.S. Pacific Northwest foredune restoration on exposure to coastal flooding under present-day and possible future extreme storm conditions, on plover conservation, and on endemic plant community conservation. In this study, we address the following questions: (1) Does beachgrass and foredune removal create synergies or tradeoffs (i.e., positive or negative covariation) between three Pacific Northwest dune services: coastal protection, plover conservation, and endemic plant conservation? (2) Which biophysical processes and interventions produce ES interactions, and do these interactions vary among sites?

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

Methods

Habitat restoration areas

We surveyed seven foredune HRAs in Oregon and southern Washington, USA, in summer and fall 2012 (Fig. 1; Appendix S1: Table S1). Within the HRAs, we established 58 cross-shore transects at beachgrass removal and nearby reference locations (6–14 per HRA) and near sites used by Zarnetske et al. (2010; Fig. 1; Appendix S1: Table S1). Beachgrass removal was conducted one to three years prior to conducting the surveys, using bulldozing, discing, herbicide, hand pulling, or burning (Appendix S1: Table S2; Zarnetske et al. 2010, Lauten et al. 2012, Pearson et al. 2013).

Cross-shore topobathymetric profiles

At each transect location, we measured topography in three cross-shore replicate transects using Network Real-Time Kinematic Differential Global Positioning Systems (NRTK dGPS; Oregon Real-Time GNSS Network, Oregon Department of Transportation, Salem, Oregon, USA; Washington State Reference Network, Washington, USA). Each of the three replicate transects was run perpendicular to the foredune and parallel to neighboring replicate transects at 10-m alongshore spacing (Fig. 1; 174 replicates within 58 transects). Topographic beach and foredune profiles were then measured along each replicate between the waterline and the landward edge of the dune field, at sub-decimeter accuracy (Fig. 2; Ruggiero et al. 2005). Corresponding bathymetric profiles were reconstructed between the shoreline and the 18-m isobaths from the best available data sources (Ruggiero et al. 2005, Carignan et al. 2009*a*, *b*, Stevens et al. 2012, Di Leonardo and Ruggiero 2015).

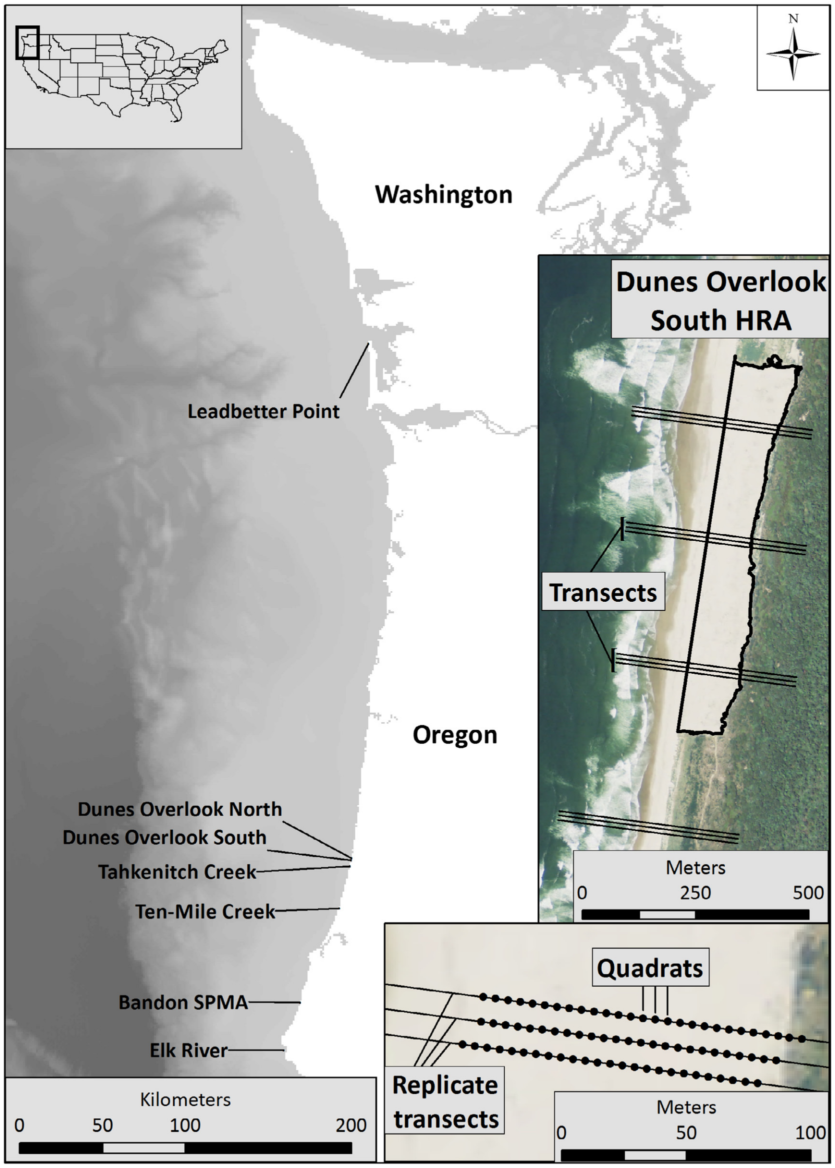

Fig. 1. Dune habitat restoration areas (HRAs) in Oregon and southern Washington, USA, and survey design (Appendix S1: Table S1). Aerial photograph of Dunes Overlook South shows transect placement within beachgrass removal and nearby reference locations. Black lines show transects; points indicate vegetation survey quadrats.

Nearshore and foredune metrics and statistics

We classified each topobathymetric transect using metrics of nearshore and foredune morphology. Nearshore morphology was classified into nearshore slope, the mean slope between the horizontal locations of the 18-m isobaths and mean low water (MLW); foreshore slope, mean slope between MLW and mean high water (MHW); and backshore slope, mean slope between MHW and the 4-m contour above local mean sea level (MSL). Foredune morphology was also classified into foredune toe (d_{toe}), foredune crest (d_{crest}), and foredune heel (d_{heel}) elevations and positions (Fig. 2) using methods described by Mull and Ruggiero (2014), where d_{crest} is the maximum foredune elevation; d_{toe} is the inflection point between the concave-up backshore and concave-down foredune and

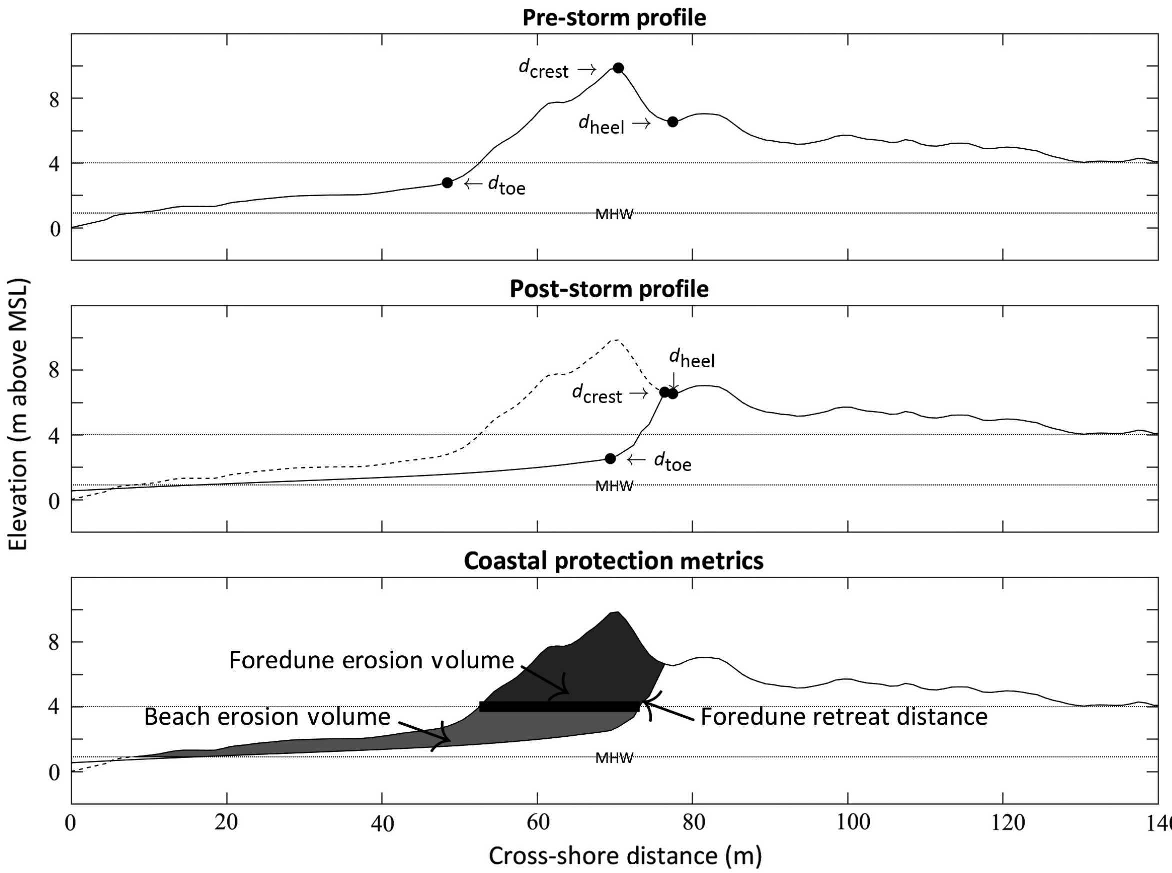

Fig. 2. An example of pre- and post-storm cross-shore profiles at a Ten-Mile Creek habitat restoration area (HRA). Foredune toe (d_{toe}), foredune crest (d_{crest}), and foredune heel (d_{heel}) positions are indicated for both the pre-storm and post-storm profiles. Shading indicates the cross-sectional area eroded during the simulated storm (dark gray = foredune erosion volume; medium gray = beach erosion volume; black line = foredune retreat distance).

approximates the most-seaward vegetation line; and d_{heel} is the landward extent of the foredune.

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

XBeach model and extreme storm scenarios

XBeach is a process-based numerical model of wave propagation, sediment transport, and nearshore, beach, and dune morphological change (Roelvink et al. 2009). To assess storm-related flooding and erosion exposure, we developed a one-dimensional cross-shore XBeach model for each of the topobathymetric cross-shore profiles. We employed a variable cross-shore grid resolution of 25 m to 1 m, with increasing grid resolution near foredunes, and incorporated median sediment grain size estimates from a regional database of physical shoreline characteristics (Peterson et al. 1994) as non-default parameters in XBeach simulations. All other XBeach model parameters were set to default values. Upon running model simulations, we stored values of bed level and wave height for each 56-h storm scenario.

To simulate possible changes to regional extreme storms, we considered nine storm scenarios with three levels of significant wave height

(SWH) and peak wave period (T), and three levels of storm surge. For a present-day approximately 30-yr return-level storm event (Mull and Ruggiero 2014), we utilized a 56-h storm hydrograph from the "storm of record," the 2–3 March 1999, extratropical storm (SWH; T, tide; and surge). Based on wave buoy and tide gauge measurements, the 2–3 March storm event produced SWH = 13.3 m, T = 16.7 s, and a maximum storm surge = 1.6 m. To simulate possible changing storminess patterns on extreme storms, we varied maximum SWH by −1.5 to +2 m (11.8–15.3 m), T by ±3 s (13.7–19.7 s; see Seabloom et al. 2013), and storm surge by ±0.5 m (1.1–2.1 m).

Coastal protection metrics and statistics

Using XBeach model outputs, we measured foredune flooding incidence, foredune erosion volume, and foredune retreat distance metrics between pre- and post-storm cross-shore profiles as metrics of flooding and erosion exposure (Fig. 2). Foredune flooding was identified by the incidence of sediment transport landward of the d_{crest} position, indicating wave overtopping of d_{crest}. Foredune erosion volume represents the change in sediment volume above the 4-m contour relative to MSL in pre- and post-storm profiles. Foredune retreat distance denotes the change in the 4-m contour's cross-shore position between the pre- and post-storm profiles. The 4-m contour approximates the location of d_{toe}, delineating the beach (<4 m elevation) from the foredune (≥4 m elevation).

To examine how flooding incidence relates to nearshore morphometrics (nearshore, foreshore, and backshore slope), foredune morphometrics (d_{toe} elevation, d_{crest} elevation), and storm characteristics (SWH, T, surge), we modeled flooding incidence against these metrics using a mixed-effects binomial regression model using lme4 v1.1-9 (Bates et al. 2015). Transect was included as a random intercept to account for the nested sampling design. To assess multicollinearity among explanatory variables, we calculated the variance inflation factor (VIF) and removed highly multicollinear variables (VIF > 5) from the model. To similarly examine how foredune retreat relates to nearshore morphometrics, foredune morphometrics, and storm characteristics, we modeled foredune retreat distance against these metrics using a linear mixed model (nlme v3.1). We included a random intercept of replicate-transect nested within transect to reflect the nested sampling design, and a constant variance function to account for heteroskedasticity among HRA site × treatment combinations.

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

Western snowy plover conservation analysis

To assess plover productivity at each HRA, we obtained data on counts of adult breeding males, counts of fledglings, and whether predator controls were applied for each HRA and year (1992–2014) from annual plover population monitoring reports (Lauten et al. 2014, Pearson et al. 2015). Monitoring of breeding plover populations in Oregon and Washington occurs at all sites where plover nesting activity has been detected. Data were visually assessed for temporal autocorrelation using autocorrelation function plots. We performed a Bayesian hierarchical Poisson regression using a log-link function with fledgling count as the response variable, log(count of breeding males) as an offset, and HRA-level intercept and predator management as explanatory variables in rstan v2.5.0 (Stan Development Team 2014). Markov chain Monte Carlo (MCMC) samples of parameters were thinned and 95% posterior intervals calculated.

Endemic foredune plant conservation analysis

To assess the effects of beachgrass removal on the dune plant community, we visually estimated percent areal cover of all plant species using 0.25-m^2 quadrats at 5-m intervals along the cross-shore replicate transects (Fig. 1). Measurements extended from the seaward vegetation line to d_{heel}. To explore effects of beachgrass removal on plant community composition, we compared plant species richness and abundance between beachgrass removal and reference areas for endemic foredune plants, exotic foredune plants, native backdune plants, and exotic backdune plants (Appendix S1: Table S3) using a Bayesian Poisson regression model with HRA site as a random effect. Richness estimates were rarefied with a bootstrap function (vegan::specpool) and rounded to the nearest integer prior to modeling (Oksanen et al. 2013). We further estimated impacts of beachgrass removal on beachgrass and native dune grass percent cover using a Bayesian beta regression model with a non-informative prior. Finally, we assessed responses of individual species incidence to beachgrass removal using a Bayesian logistic regression model with a weakly informative prior Cauchy (0, 2.5) distribution to manage complete separation at some HRA sites (Gelman et al. 2008).

Results

Coastal protection service

Nearshore, beach, and foredune morphology are important determinants of coastal hazard exposure, and significantly contribute to differences in flooding and erosion exposure among HRA sites and with beachgrass removal. The seven HRA sites examined in this study had variable nearshore and foredune geomorphology. Nearshore slope, foreshore slope, and backshore slope varied by HRA (Fig. 3; Appendix S1: Tables S4, S5) and generally increased from northern to southern HRAs. Mean foredune toe (d_{toe}) and crest (d_{crest}) height also varied among sites and with beachgrass removal (Appendix S1: Table S6). Consequently, the northernmost HRA, Leadbetter Point, exhibited a shallow-sloping nearshore extent with comparatively short reference area foredunes, while southerly sites

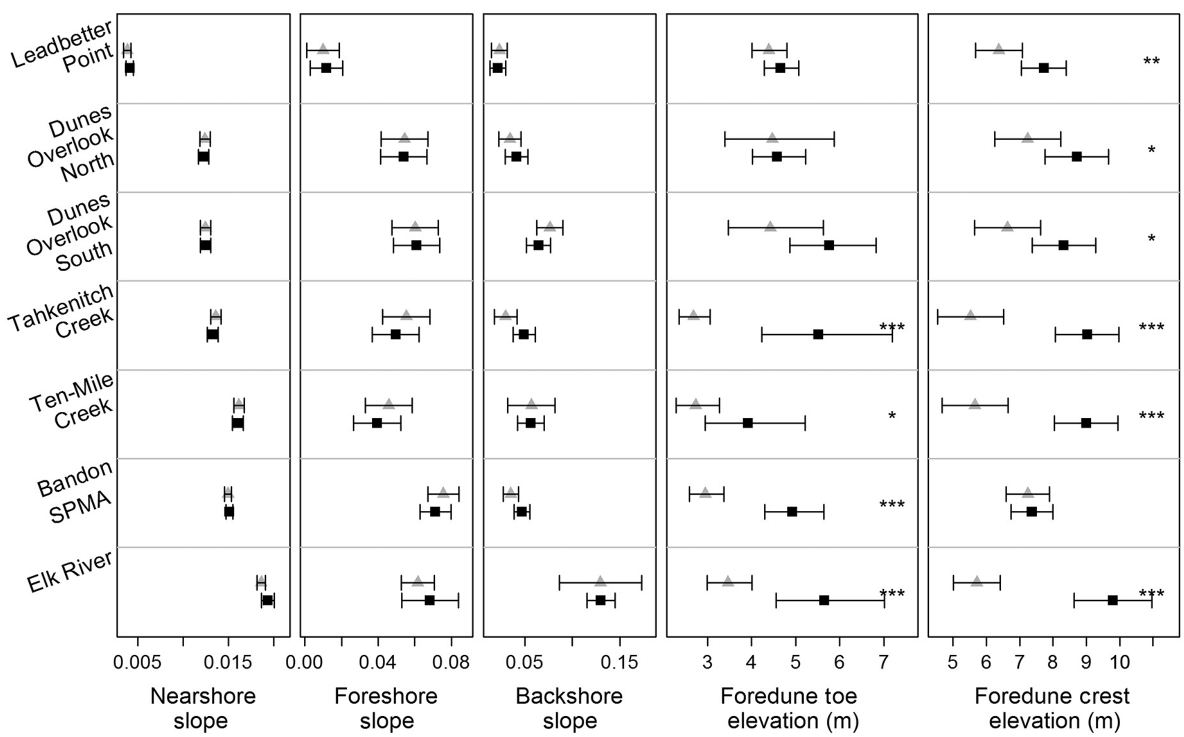

Fig. 3. Dune geomorphology at beachgrass removal (gray triangles) and reference (black squares) areas at seven habitat restoration area (HRA) sites (Fig. 1; Appendix S1: Table S1). Error bars indicate 95% confidence intervals. Asterisks indicate significant difference within HRA sites: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

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

The among-site variation in nearshore morphology and within-site elevation differences alter flooding and erosion exposure to present-day and possible future extreme storm conditions. For flooding exposure, the odds of backdune flooding (wave overtopping of d_{crest}) was positively associated with nearshore slope ($P < 0.0001$) and storm surge ($P < 0.0001$), negatively associated with d_{crest} elevation ($P < 0.0001$) with d_{crest} elevation × surge ($P = 0.058$) and d_{crest} elevation × nearshore slope ($P < 0.0001$) interactions, and not associated with d_{toe} elevation ($P = 0.31$), indicating that steeper-sloping nearshore extents, shorter foredunes, and higher storm surge increase the odds of flooding (Fig. 4). Similarly, foredune retreat (landward retreat of the 4-m contour; Fig. 2) during XBeach simulations was also associated with geomorphology, storm wave intensity (SWH, T), and surge. Foredune retreat distance was positively associated with nearshore slope ($P < 0.0001$), foreshore slope ($P < 0.0001$), backshore slope ($P < 0.0001$), storminess ($P < 0.0001$), and surge ($P < 0.0001$). Foredune retreat was further influenced by interactions between numerous variables, including d_{crest} elevation × backshore slope ($P = 0.019$), d_{crest} elevation × storminess ($P < 0.0001$), and d_{crest} elevation × surge ($P < 0.0001$), indicating that stronger storms, steeper sloped profile, and lower foredunes increased foredune retreat distances (Fig. 5).

When examining flooding and erosion exposure within and among HRA sites, we found that the odds of backdune flooding differed among HRA site ($P = 0.0007$), with beachgrass removal ($P = 0.0006$), and with storm surge ($P < 0.0001$; Fig. 6). Specifically, during a present-day extreme storm, the odds of overtopping ranges from 0.002 (±1 SE: 0.0006–0.004) to 0.06 (0.03–0.12) at each HRA site. When reframed in terms of absolute

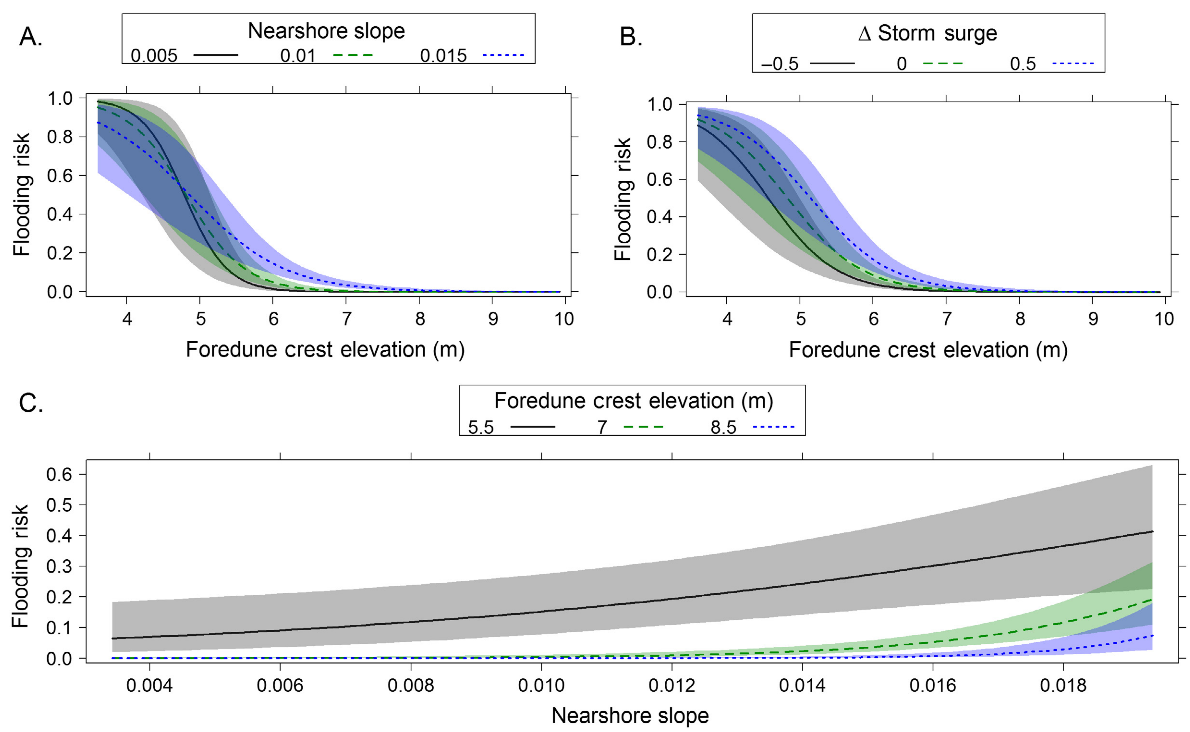

Fig. 4. Interactive effect of (A, C) nearshore slope × d_{crest} elevation and (B) Δ storm surge × d_{crest} elevation on absolute flooding risk. Bands indicate confidence intervals.

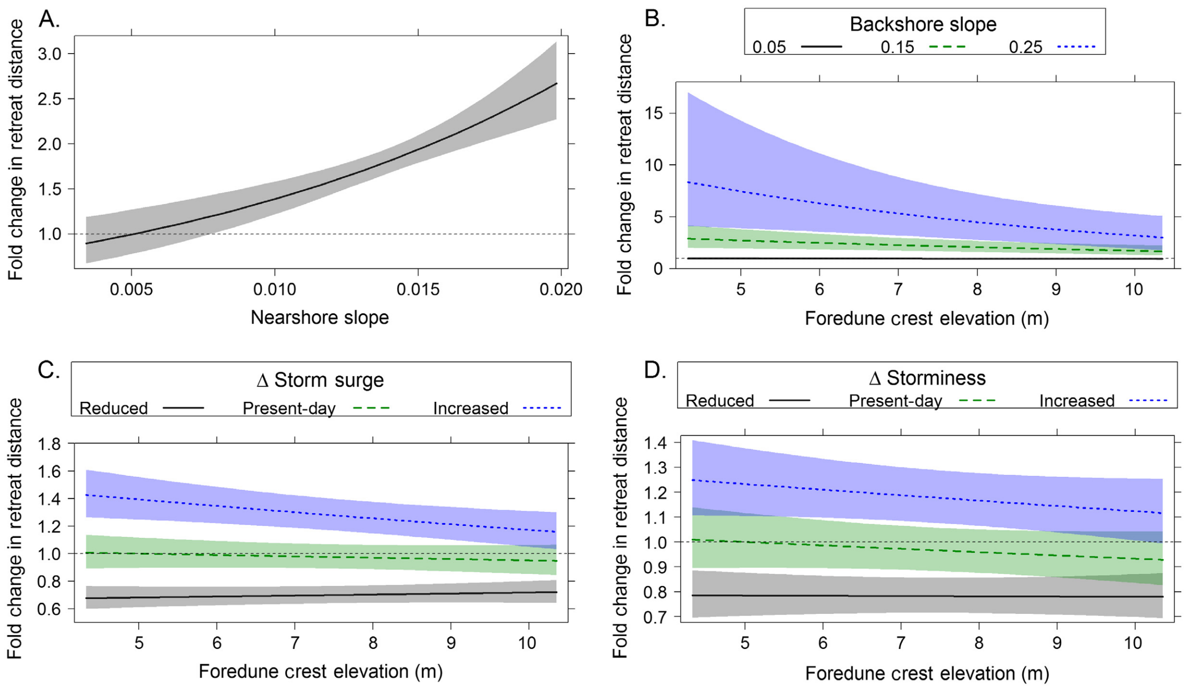

Fig. 5. (A) Main effect of nearshore slope on foredune retreat distance. Interactive effect of (B) backshore slope × d_{crest} elevation, (C) Δ storm surge × d_{crest} elevation, and (D) Δ storminess × d_{crest} elevation on foredune retreat distance. Fold change in foredune retreat distance measures the relative amount of retreat for foredunes under different conditions as compared to a reference condition (conditions with a predicted 1×-fold change). Bands indicate confidence intervals.

risk of overtopping (i.e., expected proportion of overtopped transects during an extreme storm event), overtopping risk ranged from 0.002 (±1 SE: 0.0006–0.004) to 0.06 (0.03–0.11) at each HRA site. Beachgrass removal and elevated storm surge further increased the relative odds of overtopping by 6.9-fold (4.0–12.6) and 4.2-fold (3.4–5.3), respectively, relative to the present-day storm scenario. Foredune retreat exhibited similar patterns, where retreat distance varied among HRA sites ($P < 0.0001$) and increased with wave intensity ($P < 0.0001$), surge ($P < 0.0001$), and with beachgrass removal ($P < 0.0001$), with significant HRA site × wave intensity ($P < 0.0001$), HRA site × surge ($P < 0.0001$), beachgrass removal × surge ($P < 0.0001$), and wave intensity × surge interactions ($P < 0.0001$). For foredune retreat, a present-day extreme storm caused between 3.0 m (±1 SE: 2.6–3.3 m) and 26.0 m (23.4–28.9 m) of foredune retreat (mean retreat distance: 13.7 ± 0.3 m), depending upon the HRA site. Stronger wave intensity increased retreat by 14% (9–20%) to 23% (22–24%), while higher surge increased retreat by 17% (16–18%) to 29% (27–31%) at six HRA sites (mean increase: 24% ± 2%), and by 149% (137–162%) at Leadbetter Point. Beachgrass removal further boosted foredune retreat by 26% (19–35%), while higher surge intensified retreat at removal areas by 6% (5–7%).

Plover conservation service

Western snowy plover productivity (fledglings per breeding adult male) responded positively to beachgrass removal and predator control interventions, although this varied among HRA sites (Fig. 7). Among the HRAs examined, mean productivity ranged from 0.4 (Bandon Snowy Plover Management Area [SPMA]; 95% posterior interval: 0.3, 0.6) to 0.9 fledglings per male (Ten-Mile Creek; 0.7, 1.1) in years prior to predator management. During years with lethal predator controls, mean plover productivity at HRAs rose by 1.4- to 2.2-fold. No plovers have been observed nesting at Elk River since monitoring began (Lauten et al. 2014).

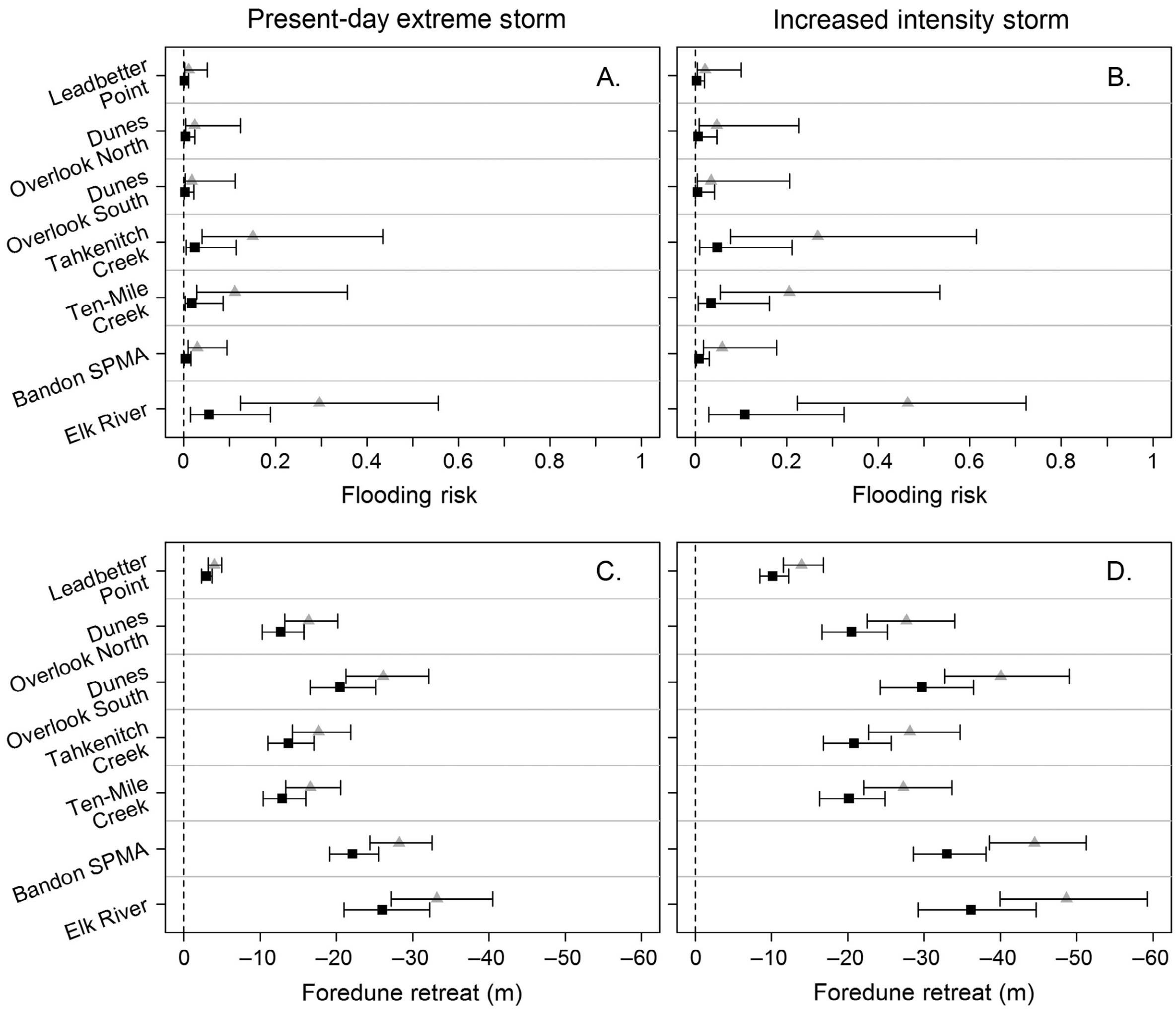

Fig. 6. (A, B) Flooding risk (probability of flooding) at beachgrass removal (gray triangles) and reference (black squares) sites under (A) a present-day extreme storm scenario and (B) an increased wave intensity and surge extreme storm scenario. (C, D) Predicted foredune retreat at beachgrass removal and reference areas under (C) a present-day extreme storm scenario and (D) an increased wave intensity and surge extreme storm scenario. Error bars indicate 95% confidence interval.

Endemic dune plant conservation service

Endemic dune plant metrics differed in restored vs. reference areas. Beachgrass removal was associated with an 84% decrease in native backdune plant richness (95% posterior interval: 75–91% decrease), a 49% decrease in exotic backdune plant richness (27–70% decrease), and no change in either endemic beach and foredune plant richness (42% decrease–57% increase) or exotic beach and foredune plant richness (11% decrease–110% increase). As expected, invasive beachgrass removal reduced beachgrass cover, although the magnitude of reductions varied by site (Fig. 8; Appendix S1: Table S7). However, among historically important beach and foredune plant species, beachgrass removal also significantly reduced native dune grass cover (*Elymus mollis*) at most HRA sites (Fig. 8) and did not affect the incidence of the native forbs *Abronia latifolia*, *Ambrosia chamissonis*, and *Calystegia soldanella* (Appendix S1: Table S7). Nevertheless, for the threatened pink sand verbena, beachgrass removal areas were

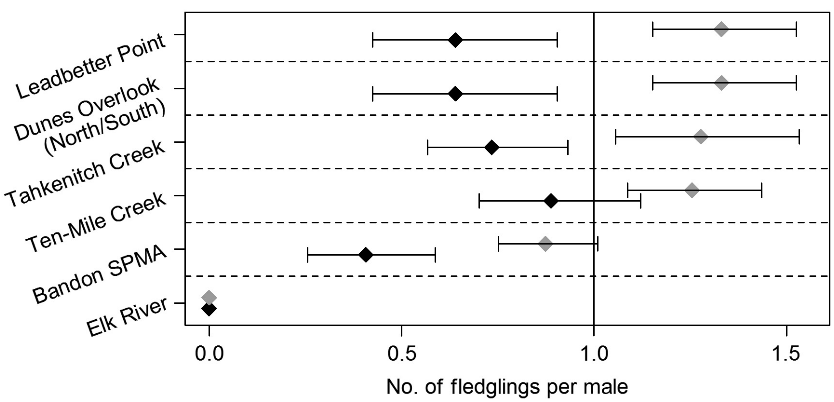

Fig. 7. Plover productivity at habitat restoration areas during years without predator removal (black diamonds) and with plover predator removal (gray diamonds). Error bars indicate 95% posterior intervals. Dunes Overlook plover productivity encompasses both the Dunes Overlook North and South sites.

associated with up to an 8.7-fold increase in the odds of incidence when compared to reference areas, depending upon the HRA site (Fig. 8; Appendix S1: Table S7).

Biophysical valuation of tradeoffs

We examined variation and covariation among the three ESs in response to foredune restoration. Coastal protection metrics exhibited tradeoffs

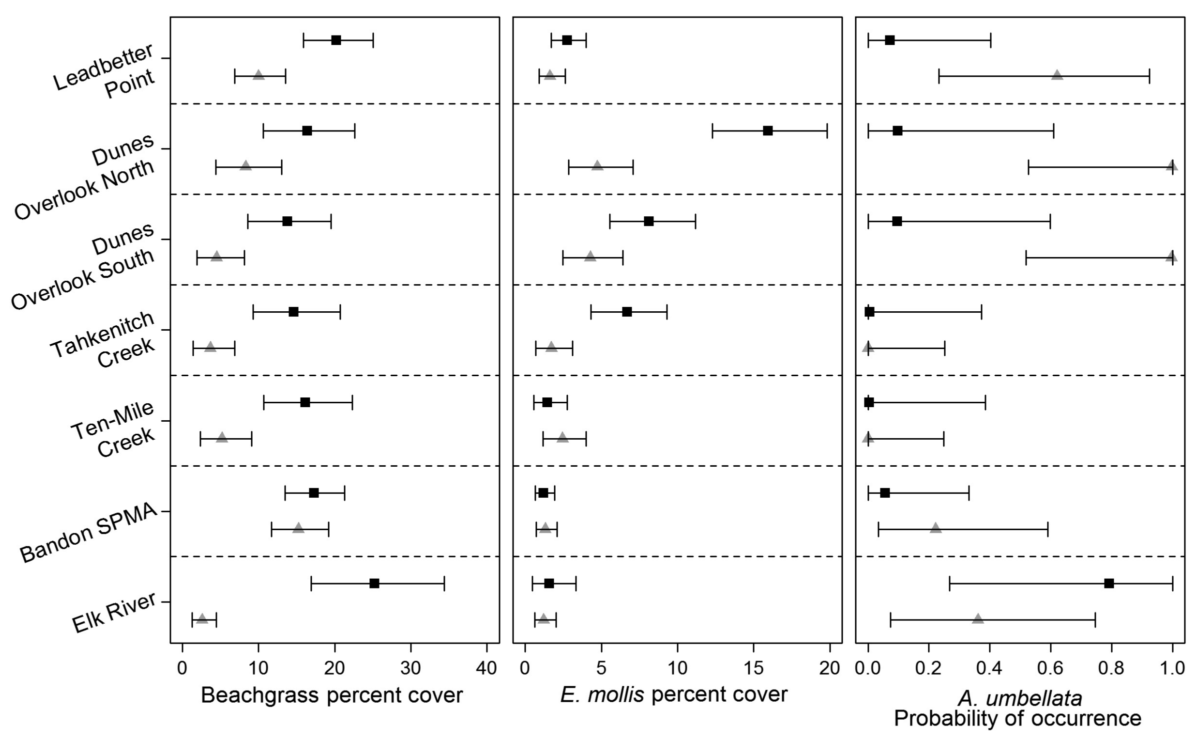

Fig. 8. (A) Beachgrass percent cover; (B) native dune grass percent cover; and (C) pink sand verbena probability of occurrence at beachgrass removal (gray triangles) and reference (black squares) areas at seven habitat restoration area sites (Fig. 1; Appendix S1: Table S1). Points indicate median posterior estimates; error bars indicate 95% posterior intervals.

with plover productivity, where foredune restoration reduced coastal protection and increased plover productivity. However, the strength of the tradeoff varied both among sites and among coastal protection metrics (Fig. 9). In contrast, most plant conservation metrics (e.g., richness, incidence of endemic species) exhibited no relationship with either plover productivity or coastal protection (Fig. 9H), although *Abronia umbellata* incidence positively covaried with plover productivity (Fig. 9I) and negatively covaried with coastal protection metrics. Although quantification of demand for ESs was beyond the scope of this study, see Appendix S2 for a discussion of demand for coastal protection and conservation ESs in the Pacific Northwest coastal dune system.

Discussion

Recent reviews on the science of ESs call for an improved understanding of their patterns and processes to benefit natural resource and conservation management (MEA 2005, Bennett et al. 2009). As researchers identify more ESs and their interactions, managing individual ESs within a complex ES network quickly becomes untenable. Moreover, because of this interconnectedness among ESs, management of individual ESs in isolation increases the chance for negative impacts on non-target ESs. Consequently, systematic assessments can help to avoid or mitigate negative externalities and to identify possible interventions that improve provisioning of multiple ESs for multiple users (Lester et al. 2013, Needles et al. 2015). Methodologically, ES interactions may be identified by examining potential covariation among ESs and their underlying drivers (i.e., ecosystem processes or functions). Covariation among ESs indicates either the presence of a shared driver (i.e., an ecosystem process that affects multiple ESs) or a direct modification of one ES by another (Bennett et al. 2009). While shared drivers provide leverage points for altering ES supply, non-shared drivers and context-dependent relationships are also important for ES management.

Shared drivers: plover–coastal protection tradeoff

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

Invasive beachgrasses harm plover productivity, yet build foredunes that reduce risk of wave overwash and erosion. Plovers preferentially select nesting habitat with low vegetation cover (1–18%; Zarnetske et al. 2010) and in areas with ≥100 m of open space, possibly to facilitate courtship and early predator detection (Muir and Colwell 2010, Pearson et al. 2016). Throughout the U.S. Pacific Northwest, though, beachgrass cover exceeds 25% across the foredune itself, with near-complete monopolization of space near the foredune crest (Hacker et al. 2012). This elimination of open space by beachgrasses not only inhibits plover nest initiation, but also provides habitat for multiple mammalian and avian predators. In turn, beachgrass removal has re-created open nesting habitat and remains essential for plover productivity and recovery (Fig. 9A; USFWS 1993, 2007, Muir and Colwell 2010, Zarnetske et al. 2010, Dinsmore et al. 2014, Pearson et al. 2016).

Beachgrasses also increase coastal protection ES by creating foredunes via sand accretion (Hesp 1989, Zarnetske et al. 2012). In the Pacific Northwest, invasive *Ammophila* spp. effectively capture sand, leading to development of tall, stable foredunes that range from 3 to 18 m in height (Hacker et al. 2012). Correspondingly, mechanical beachgrass removal reduces both invasive beachgrass abundance (Fig. 8) and foredune height (Fig. 3), resulting in a 6.9-fold increase in the odds of flooding and a 26% greater foredune retreat distance for a representative 30-yr return-level storm event (Fig. 6). Consequently, both plover conservation and coastal protection ESs share a common driver of beachgrasses that unavoidably create an ES tradeoff.

Non-shared drivers: plover–coastal protection tradeoff

Even though ESs may covary, they are often also affected by non-shared drivers, ecosystem

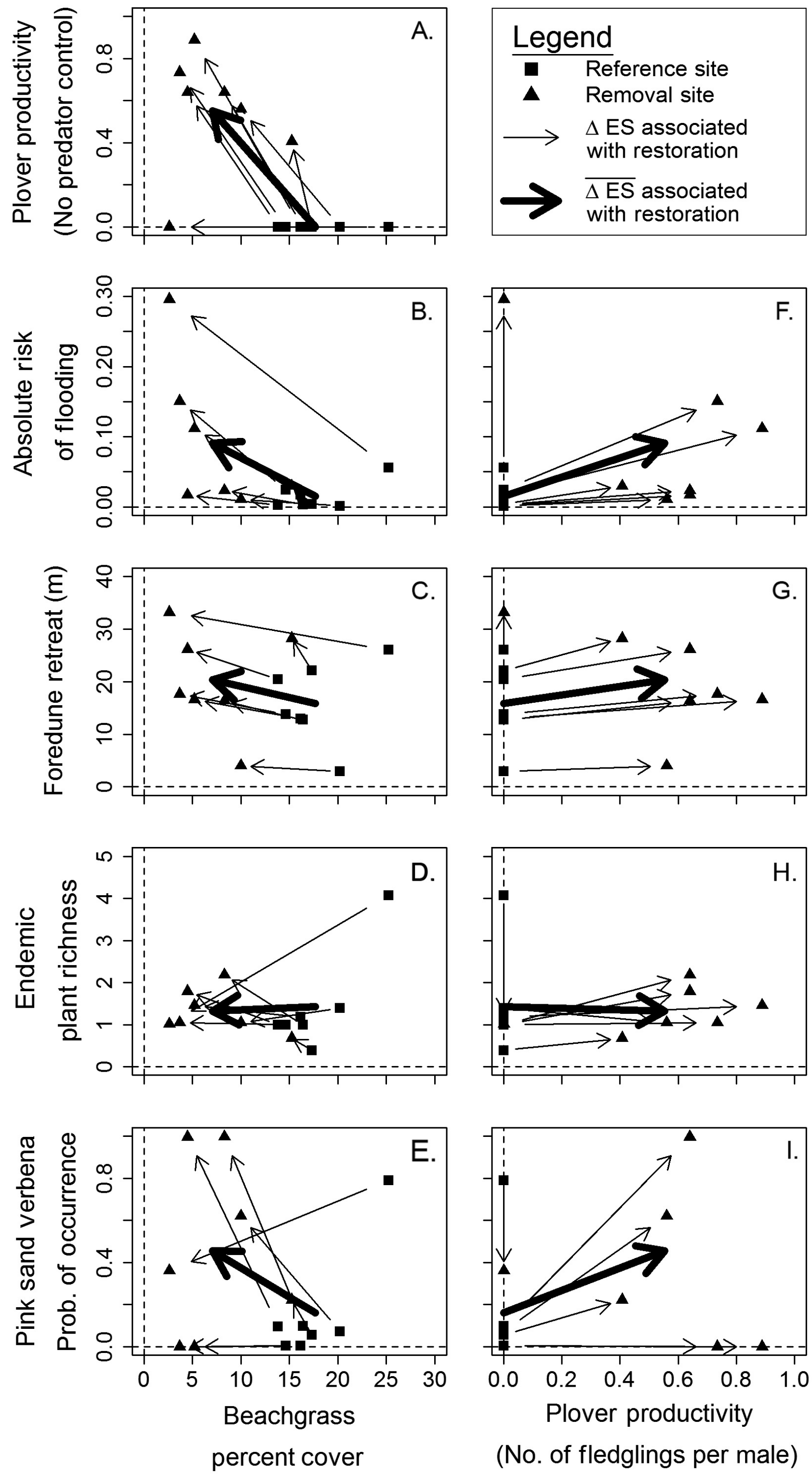

Fig. 9. (A–E) Comparison of ecosystem service (ES) metrics with beachgrass percent cover at paired beachgrass removal (black triangles) and reference (black squares) areas at seven habitat restoration area sites (Fig. 1;

(*Fig. 9. Continued*)

Appendix S1: Table S1). (F–I) Pairwise comparison of plover productivity with coastal protection and endemic plant conservation ES metrics. Thin arrows indicate ΔES supply at each site. Bold arrows indicate mean change in ES ($\overline{\Delta \mathrm{ES}}$) metric between removal and reference areas.

processes that only affect one ES in a pairwise relationship. These non-shared drivers may provide an opportunity for mitigating tradeoffs by permitting manipulation of one ES without cost to the other. For the coastal protection–plover tradeoff, while beachgrass removal and foredune shortening function as a shared driver in the coastal protection–plover productivity tradeoff, tradeoff intensity differed among the seven restoration areas (Fig. 9F, G). This variation was the consequence of important non-shared drivers that produce spatial variation in coastal protection and plover production.

For coastal protection, nearshore geomorphology mediates the intensity of flooding and erosion exposure (Figs. 3, 4), but does not affect plover productivity. Regions with shallow-sloping nearshore environments and wide beaches (i.e., dissipative beaches; Wright and Short 1984) provide greater area for wave energy dissipation to occur than regions with moderate- to steep-sloped nearshore environments and narrow beaches (i.e., intermediate and reflective beaches). Thus, under comparable wave conditions, dissipative beaches typically experience lower wave runup elevations than reflective beaches (Stockdon et al. 2006). If beaches do not dissipate all the wave energy they experience, foredunes provide a second line of defense by reflecting or dissipating residual wave runup and by widening beaches via sediment erosion from the foredune to the beach (Larson et al. 2004, Roelvink et al. 2009).

In our study, HRAs on dissipative beaches (e.g., Leadbetter Point) exhibited little flooding and erosion exposure as compared to HRAs on intermediate and intermediate-reflective beaches (e.g., Bandon SPMA, Elk River). Moreover, while beachgrass removal and associated dune shortening on dissipative beaches increased flooding and erosion exposure slightly, similar shortening on intermediate and intermediate-reflective beaches produced sizeable increases in exposure (Fig. 6). These results suggest that nearshore geomorphology, a non-shared driver, may significantly alter each site's coastal hazard exposure and that nearshore geomorphology may also mediate the effects of dune shortening on coastal hazard exposure (Figs. 4, 5). Thus, managers can mitigate tradeoffs between plover productivity and coastal hazard exposure by incorporating nearshore geomorphological information into HRA site selection processes. Although not examined in this study, managers can also minimize vulnerability to coastal hazards by locating restoration sites in areas where flooding and erosion events would have tolerable impacts on coastal development and ES supply (Appendix S2).

Similarly, for plover conservation, numerous non-shared drivers influence plover productivity, without influencing coastal protection. In addition to beachgrass cover, plover productivity is significantly affected by predation pressure, recreational beach use, habitat quality, and plover behavior (USFWS 1993, 2007, 2012, Lafferty et al. 2006, Colwell et al. 2011, Pearson et al. 2016). Predators affect plover productivity at multiple stages throughout nesting, causing nest abandonment and depredation of eggs, chicks, and adults. In response, plover managers have employed numerous predator control methods, including predator exclosures and both non-lethal and lethal predator removal (Pearson et al. 2016). At this study's seven HRAs, each of these predator controls has been employed in varying intensity, and predator exclosures have significantly improved nest survival (Zarnetske et al. 2010, Pearson et al. 2016). Although we did not control for predator exclosure intensity in our analysis, plover productivity appreciably rose during years when lethal predator controls were employed, although its efficacy varied among sites (Fig. 9). While predator exclosures may partly explain differences in site-specific responses to lethal predator controls, it is also likely that predation pressure varied among sites (Hardy and Colwell 2012, Pearson et al. 2016) and may have produced site-specific responses to predator controls.

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

Context dependence: endemic plant conservation relationships

While shared and non-shared drivers are important sources of ES variation and covariation, context dependence may also control ES interactions. Context-dependent ES interactions may arise when additional covariates interact with shared drivers to alter the sign or magnitude of ES relationships. Consequently, ESs may exhibit neutral or weak interactions under one set of conditions and strong interactions under different conditions. Context may include, but is not limited to, spatial or temporal conditions, disturbance regimes, and abiotic or biotic conditions (Koch et al. 2009). In Pacific Northwest dunes, endemic plant conservation typifies this relationship because endemic plant decline likely was driven by direct competition with beachgrasses and indirect effects of beachgrass ecosystem engineering (e.g., altered sand burial, sand scour, and salt spray regimes; Wiedemann and Pickart 2008). Yet beachgrass removal had no effect on the incidence or abundance of many historically important endemic foredune plants (e.g., *Abronia latifolia*, *Ambrosia chamissonis*, *Calystegia soldanella;* Fig. 9D; Appendix S1: Table S7). Although beachgrass removal creates habitat for endemic plants, we hypothesize that seed dispersal limitation is largely responsible for their lack of recovery.

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

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

Pink sand verbena (*Abronia umbellata*), however, deviates from this pattern. It positively covaries with plover conservation (Fig. 9I) and negatively covaries with coastal protection. Unlike other endemic species, pink sand verbena's success arises from a combination of beachgrass removal, increased disturbance (both from beachgrass removal activities and from wave overwash), seed additions, and targeted protection of overwintering plants from discing and herbicide. Through these actions, managers have alleviated beachgrass competition and dispersal limitation, and facilitated increases in pink sand verbena abundance (Fig. 8; Giles-Johnson and Kaye 2014). Consequently, a synergistic relationship exists between plover conservation and pink sand verbena conservation, due to beachgrass removal (shared driver) and reduced dispersal limitation (context dependence). For other endemic foredune plants, it is unlikely that a similar synergistic relationship would develop without seeding interventions.

Optimizing ecosystem service management

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

In other systems, ES supply can also be optimized by exploiting context dependence and non-shared drivers. In Thailand, mangroves provide coastal protection, but are often irreversibly converted to shrimp aquaculture ponds, creating a tradeoff between coastal protection and shrimp aquaculture. Spatial planning of shrimp aquaculture pond placement, though, can alleviate this tradeoff: While placement of ponds at the seaward fringe of mangroves creates a strong ES tradeoff, pond placement near the inland boundary of mangrove areas causes little reduction in coastal protection and may further enhance shrimp production (Barbier 2012). Similarly, although agriculture production ESs commonly tradeoff with water quality, placement of targeted riparian buffers can significantly diminish tradeoff intensity by minimizing sediment erosion and nutrient loading (Polyakov et al. 2005).

For natural resource, conservation, and restoration management, recognition and mitigation of ES tradeoffs may help managers meeting multiple management objectives. Although not of large concern for most HRAs examined in this western snowy plover case study (Appendix S2), conservation and restoration projects that fail to consider negative socio-economic and socio-ecological impacts of conservation policies can alienate local communities and stakeholders, cause disenfranchisement and loss of livelihood to local communities, deprive conservation groups with political allies and local enforcement, and inefficiently use limited financial resources (Adams et al. 2004, Aronson et al. 2006, Naidoo and Iwamura 2007). For some projects, these oversights may impair the efforts to conserve or restore ecosystems and may ultimately lead to project failure, as has occurred in both developing and developed countries (Bode et al. 2008, Buckley and Crone 2008, Abelson et al. 2016). Consideration and amelioration of ES tradeoffs not only ensures that an ecosystem's finite resources are managed efficiently (Naidoo and Ricketts 2006, Naidoo and Iwamura 2007), but also provides a framework for facilitating local community and stakeholder engagement and support when establishing ecological reserves and managing resources for multiple users (Davenport et al. 2010, Abelson et al. 2016, Marttila et al. 2016).

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

Acknowledgments

Thanks to S. Pearson and E. Gaines for advice and comments and D. Batson, J. Henderson, and J. Wood for help with data collection and logistics. We further thank OR and WA coastal managers, biologists, and landowners involved in western snowy plover management, including W. Ritchie, C. Burns, C. Stevenson, D. Lauten, T. Stein, and S. McKenzie. Funding was provided by an EPA STAR Grant (R833836) to SDH, PR, and EWS; an EPA STAR Graduate Fellowship (F13B20274) to RGB; and an OSU Provost's Distinguished Graduate Fellowship to RGB.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1791/full