

RESEARCH ARTICLE

Method for controlling invasive *Ammophila arenaria* in coastal dunes alters restoration trajectory

Lorraine S. Parsons^{1,2} , Savannah R. Fuqua³ , Michael K. Spaeth⁴, Benjamin H. Becker⁵

Coastal dune restoration often focuses on weed removal to reestablish native vegetation communities. Point Reyes National Seashore (PRNS) initiated large-scale dune restoration after becoming concerned about loss of dune and rare species habitat from spread of non-native *Ammophila arenaria* (European beachgrass). Two projects removed beachgrass from 146 ha of heavily invaded dunes using either mechanical removal or herbicide treatment. PRNS conducted pre- and post-restoration vegetation monitoring for 10 years post-implementation, evaluating success in (1) eradicating beachgrass and (2) reestablishing vegetation communities similar to native dunes in cover, diversity, and species composition. Both methods eradicated beachgrass with annual retreatment. However, they were less successful in rebuilding vegetation communities with comparable native species cover and/or richness. Mechanical removal areas remained largely barren expanses of sand that struggled to support native plants except for a rare perennial, Tidestrom's lupine (*Lupinus tidestromii*). Tidestrom's lupine and other rare plants now number in the hundreds of thousands. Conversely, herbicide-treated backdunes were dominated by standing dead beachgrass that resisted decomposition even after 7 years, which hampered native and rare plant establishment. Delayed decomposition was less of an issue in herbicide-treated foredunes, because sand overwash buried necromass. Restored areas also contended with subsequent invasion by secondary plant invaders. By 2021, only older herbicide-treated backdunes, and to a lesser extent, mechanical backdunes, showed signs of convergence with native dunes. Successful convergence may be hindered by lingering physical and microbial legacy effects of beachgrass invasion and treatment method. Adaptive restoration may be needed to counter effects and improve project success.

Key words: delayed decomposition, herbicide, invasive plant, legacy effect, microbia, rare plant

Implications for Practice

- Large-scale restoration projects involving non-native invasive plant removal need to be designed with potential legacy effects in mind. Weed removal alone may be insufficient to achieve objectives. Additional measures may be required to achieve successful restoration.
- Project managers need to acknowledge the threat of secondary invasion by new weeds early on and be prepared to quickly respond to this threat. Managers should prioritize removal of secondary invaders that act as facilitators for other invaders.
- Retreatment is critical to success of restoration and will need to be acknowledged as a long-term investment of resources.
- Planning should prioritize removing non-natives from relatively intact systems or recently invaded areas where legacy effects may have not yet fully developed.

Introduction

Coastal dunes worldwide have been adversely impacted by development, mining, and non-native invasive plant species introduction (Lithgow et al. 2013; Martínez et al. 2013; Nordstrom 2021). Concerns about degradation of coastal dunes and subsequent impairment or loss of ecosystem functions such as recharging groundwater and providing rare plant and wildlife

habitat (Martínez et al. 2013) have prompted numerous efforts worldwide to restore these systems. With non-native plant invasion being one of the primary impacts (Lithgow et al. 2013), many coastal dune restoration efforts have focused on invasives removal (Wiedemann & Pickart 1996; Novoa et al. 2014; Konlechner & Lord 2015). One of the most common coastal dune invaders worldwide is *Ammophila arenaria* (European beachgrass), a native of northern Europe (Weber 2003). This is particularly true on the west coast of North America, where beachgrass was planted for soil stabilization in the late 1800s and is now present in most dune systems between

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Los Angeles and British Columbia (Breckon & Barbour 1974). Despite European beachgrass being a worldwide invasives issue, until the early 2000s, most projects aimed at controlling or eradicating beachgrass were restricted to the west coast of North America (Wiedemann & Pickart 1996; Zarnetske et al. 2010; Darke et al. 2016) or New Zealand (Hesp & Hilton 2013).

Many past dune restoration projects have tacitly assumed that weed eradication alone would be sufficient to restore natural ecosystems and associated functions. However, restoration projects that rely entirely on invasives removal can be fraught with unexpected complications (Suding et al. 2004; Corbin & D'Antonio 2012; Konlechner & Lord 2015). Past invasive plant control projects conducted in grasslands, wetlands, forest, and shrubland habitats have found that, while most have been successful at reducing invasive plant abundance, they were less successful in reestablishing natives (Reid et al. 2009; Kettenring & Adams 2011). For many of these projects, long-term retreatment has been necessary to prevent primary invaders from reestablishing and new or secondary invaders from becoming established (Reid et al. 2009; Kettenring & Adams 2011), some of which may pose more risk to ecosystem health than primary ones (Pearson et al. 2016). Similar issues have plagued previous dune restoration projects, with post-restoration studies citing lower native plant cover/diversity (Zarnetske et al. 2010; Konlechner & Lord 2015; Pickart et al. 2021); increased abundance of secondary invaders (Novoa et al. 2014; Konlechner & Lord 2015); and need for frequent retreatment to prevent reinvasion (Hesp & Hilton 2013; Novoa et al. 2014; Darke et al. 2016).

Impacts of invasives may be more pervasive than simple displacement of native species (Novoa et al. 2014; Konlechner & Lord 2015). Once established, invasives can alter soil chemistry and microbiota, as well as insect-plant relationships (Bartomeus et al. 2008; Gornish et al. 2020; Pellegrini et al. 2021). Dune invasives such as *Carpobrotus edulis* (iceplant) and *Lupinus arboreus* (bush lupine) have well-documented effects on soil chemistry (Conser & Connor 2009; Novoa et al. 2014; Hetherington & Wilson 2019) and microbiota (de la Peña et al. 2010; Badalamenti et al. 2016). Indirect effects of beachgrass invasion have not been as well-studied, but in northern California systems, invasion appears to affect both soil chemistry and microbiota (Parsons et al. 2020b; Parsons & Becker 2021), as well as natural foredune structure through aggressive sand accretion (Wiedemann & Pickart 1996).

Some of these invader-mediated impacts persist long after invasives are removed, creating so-called legacy effects (Cuddington 2011; Corbin & D'Antonio 2012; Holmes et al. 2020). Removal of invasive *Phalaris aquatica* from California sagebrush and *Acacia saligna* from South African shrublands created changes in soil microbiota or chemistry, respectively, that persisted for at least 7–10 years (Nsikani et al. 2017; Pickett et al. 2019). A meta-analysis evaluating persistence of legacy effects for 42 studies involving restoration of agricultural old fields found that soil conditions and soil invertebrate richness and abundance had largely not converged with those of reference ecosystems even 50 years following

restoration (Parkhurst et al. 2022). Thus, invasives removal may not be sufficient to reverse these broader legacy effects that may hinder or even preclude successful ecosystem restoration (Reid et al. 2009; Corbin & D'Antonio 2012; Holmes et al. 2020). Persistent legacy effects for soil chemistry and microbiota have been reported in dune soils where iceplant, bush lupine, and beachgrass have been removed (Novoa et al. 2014; Hetherington & Wilson 2019; Parsons et al. 2020b).

Point Reyes National Seashore (PRNS) is a unit of the U.S. National Park Service (NPS) located on the northern California coast. By 2009, more than 60% of the park's roughly 890 ha of coastal habitat was dominated by beachgrass and iceplant (NPS 2009), which were believed to have been planted in the early to mid-1900s by previous landowners. In 2011, PRNS initiated dune restoration in a 104 gross-hectare area south of Abbotts Lagoon dominated by European beachgrass using both mechanical removal and herbicide treatment. In 2015, PRNS expanded restoration southward into the adjacent 42 gross-hectare AT&T dunes, relying primarily on herbicide to eliminate beachgrass. Due to the abundance of native dune plants directly adjacent to restored areas, only limited active revegetation was performed.

PRNS undertook dune restoration efforts with the objective of removing non-native invasive plant species “to create conditions under which native plant and wildlife species can flourish,” including 11 threatened and endangered plant and animal species listed under the U.S. Endangered Species Act (NPS 2015). To determine whether the park had been successful in both removing weeds and expanding cover of native plants, PRNS implemented a pre- and post-restoration long-term vegetation monitoring program at Abbotts and AT&T in restored and target native dune communities. Up to 11 years of vegetation monitoring data now exist for Abbotts, with 4–6 years of data available for AT&T.

In this paper, we evaluate how successful mechanical removal and herbicide treatment have comparatively been at PRNS in both (1) eradicating primary invaders such as beachgrass and (2) reestablishing the appropriate target native dune vegetation community, which is, in many cases, strongly linked to habitat support functions for rare plants and wildlife at PRNS and other west coast U.S. dune systems (Zarnetske et al. 2010; NPS 2015).

Methods

Study Site

PRNS is located approximately 48 km north of San Francisco, California, U.S.A. (Fig. 1). Dunes at PRNS are composed of a modern largely continuous foredune ridge established by European beachgrass and a complex series of undulating back-dunes and depressions associated with older, mostly stabilized parabolic dunes.

The climate at Point Reyes is Mediterranean, with hot/dry summers and cool/wet winters. Coastal areas in California are cooler and have less intra-annual variability in temperature

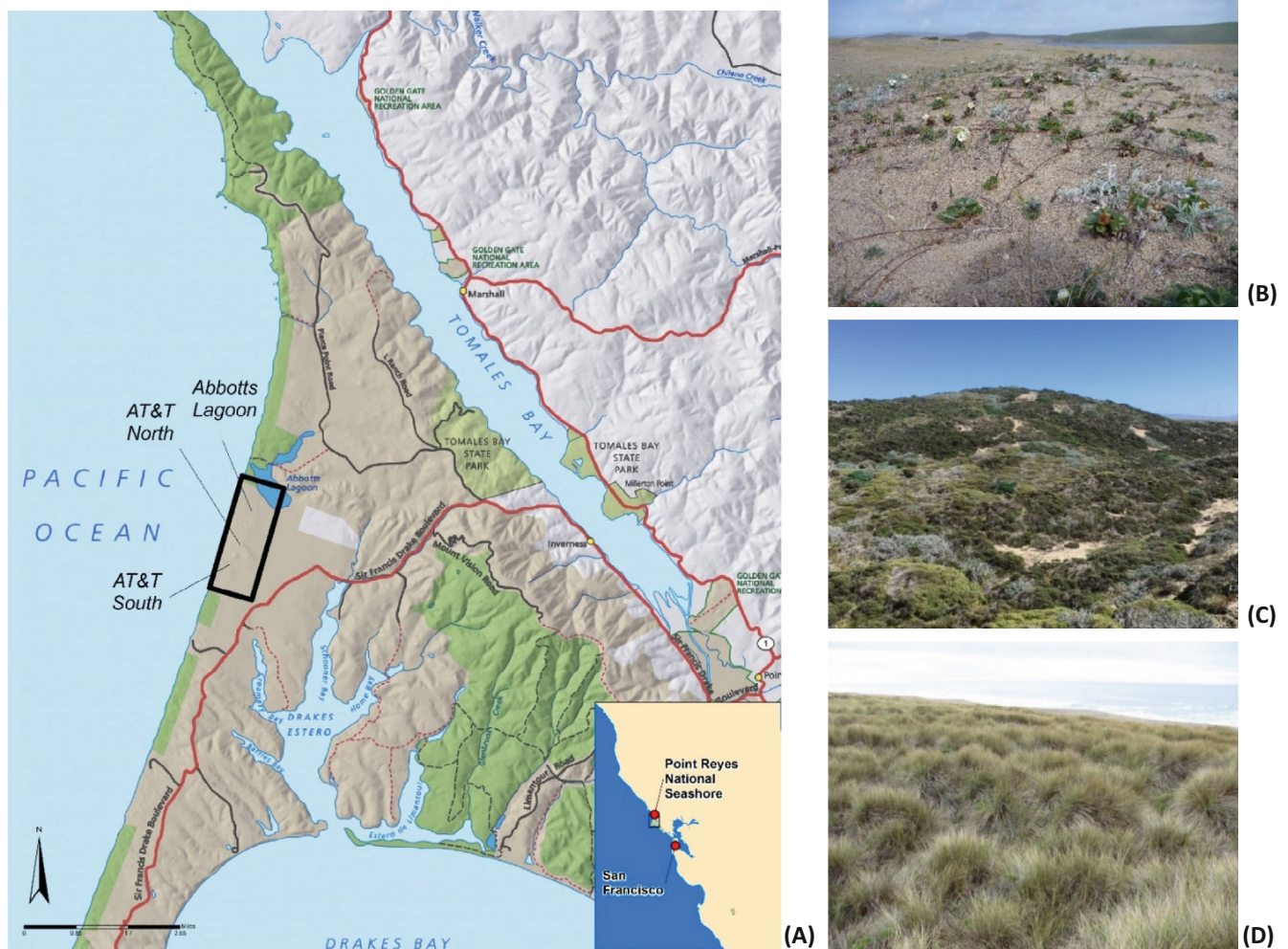


Figure 1. (A) Map of the study areas in Point Reyes National Seashore (PRNS), showing three sites (Abbotts Lagoon, AT&T North, and AT&T South) and location of PRNS along northern California coast; (B) sparsely invaded native Dune Mat; (C) sparsely invaded native Dune Scrub; and (D) heavily invaded dunes with European beachgrass.

than inland regions, with fog, winds, and salt spray being important climatic influences and nutrient sources for soils (Clayton 1972; Holton et al. 1991; Ingraham & Matthews 1995). Annual temperature averages 12.1°C, and precipitation near the project area averages 54 cm/year (2006–2021; WRCC 2021), although large interannual variability in rainfall exists.

Native dunes at PRNS represent a range of successional stages from early to mid-successional communities such as foredunes and native Dune Mat, often characterized as “yellow dunes,” to later successional ones such as backdunes (“gray” or “brown” dunes) and native Dune Scrub. Dune Mat (Fig. 1B) occurs closer to the ocean in foredunes or at lower elevations inland, while native Dune Scrub (Fig. 1C) is situated further inland (>300 m from ocean) in backdunes or higher elevations along the coast. Uninvaded foredunes and Dune Mat are sparsely vegetated, open sand habitats supporting herbaceous primary successional Dune Mat species such as *Elymus mollis* (American dunegrass), *Abronia latifolia* (sand verbena), *Calystegia soldanella* (beach morning glory), as

well as mid- to late-successional ones such as *Eriogonum latifolium* (coast buckwheat; Buck-Diaz et al. 2021). Dune Scrub is a dense, shrub-dominated habitat characterized by *Lupinus chamissonis* (chamisso lupine) and *Ericameria ericoides* (mock heather; Buck-Diaz et al. 2021), which at PRNS is often intermixed with *Baccharis pilularis* (coyotebrush) and bush lupine.

A range of invasion conditions exist within PRNS’ dunes from sparsely to moderately to heavily invaded, with the highly clonal nature of beachgrass (and iceplant) favoring eventual establishment of dense monocultures exceeding 77% invasives cover (Fig. 1D). Some highly invaded systems retain vestiges of Dune Mat or Dune Scrub that have only been very sparsely invaded despite being surrounded by beachgrass or iceplant for decades. With restoration, heavily invaded beachgrass dunes are expected to evolve into either Dune Mat (foredunes, lower elevation areas) or Dune Scrub (backdunes, higher elevation areas; Fig. 1B & 1C).

Concerned about loss of native dunes and associated rare plants and wildlife, PRNS embarked in 2001 on a restoration

program to remove beachgrass and, to a lesser extent, iceplant. By 2018, approximately 110 ha of invasive beachgrass and 11 ha of iceplant had been removed from invaded nearshore foredunes and inland backdunes at PRNS. Most of the park's beachgrass restoration efforts have focused on a combination of manual removal, mechanical removal, and chemical treatment. The park initially attempted manual removal to eradicate beachgrass, but had poor success, probably due partially to the fact that beachgrass rhizomes are extremely long (0.9–2.5 m; Parsons et al. 2020a).

PRNS eliminated European beachgrass at the Abbotts project area (122°57'33.46"W 38°6'36.272"N; Fig. 1) using first mechanical removal and later herbicide treatment, because mechanical removal was very costly and remobilized sands that buried adjacent native habitats and ranchlands. The subsequent AT&T project (122°57'51.737"W–38°5'47.147"N) primarily relied on herbicide treatment to eliminate beachgrass (Fig. 1). Mechanical removal at Abbotts in 2011 totaled 30.0 net hectares of foredunes and backdunes and involved use of excavators and bulldozers to invert or “flip” the surface 1–1.5 m of the most rhizome-contaminated soils with less-contaminated soils 2–3 m below the soil surface (Table 1). When possible, areas or “pockets” within dense beachgrass stands supporting native dune plants were not excavated. Herbicide was used to treat 20.5 net hectares at Abbotts primarily in 2012 (although foredunes and some backdunes were treated in 2011); 15.1 net hectares at AT&T North in 2016; and 6.9 net hectares at AT&T South in 2018 (Table 1). Backdunes represented more than 70% of herbicide treatment areas at Abbotts and AT&T North. Chemical treatment was performed using backpacks with a single nozzle wand and focused spraying onto beachgrass of 1% imazapyr (Habitat); 2% glyphosate (Roundup Custom);

1.5% modified vegetable oil surfactant (Competitor); and 1% blue dye (various manufacturers). Native plants were avoided to the maximum extent practicable. Herbicide retreatment has been performed annually. As both systems incorporate sparsely invaded native dune areas that serve as propagule sources for adjacent restored areas, PRNS did not perform active revegetation, except for limited transplanting of American dunegrass.

Vegetation Monitoring

Dunes were stratified using restoration status, method, and successional status for random selection of 2 × 1-m vegetation monitoring plot locations at Abbotts and AT&T using ArcGIS (ESRI, Redlands, CA, U.S.A.). At Abbotts, plots were installed in mechanical foredunes/backdunes, herbicide-treated backdunes, and native Dune Mat (Table 1). A few herbicide-treated foredune plots were established later at Abbotts in 2019 (Table 1). At AT&T, plots were established in foredune/backdune areas chemically treated in 2016 (North) and 2018 (South) and native Dune Scrub (North; Table 1). Fewer plots were established in foredunes due to their smaller areal extent. Plots were monitored prior to restoration and annually thereafter, generating 9–10 years of post-restoration data for Abbotts and 3–5 years for AT&T.

We used a 2 × 1-m PVC quadrat divided into 10 × 10-cm grids for cover estimation by point-intercept, with a range of 86–171 crosspoints sampled depending on habitat (i.e., more points monitored in sparsely vegetated habitats). Plant species (alive and dead) were recorded once regardless of the number of “hits” at a particular crosspoint, along with functional groups such as bareground, thatch (intact dead beachgrass stems >10 cm), and detritus (litter <10 cm). Plants were grouped into

Table 1. Summary of coastal dune restoration areas and approaches in northern areas of Point Reyes National Seashore (PRNS) and associated pre- and post-restoration vegetation monitoring effort and statistical analysis approach. Restoration type refers to mechanical removal or herbicide treatment of *Ammophila arenaria* (European beachgrass) in heavily invaded dunes. Successional stage refers to foredune (Fore) or backdune (Back). Monitoring data show the year of the initial treatment (Restoration Year), the number of years of post-restoration monitoring, and number of monitoring plots. Analysis summarizes the analytical approach, including whether analyses of pre- versus immediate post-restoration were performed (Yes “Y” or No “N”). Analysis group indicates which sites were analyzed together—mechanical sites (M), herbicide foredune sites (HF), and herbicide backdune sites (HB)—for analysis of intermediate and long-term changes in vegetation data collected from primarily odd-numbered monitoring years. Habitat convergence analyses involved comparisons of 2021 post-restoration monitoring data with data from target native habitats, either Dune Mat or Dune Scrub. NA, not applicable.

	Site Characteristics				Monitoring			Analysis		
	Site Name	Restoration Type	Successional Stage	Net Area (ha)	Restoration Year	Years		Pre-/Post-Analysis?	Analysis Group	Convergence Type
						Monitor (Postrest.)	# Plots			
Restoration sites heavily invaded by European beachgrass	Abbotts	Mechanical	Fore	8.8	2011	10	12	Y	M	Dune Mat
	Abbotts	Mechanical	Back	11.3	2011	10	14	Y	M	Dune Mat
	Abbotts	Herbicide	Fore	4.0	2011	2	4	N	HF	Dune Mat
	Abbotts	Herbicide	Back	16.5	2012	9	13	Y	HB	Dune Scrub
	AT&T-N	Herbicide	Fore	4.1	2016	5	4	Y	HF	Dune Mat
	AT&T-N	Herbicide	Back	11.0	2016	5	13	Y	HB	Dune Scrub
	AT&T-S	Herbicide	Fore	4.3	2018	3	2	Y	HF	Dune Mat
	AT&T-S	Herbicide	Back	2.6	2018	3	4	Y	HB	Dune Scrub
Target sites sparsely invaded native dunes	Abbotts	NA	Fore, Back	20.8	NA	10	23	NA	M, HF	Dune Mat
	AT&T-N	NA	Back	4.1	NA	3	17	NA	HB	Dune Scrub

native, non-native, and secondary invader species. Native and non-native species richness was calculated from the total number of native and non-native species present in 2-m² plots regardless of whether “hit” directly by intercept sampling with the total divided by 2. Diversity was assessed using Shannon–Weiner diversity index and Pielou species evenness index.

Statistical Analyses

Cover and Diversity. We addressed if restoration met our primary objectives: (1) eradication of European beachgrass, and (2) establishment of vegetation communities similar to target native dune habitats. In addition to beachgrass cover, 10 other vegetation-related cover, richness, and species diversity dependent variables were analyzed. These included native, non-native, and secondary invader cover; bareground, dead beachgrass, and detritus cover; native and non-native species richness; and species diversity and evenness. All analyses included distance from the ocean as a covariate, because distance is often linked to successional stage and can influence dependent variables. To assess beachgrass eradication success, we compared pre (year 0)- and immediate post (year 1)-restoration using treatment (mechanical, herbicide) and time as fixed effect factors.

For evaluating convergence of restored areas with target habitats, we split analyses based on appropriate native target habitat (Dune Mat, Dune Scrub) with herbicide-treated backdunes grouped with later successional Dune Scrub and herbicide-treated foredunes and mechanical foredunes and backdunes grouped with earlier successional Dune Mat (Table 1). Convergence was assessed for odd-numbered monitoring years starting at post-restoration year 3 through year 9 (Abbotts herbicide) or 10 (Abbotts mechanical) using a fixed effect factor combining time (since treatment), treatment status (restored, native), and, for herbicide-treated backdunes, site (i.e. Abbotts, AT&T North, AT&T South). AT&T was restored more recently, so only post-restoration years 3 and 5 are available for convergence analyses (Table 1). For target habitats, we relied on pre-restoration data (2010) for Dune Mat, as sand remobilization from mechanical removal affected adjacent native dune areas after restoration: Dune Scrub data came from 2021. Because herbicide-treated foredunes at Abbotts were only monitored during later monitoring years, convergence analyses were run separately for Abbotts and AT&T foredunes using only 2021 data (Table 1).

We performed multivariate and univariate analyses using the relevant fixed effect factors. When group dispersion was appropriately homogenous (evaluated using betadisper function), we conducted permutational multivariate analysis of variance (PERMANOVA) for the 11 cover, richness, and diversity variables (PERMANOVA; vegan package; Oksanen et al. 2022). To further evaluate change in dependent variables, we used generalized linear model (GLM), employing alternative distributions when necessary using bestNormalize (Peterson 2022) packages. The final model was based on residual plots, Akaike information criteria value, and data dispersion. When data did not meet parametric assumptions, we conducted the non-parametric randomization approach Permutation (lmperm; Wheeler & Torchiano 2016). Post hoc pairwise comparisons

were assessed with pairwiseAdonis (Martinez 2020) for PERMANOVA; emmeans (Lenth et al. 2022) for GLM; or pairwise permutation in rcompanion package (Mangiafico 2023) for Permutation, with adjustment for multiple testing using false discovery rate method (Benjamini & Hochberg 1995). Results of main and conditional effects of statistical analyses are presented in the text, while results of post hoc pairwise comparisons are presented in Tables S1–S3. Means and SE for variables analyzed are presented in Tables S4 and S5.

Vegetation Species Composition. To better understand changes in species composition following restoration and convergence with target communities, we conducted unconstrained ordination with non-metric multidimensional scaling (NMDS; vegan package; Oksanen et al. 2022) on species data from Abbotts areas treated mechanically and with herbicide from post-restoration year 10 and year 9 (2021), respectively, and from adjacent Dune Mat. A separate NMDS analysis was run that specifically evaluated herbicide-treated backdunes at Abbotts (year 9), AT&T North (year 5), and AT&T South (year 3) in 2021 with Dune Scrub. Analysis of similarities (ANOSIM) (vegan package) was performed to evaluate whether NMDS group differences were significant. To identify species associated with restored and target habitats, we applied a Dufrêne–Legendre indicator species analysis (ISA; indispes package; De Cáceres 2022) to data used in the 2021 NMDS analyses described earlier.

All analyses were done in R (R Core Team 2022; version 4.1.3).

Results

Beachgrass Eradication and Immediate Post-Restoration Changes

Both mechanical removal and herbicide treatment performed extremely well in eradicating European beachgrass, although there appeared to be potentially an interaction between treatment method and time (pre/post; GLM, $\beta = 0.400$, $SE = 0.176$, $t = 1.927$, $p = 0.057$). The initial year following treatment, beachgrass cover at Abbotts dropped from 79.5 to 0% in mechanical areas and from 81.6 to 1.9% in herbicide treatment areas. At AT&T, beachgrass cover fell after herbicide treatment from 77.3 to 3.7%. Cover of all non-native species—most of which was beachgrass prior to restoration—also dropped after restoration (GLM, $\beta = 1.41$, $SE = 0.11$, $t = 12.70$, $p = 0.001$; Fig. 2A & 2B). For all other variables except native cover and Shannon diversity, there was a significant interaction between treatment type and time (GLM, all $\beta > -1.196$, all $SE < 0.311$, all $t > -6.858$, all $p < 0.05$), with changes following mechanical removal being more extreme (Table S1). There were no changes in cover of bareground (adj. $p = 0.497$; Fig. 2G) or detritus (adj. $p = 0.114$) or in non-native species richness (adj. $p = 0.156$) in herbicide-treated backdunes at Abbotts or AT&T immediately after restoration (Table S2). In contrast, mechanical removal of beachgrass through burial affected almost every cover-, richness-, and diversity-related variable

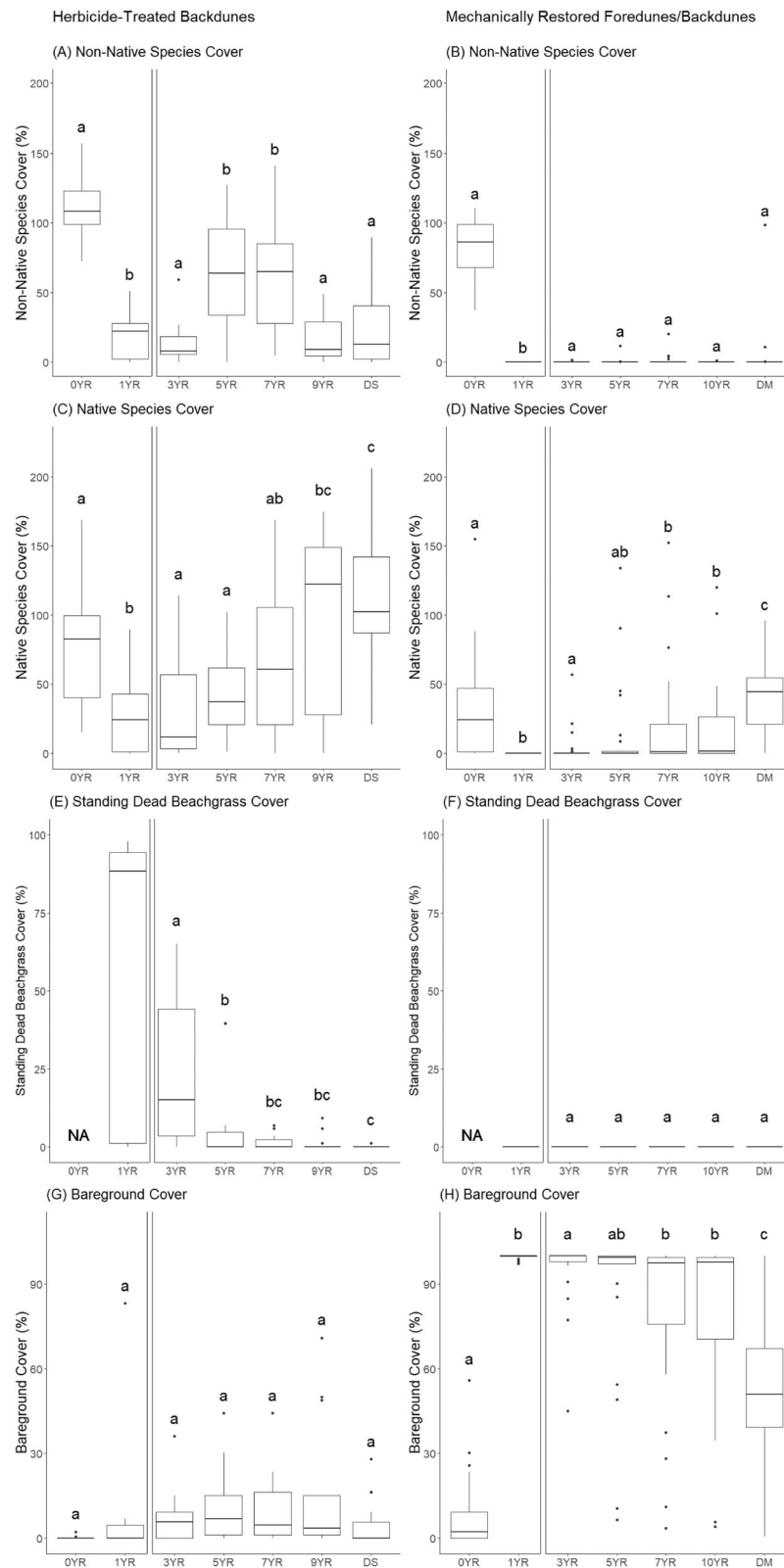


Figure 2. Boxplots displaying the median and 25th and 75th percentiles for selected cover (%) data for the Abbotts herbicide-treated backdunes (BD) and mechanically restored foredune (FD) and BD areas from prerestoration (0YR) through 9–10 years postrestoration. Significant differences ($p < 0.05$) for analyses involving (1) pre- and immediate postrestoration (0YR–1YR) and (2) postrestoration (3YR to 9 or 10YR) and convergence with target native habitats—Dune Scrub (“DS”) and Dune Mat (“DM”)—are denoted by different lowercase alphabet letters. NA=not applicable, as variable not monitored that year.

(all $p/\text{adj. } p < 0.05$; Table S1; Fig. 2). Unlike mechanical removal where beachgrass burial instantaneously boosted bareground cover by more than 1,000% ($\bar{X} = 99.4\%$), bareground climbed only 3.3% within all herbicide-treated areas immediately post-restoration (Fig. 2G & 2H). Dead beachgrass cover immediately post-restoration was non-existent in mechanical areas (Fig. 2F), but ranged in herbicide-treated areas between 62.3% at Abbotts (Fig. 2E) and 79.3% at AT&T. Despite efforts to avoid nontarget species during herbicide application and mechanical removal (i.e. not excavating native dune “pockets” within beachgrass), native species cover (GLM, $\beta = 0.80$, $\text{SE} = 0.15$, $t = 5.22$, $p = 0.001$; Fig. 2C & 2D) and richness declined immediately after treatment, with declines in native species richness much greater in mechanical areas due to extensive plant burial (adj. $p < 0.0001$; Tables S1, S2, & S4). Annual retreatment helped to maintain post-restoration beachgrass cover low in subsequent years, averaging 0% in mechanical areas at Abbotts and less than 2.3% in herbicide treatment areas at Abbotts and AT&T.

Convergence with Target Native Dune Communities

Mechanical Removal. Bareground cover remained high ($\bar{X} = 87.9\%$), and native species cover ($\bar{X} = 3.9\%$) and richness ($\bar{X} = 0.3$ species [spp]/m²) remained low for the first 3 years post-restoration (Fig. 2D & 2H). Starting in year 5, however, native species establishment accelerated, with native species richness (0.9 spp/m²; adj. $p = 0.012$) and Shannon–Weiner diversity (0.30; adj. $p = 0.049$) climbing in year 7 (Table S1). Native species cover also increased in later years, reaching 20.0% in year 7 (adj. $p = 0.020$; Fig. 2D; Table S1). Bareground cover continued to be high even by year 10, particularly in fore-dune areas, although it did drop somewhat in years 7 and 10 relative to year 3 (all adj. $p = 0.029$; Tables S1 & S4; Fig. 2H).

In addition to native species, secondary invaders such as *Cakile maritima* (European searocket) also began encroaching into mechanically restored dunes, with abundance skyrocketing in 2016. Additional secondary invaders included iceplant and *Sonchus* species (sow thistle). The proliferation of secondary invaders was not reflected in non-native species cover (lmPerm, $df = 4$, $p = 0.232$; Fig. 2B) or richness (all adj. $p > 0.19$; Table S1); high spatial variability in secondary invader abundance may have obscured our ability to detect this change.

Ten years post-restoration, mechanical areas have not fully converged with the target native community, Dune Mat (PERMANOVA, $df = 1$, $F = 6.34$, $p = 0.002$, $r^2 = 0.12$; beta-disper, $F = 1.61$, $p = 0.21$). Apart from non-native species cover, detritus cover (adj. $p = 0.397$), and non-native species richness (adj. $p = 0.328$), mechanical plots showed little statistical equivalence with native plots by year 10 (Table S1).

In terms of species composition, mechanical plots showed overlap with Dune Mat plots in year 10, although some remained distinct (NMDS, final stress = 0.06, Bray–Curtis, three-dimensional (3D); Fig. 3). Mechanical plots showing overlap were largely in backdune areas that developed a more characteristic Dune Mat species assemblage (Fig. 1B), while non-overlapping plots corresponded to those in foredunes with

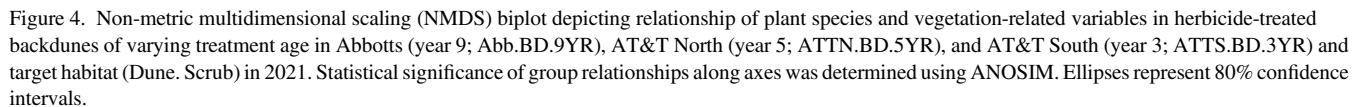
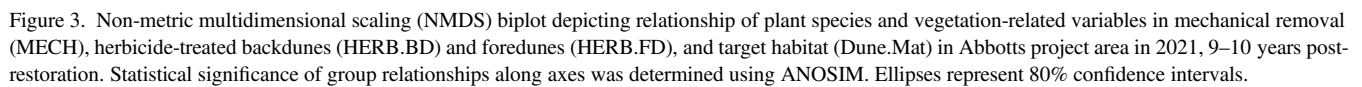
higher bareground cover that are still struggling to establish vegetation (Fig. 3). Axis 1 highlighted differences between herbicide-treated backdune and other plots, as well as convergence of mechanical removal/herbicide-treated foredune plots with Dune Mat (ANOSIM, $p = 0.0001$; Fig. 3).

Based on ISA, mechanically restored areas continued to be differentiated from other Abbotts areas based on bareground cover ($p < 0.05$), with Dune Mat characterized by higher abundance of beach morning glory, *Monardella sinuata* ssp. *nigrescens* (curly leaved monardella), and *Poa douglasii* (Douglas’ blue grass; all $p < 0.05$).

Herbicide Treatment—Backdunes. Herbicide-treated backdunes diverged markedly from mechanically restored areas in terms of post-restoration outcomes. In stark contrast to mechanical areas, bareground cover in herbicide-treated backdunes at Abbotts was minimal following restoration and increased only incrementally over time (Fig. 2G). While it seemingly doubled between year 3 (7.8%) and year 9 (16.6%), this change was not significant (adj. $p = 0.585$; Table S2).

Bareground remained low following restoration because cover of dead beachgrass (Fig. 2E) and, to a much lesser extent, iceplant and shrubs such as bush lupine and coyotebrush remained very high. Herbicide treatment resulted in extensive standing dead beachgrass or necromass in backdunes that decomposed very slowly. By year 3 following restoration, standing dead beachgrass accounted for between 22.7 (Abbotts; Fig. 2E) and 37.6% (AT&T North) cover, which represented about 50% of the necromass present immediately after treatment (Tables S4 & S5). By year 5, necromass had dropped considerably at Abbotts relative to year 3 ($\bar{X} = 4.7\%$ cover; adj. $p = 0.004$; Fig. 2E), but not at AT&T North ($\bar{X} = 30.5\%$ cover; adj. $p = 0.260$; Table S2). Nine years following restoration, standing dead beachgrass at Abbotts was infrequent ($\bar{X} = 1.3\%$), although scattered clumps still persisted (Fig. 2E). Once it finally started to decompose, dead beachgrass transformed into thick layers of large pieces of litter or “thatch” (>10 cm). Thatch was not monitored during initial years, but even by year 7, thatch and, separately, detritus still accounted for 8.8 and 53.3% cover, respectively, at Abbotts, with thatch cover dropping to 2.0% by year 9. At AT&T, where thatch was monitored from the onset, it averaged between 22.9 (year 3, AT&T South) and 28.6% (year 5, AT&T North).

As beachgrass represented a large percentage of invaders present, non-native cover at Abbotts plummeted after restoration, averaging 13.6% in year 3, but, by year 5, it had jumped to 58.3% (adj. $p = 0.001$; Table S2; Fig. 2A). Non-native plant species richness also appeared to double at Abbotts between years 3 and 5, although this was marginally significant (adj. $p = 0.058$; Table S2). This dramatic increase in non-native cover in year 5 (2017) largely came from proliferation of secondary invaders (50.8%; adj. $p = 0.0001$; Table S2). Restored backdunes attracted a different suite of secondary invaders than mechanical areas. European searocket was largely non-existent, but non-native annuals such as *Senecio sylvestris* (common groundsel), *Bromus diandrus* (ripgut brome), and *Festuca*



While native species were avoided during treatment, beachgrass often grew intermixed with them, complicating efforts to preclude impacts. At Abbots, native species cover in year 3 (30.6%) averaged less than half that recorded pre-restoration (70.8%; Fig. 2C). In subsequent years, native cover steadily climbed, particularly in years 7 (64.1%) and 9 (95.5%), although only the latter was significant (adj. $p = 0.004$; Table S2; Fig. 2C). Increases in native species richness (all adj. $p \leq 0.024$) and Shannon diversity (all adj. $p \leq 0.037$) during this same period were significant, but less dramatic (Tables S2 &

S4). Native cover at AT&T was also impacted by treatment, dropping 41–82% immediately post-restoration, and no significant rebound occurred between years 3 and 5, at least at AT&T North (adj. $p = 0.625$; Table S2).

Multivariate analyses of cover, richness, and diversity data from these sites point to convergence with the target native community, Dune Scrub, occurring at least for Abbotts by year 9 (PERMANOVA, $df = 7$, $F = 4.53$, $p = 0.001$, $r^2 = 0.25$; pairwise, adj. $p = 0.62$) and possibly even by year 7 (adj. $p = 0.11$). All other year/site combinations showed continued divergence from native vegetation conditions (all adj. $p < 0.03$) and a varying amount of overlap with other backdune herbicide treatment year/site combinations (all adj. $p > 0.05$).

By year 9, herbicide-treated backdunes at Abbotts showed no significant differences from Dune Scrub for almost all measures of cover, richness, and diversity (all adj. $p > 0.144$; Table S2). Non-native species richness at Abbotts reached equivalence with target habitats by year 7 (adj. $p = 0.091$), while Shannon diversity achieved equivalence even earlier (year 5; adj. $p = 0.317$; Table S2). At AT&T North, the Shannon index and non-native species cover also quickly converged with that of Dune Scrub, becoming equivalent by year 3 (adj. $p = 0.317$) and year 5 (adj. $p = 0.623$), respectively (Table S2). In 2021, no significant differences were detected between the target habitat and any treatment area for cover of secondary invaders, bareground, and detritus and for non-native species richness and evenness (all adj. $p > 0.09$; Table S2). Only native species richness continued to differ between all treatment areas and Dune Scrub in 2021 (all adj. $p \leq 0.004$; Table S2).

Consistent with PERMANOVA analysis results, Abbotts backdunes showed strong overlap with Dune Scrub by year 9 (NMDS, final stress = 12.10, Bray–Curtis, 3D; Fig. 4). Axis 1 provided most of the separation between Abbotts treated backdunes/Dune Scrub and AT&T treated backdunes (ANOSIM, $p = 0.0001$; Fig. 4). Some Abbotts plots diverged considerably from Dune Scrub communities: These were closer to the foredunes spatially and had higher bareground cover (Fig. 4; middle- to upper right).

Species assemblages in Dune Scrub differentiated from restored backdunes based on higher abundance of chamisso lupine and coast buckwheat (ISA, all $p < 0.05$). Abbotts treated backdunes supported more bush lupine and ripgut brome than recently treated backdunes, which had higher cover of dead beachgrass, dead coyotebrush, thatch, and fescue brome (ISA, all $p < 0.01$).

Herbicide Treatment—Foredunes. Multivariate analyses suggest possible convergence of both Abbotts (year 9) and the younger AT&T North (year 5) foredunes with native Dune Mat in 2021 (PERMANOVA, $df = 3$, $F = 4.36$, $p = 0.001$, $r^2 = 0.36$; pairwise, all adj. $p > 0.07$). Convergence appeared to occur more rapidly in herbicide-treated foredunes than backdunes, as even younger treated areas at AT&T were already statistically equivalent with target habitat for cover of native species (ImPerm, $df = 3$, $p = 0.967$), non-native species (ImPerm, $df = 3$, $p = 0.627$), and secondary invaders (ImPerm,

$df = 3$, $p = 0.927$), as well as Shannon diversity (ImPerm, $df = 3$, $p = 0.133$). Convergence unfolded more slowly for certain variables, as only older treated foredunes at Abbotts showed equivalence with Dune Mat for cover of bareground (ImPerm, adj. $p = 0.971$), dead beachgrass (ImPerm, adj. $p = 0.079$), and detritus (ImPerm, adj. $p = 0.094$; Table S3). However, only AT&T North foredunes supported similar numbers of native species to target habitats (ImPerm, adj. $p = 0.431$; Table S3). In terms of species assemblages, NMDS analysis showed herbicide-treated foredune plots at Abbotts strongly overlapping Dune Mat ones, although the small sample size may conflate convergence (Fig. 3). Bareground represented the only significant indicator for treated foredunes at Abbotts relative to other Abbotts areas (ISA, $p = 0.005$). In year 9, bareground cover averaged 59.5% in foredunes at Abbotts compared to 16.6% in backdunes, with foredunes subject to frequent sand overwash from the adjacent beach.

Discussion

The goal of most restoration projects is to create systems that closely resemble native ones both in terms of appearance and function. To achieve that goal, two primary objectives must be met. First, invasive non-native plants that have impaired habitat quality need to be successfully eradicated and prevented from reestablishing. Second, plant species characteristic of native ecosystems need to be successfully reestablished. While these objectives are focused more on surficial attributes of restoration success such as absence of threats (e.g. invasives), species composition, and structural diversity (Gann et al. 2019), the expectation is that, once they are realized, restored areas should over time develop higher-order ecosystem functions and services characteristic of natural systems such as rare species support and sea level rise protection.

At PRNS, both mechanical removal and herbicide treatment performed extremely well in almost instantaneously eliminating European beachgrass, with retreatment needs greatly reduced generally by year 3. The magnitude of this accomplishment cannot be overstated, given how entrenched beachgrass was in these areas and adjacent dunes. However, while the battle against primary invaders appeared largely won, a new battle ensued against a much larger suite of secondary invader species, many of whom had subsisted at low abundance prior to restoration. “Sleeper weeds” such as European searocket often linger in this seemingly innocuous lag phase until conditions are optimal and then rapidly explode (Groves 1999), fueled in some instances by a change in biotic or abiotic resources or landscape disturbance. Often, sleeper weeds are ones such as European searocket and European beachgrass that function within their native range as primary successional species, uniquely adapted to colonizing areas with frequent natural disturbance such as shorelines (Davy & Figueroa 1993). Ecosystem restorations can ignite an explosion in abundance of disturbance-adapted species, as the restoration process increases resource availability (Kettenring & Adams 2011). Our inability to bring searocket under control in the Abbotts mechanical areas, if not the other project areas, during its rapid expansion phase points to this

species is likely becoming a permanent fixture and a long-term control issue at Abbotts due to its prolific seedbank. More troublesome yet is that some secondary invaders likely facilitate others: In PRNS dunes, nitrogen (N)-fixing bush lupine is often strongly associated with iceplant and New Zealand spinach (Parsons et al. 2020a). While this synergetic association may not lead to an “invasional meltdown” (Simberloff 2006) or full-scale re-invasion of restored dunes by either primary or secondary weeds, it is certainly concerning and illustrative of the challenges posed in trying to restore entire ecosystems, particularly those that were dominated by invasives for decades.

Encroachment by secondary invaders complicated efforts to re-create native dune ecosystems. As these new weeds are not as tenacious as European beachgrass (or iceplant) in terms of forming dense monocultures, native species have been able to expand within restored dunes. However, 10 years after restoration was implemented at Abbotts, some of the restored areas have still not converged with their appropriate target native habitat in terms of native plant cover, richness, diversity, and species assemblages, although herbicide-treated backdunes do appear to be converging with their target habitat, Dune Scrub. In some senses, mechanical removal may have been too extreme in terms of resetting the successional clock, while herbicide treatment, at least in backdune areas, was not extreme enough. With mechanical removal, all non-native—and native—species were eliminated instantaneously, leaving vast expanses of open sand that remained largely unvegetated for years due to the vagaries of climate and other factors. Massive sand remobilization fostered dune processes and soil conditions that were initially too primordial except for the hardiest of pioneering species such as the rare *Lupinus tidestromii* (Tidestrom’s lupine), a N-fixer (Parsons et al. 2020a). Tidestrom’s lupine appears to have facilitated eventual establishment of other native species by year 7, at least in the mechanical backdunes (Parsons et al. 2020a), leading to an increase in species richness, although not cover, of natives.

In stark contrast, herbicide treatment left vast stands of dead beachgrass and, to a much lesser extent, other plant biomass that seemed impervious to decomposition. Based on data from all PRNS dune restoration projects, it takes at least 2–3 years for standing dead beachgrass to decompose to approximately 50% of pre-treatment live cover (Parsons et al. 2020a). Between the standing dead biomass and thick thatch, there is little opportunity in terms of bareground to allow for native plant colonization, including rare plant species such as Tidestrom’s lupine. Rare plant establishment within herbicide-treated areas has been extremely slow and limited to open areas within treated beachgrass stands (Parsons et al. 2020a). The only exception to delayed decomposition and native reestablishment occurred in herbicide-treated foredunes where beach overwash blanketed dead beachgrass culms and thatch with new sand that provided substrate for natives (and secondary invaders) to more quickly gain hold.

This persistent necromass phenomenon following herbicide treatment has not been well-documented, even though it has occurred in other beachgrass removal projects in northern and central California (e.g. Manchester, Año Nuevo; T. Fuller 2022, California Department of Parks and Recreation [CDPR],

Mendocino, CA, U.S.A., personal communication; T. Hyland 2022, CDPR, Santa Cruz, CA, U.S.A., personal communication). Findings of other studies generally point to comparatively speedier decomposition of invasives relative to natives: A meta-analysis of 94 studies conducted in various habitats found that invasion increased litter decomposition rates by 117% (Liao et al. 2008). This meta-analysis did not incorporate studies in which herbicide treatment was performed, but for studies that did, decomposition of dead aboveground biomass was not delayed (Reynolds et al. 2017; Robichaud & Rooney 2021), although dead rhizomes in one instance persisted for at least 6 years (Reynolds et al. 2017).

Long-term persistence of standing dead biomass and thatch could be regarded as a physical legacy effect that impedes evolution of herbicide-treated backdunes into target habitats. While belowground effects are most commonly documented, invasive species can also exert effects by physically changing ecosystems (Cuddington 2011). Dense stands of live beachgrass usurp space for natives and suppress plant germination by preventing light from reaching the soil surface, and these invasive impacts can persist after restoration when decomposition of standing dead biomass and litter is delayed (Facelli & Pickett 1991).

Issues with delayed beachgrass decomposition and native dune convergence may be strongly linked to legacy effects of both invasion and treatment approach on soil microbia and chemistry. Research recently conducted at PRNS within the Abbotts-AT&T study areas has shown that beachgrass invasion alters both soil microbia and chemistry and that some effects persist after restoration (Winsemius et al. 2015; Parsons et al. 2020b; Parsons & Becker 2021). Even mechanical removal, which should have seemingly negated the potential for legacy effects, was not immune to problems, as treatment also affected soil microbia and chemistry (Winsemius et al. 2015; Parsons et al. 2020b; Parsons & Becker 2021). Of 15 soil chemistry variables exhibiting “treatment” effects—changes associated with treatment method, not invasion legacy—13 occurred exclusively in mechanical restoration areas (Parsons & Becker 2021). A soil inoculum study conducted at PRNS after mechanical removal found that, while germination of several native plants in “flipped” soils was comparable to that in native dune soils, aboveground biomass was considerably reduced, and it concluded that parasitic microbes in flipped soils could be potentially responsible (Winsemius et al. 2015).

Microbial changes following beachgrass invasion and treatment could also be slowing decomposition within backdunes. Within PRNS’ study areas, abundance of wood saprophytic fungi was lower in treated backdunes than in invaded dunes, with fungal recovery not evident in herbicide-treated areas even after 8 years (Yang et al. 2022). Saprophytic fungi are a key driver in the decomposition process, initiating decomposition of cellulose, lignin, and lignocellulose (Francioli et al. 2021). Beachgrass sampled at AT&T had high C:N ratios (70.8:1) and lignocellulose content, while levels of lignin, other phenols, and silicon fell towards the lower end of the range generally reported for grasses (Parsons et al. 2020a). Abundance of cellulose-decomposing cellulolytic bacteria, which was high in

heavily invaded dunes, also dropped immediately after herbicide treatment (Parsons et al. 2020b), but cellulolytic bacteria abundance and related enzymatic activities appeared to potentially rebound by years 4–8 (B. Yang 2022, University of Arizona, Tucson, AZ, U.S.A., personal communication). Microbially mediated decomposition may be further hampered by extremely low N in dune soils (Barbour et al. 1985; Holton et al. 1991; Parsons & Becker 2021). Microbes must scavenge N within soils to enable breakdown of litter with higher C:N ratios (>25:1), which in N-poor soils leads to immobilization rather than mineralization of N in litter and delays in decomposition (Brady & Weil 1999). While reversing microbial legacy effects of invaders is certainly desirable, reduced abundance of cellulolytic bacteria and saprophytic fungi while extensive necromass is still present may be strongly hindering restoration efforts, at least in the short term.

As researchers and land managers have come to realize, weed removal alone is not sufficient to restore most ecosystems due to the potential for legacy effects. Projects contending with legacy effects may require implementation of additional restoration measures such as soil amelioration or removal of biomass (Suding et al. 2004; Wolfe & Klironomos 2005; Kardol & Wardle 2010). PRNS is currently collaborating with researchers on an experiment to determine if inoculation with whole soils from native Dune Scrub might reintroduce or augment microbial decomposers in treated backdunes and speed up litter decomposition. Alternatively, demand on decomposers could be reduced through mechanically breaking up or burning dead beachgrass. The former was attempted previously at Abbotts shortly after initial treatment using bulldozers or mowing. While necromass was reduced, so was native species richness and diversity relative to unmanipulated treated backdunes (Parsons et al. 2020a).

In summary, while herbicide-treated backdunes have been slow to evolve due to persistent necromass, they do appear to be headed towards eventual convergence with native dune habitats, at least in terms of vegetation. Adaptive restoration measures focused on minimizing or eliminating legacy effects may accelerate this convergence process. Mechanical backdunes, if not foredunes, also appear to have developed species assemblages similar to native Dune Mat, albeit perhaps more slowly due in part to effects of mechanical restoration on soil chemistry and microbiota (Winsemius et al. 2015; Parsons et al. 2020b; Parsons & Becker 2021). Ultimately, problems with entrenched secondary invaders such as European searocket in Abbotts mechanical areas may prove insurmountable due to the extensive, and perhaps unsustainable, amount of long-term retreatment required due to the delayed control response at this site.

Despite these issues, the Abbotts mechanical project has succeeded in achieving one of the project's other high-priority objectives—reinstating ecosystem functions such as support of rare species. Hundreds of thousands of federally listed rare plants such as Tidestrom's lupine and *Layia carnosa* (beach layia) have colonized mechanically restored areas (Parsons et al. 2020a). The federally listed shorebird, *Charadrius alexandrinus nivosus* (Western snowy plover), also utilizes mechanically restored areas and adjacent beaches (M. Lau 2022, NPS, Point Reyes Station, CA, U.S.A., personal

communication). Situations such as this where there are mixed restoration results may eventually push land managers to retroactively reevaluate how project success is defined, particularly when high priority objectives such as rare species recovery are being met.

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LITERATURE CITED

- Badalamenti E, Gristino L, Laudicina VA, Novara A, Pasta S, La Mantia T (2016) The impact of *Carpobrotus* cfr. *acinaciformis* (L.) L. bolus on soil nutrients, microbial communities structure and native plant communities in Mediterranean ecosystems. *Plant and Soil* 409:19–34. <https://doi.org/10.1007/s11104-016-2924-z>
- Barbour MG, De Jong TM, Pavlik BM (1985) Marine beach and dune plant communities. Pages 296–322. In: *Physiological ecology of North American plant communities*. Springer Netherlands, Dordrecht, The Netherlands
- Bartomeus I, Bosch J, Vilà M (2008) High invasive pollen transfer, yet low deposition on native stigmas in a *Carpobrotus*-invaded community. *Annals of Botany* 102:417–424. <https://doi.org/10.1093/aob/mcn109>
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 57:289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Brady NC, Weil RR (1999) *The nature and properties of soils*. 12th ed. Prentice Hall, Prentice, New Jersey
- Breckon GJ, Barbour MG (1974) Review of North American Pacific coast beach vegetation. *Madrono* 22:333–360
- Buck-Diaz J, Sikes K, Evens JM (2021) Vegetation classification of alliances and associations in Marin County, California. *California Native Plant Society*. https://www.cnps.org/wp-content/uploads/2021/09/marin_co_veg_classification-2021.pdf
- Clayton JL (1972) Salt spray and mineral cycling in two California coastal ecosystems. *Ecology* 53:74–81. <https://doi.org/10.2307/1935711>
- Conser C, Connor EF (2009) Assessing the residual effects of *Carpobrotus edulis* invasion, implications for restoration. *Biological Invasions* 11:349–358. <https://doi.org/10.1007/s10530-008-9252-z>
- Corbin JD, D'Antonio CM (2012) Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. *Invasive Plant Science and Management* 5:117–124. <https://doi.org/10.1614/IPSM-D-11-00005.1>
- Cuddington K (2011) Legacy effects: the persistent impact of ecological interactions. *Biological Theory* 6:203–210. <https://doi.org/10.1007/s13752-012-0027-5>
- Darke IB, Walker IJ, Hesp PA (2016) Beach–dune sediment budgets and dune morphodynamics following coastal dune restoration, Wickaninnish Dunes, Canada. *Earth Surface Processes and Landforms* 41:1370–1385. <https://doi.org/10.1002/esp.3910>
- Davy AJ, Figueroa ME (1993) The colonization of strandlines. *Special Publication-British Ecological Society* 12:113–131
- De Cáceres M (2022) Package “indicspecies.” R package version 1.7.12. <https://emf-craef.github.io/indicspecies/>
- Facelli JM, Pickett STA (1991) Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* 57:1–32. <https://doi.org/10.1007/BF02858763>
- Francioli D, van Rijssel SQ, van Ruijven J, Termorshuizen AJ, Cotton TE, Dumbrell AJ, Raaijmakers JM, Weigelt A, Mommer L (2021) Plant

- functional group drives the community structure of saprophytic fungi in a grassland biodiversity experiment. *Plant and Soil* 461:91–105. <https://doi.org/10.1007/s11104-020-04454-y>
- Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al. (2019) International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27:S1–S46. <https://doi.org/10.1111/rec.13035>
- Gornish ES, Franklin K, Rowe J, Barberán A (2020) Buffelgrass invasion and glyphosate effects on desert soil microbiome communities. *Biological Invasions* 22:2587–2597. <https://doi.org/10.1007/s10530-020-02268-8>
- Groves RH (1999) Sleeper weeds. Pages 632–636. In: *Proceedings of the 12th Australian weeds conference*. Tasmanian Weed Society, Devonport, Australia
- Hesp PA, Hilton MJ (2013) Restoration of foredunes and transgressive dunefields: case studies from New Zealand. Pages 67–92. In: Martínez LM, Gallego-Fernández JB, Hesp PA (eds) *Restoration of coastal dunes*. Springer, Berlin, Heidelberg, Germany. https://doi.org/10.1007/978-3-642-33445-0_5
- Hetherington JK, Wilson JB (2019) Short-term soil nutrient and plant community responses to the eradication of a nitrogen fixing tree, *Lupinus arboreus*. *Journal of Coastal Conservation* 23:49–58. <https://doi.org/10.1007/s11852-018-0635-8>
- Holmes PM, Esler KJ, Gaertner M, Geerts S, Hall SA, Nsikani MM, Richardson DM, Ruwanga S (2020) Biological invasions and ecological restoration in South Africa. Pages 665–700. In: van Wilgen B, Measey J, Richardson D, Wilson J, Zengeya T (eds) *Biological invasions in South Africa*. Springer, Cham, Switzerland
- Holton B, Barbour MG, Martens SN (1991) Some aspects of the nitrogen cycle in a Californian strand ecosystem. *Madrono* 38:170–184
- Ingraham NL, Matthews RA (1995) The importance of fog-drip water to vegetation: Point Reyes Peninsula, California. *Journal of Hydrology* 164:269–285. [https://doi.org/10.1016/0022-1694\(94\)02538-M](https://doi.org/10.1016/0022-1694(94)02538-M)
- Kardol P, Wardle DA (2010) How understanding aboveground–belowground linkages can assist restoration ecology. *Trends in Ecology & Evolution* 25:670–679. <https://doi.org/10.1016/j.tree.2010.09.001>
- Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *Journal of Applied Ecology* 48:970–979. <https://doi.org/10.1111/j.1365-2664.2011.01979.x>
- Konlechner TM, Lord JM (2015) Plant community response following the removal of the invasive *Lupinus arboreus* in a coastal dune system: community response following *L. arboreus* removal. *Restoration Ecology* 23: 607–614. <https://doi.org/10.1111/rec.12234>
- Lenth R, Buerkner P, Giné-Vázquez I, Herve M, Jung M, Love J, Miguez F, Riebl H, Singmann H (2022) Package “emmeans”. Version 1.8.3. <https://cran.r-project.org/web/packages/emmeans/index.html>
- Liao C, Peng R, Luo Y, Zhou X, Wu X, Fang C, Chen J, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* 177:706–714. <https://doi.org/10.1111/j.1469-8137.2007.02290.x>
- Lithgow D, Martínez ML, Gallego-Fernández JB, Hesp PA, Flores P, Gachuz S, Rodríguez-Revelo N, Jiménez-Orocio O, Mendoza-González G, Álvarez-Molina LL (2013) Linking restoration ecology with coastal dune restoration. *Geomorphology* 199:214–224. <https://doi.org/10.1016/j.geomorph.2013.05.007>
- Mangiafico S (2023) Package “rcompanion.” Version 2.4.30. <https://cran.r-project.org/web/packages/rcompanion/index.html>
- Martínez AP (2020) pairwiseAdonis: pairwise multilevel comparison using adonis. R package version 0.4. <https://github.com/pmartinezarbizu/pairwiseAdonis>
- Martínez ML, Hesp PA, Gallego-Fernández JB (2013) Coastal dunes: human impact and need for restoration. Pages 1–14. In: Martínez M, Gallego-Fernández J, Hesp P (eds) *Restoration of coastal dunes*. Springer, Berlin, Heidelberg, Germany. https://doi.org/10.1007/978-3-642-33445-0_1
- Nordstrom KF (2021) *Beach and dune restoration*. Cambridge University Press. <https://doi.org/10.1017/9781108866453>
- Novoa A, González L, Moravcová L, Pyšek P (2014) Constraints to native plant species establishment in coastal dune communities invaded by *Carpobrotus edulis*: implications for restoration. *Biological Conservation* 164:1–9. <https://doi.org/10.1016/j.biocon.2013.04.008>
- NPS (National Park Service) (2009) Abbots lagoon area dune restoration plan environmental assessment. https://www.nps.gov/pore/learn/management/upload/planning_dunere restoration_ea_090209.pdf
- NPS (National Park Service) (2015) Coastal dune restoration environmental assessment. https://www.nps.gov/pore/learn/management/upload/planning_dunere restoration_project_ea_150109.pdf
- Nsikani MM, Novoa A, van Wiglen BW, Keet J-H, Gaertner M (2017) *Acacia saligna*’s soil legacy effects persist up to 10 years after clearing: implications for ecological restoration. *Austral Ecology* 42:880–889. <https://doi.org/10.1111/aec.12515>
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, et al. (2022) *Vegan: community ecology package*. Version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Parkhurst T, Prober SM, Hobbs RJ, Standish RJ (2022) Global meta-analysis reveals incomplete recovery of soil conditions and invertebrate assemblages after ecological restoration in agricultural landscapes. *Journal of Applied Ecology* 59:358–372. <https://doi.org/10.1111/1365-2664.13852>
- Parsons LS, Becker BH (2021) Invasion by *Ammophila arenaria* alters soil chemistry, leaving lasting legacy effects on restored coastal dunes in California. *Invasive Plant Science and Management* 14:75–91. <https://doi.org/10.1017/imp.2021.16>
- Parsons L, Ender C, Spaeth M (2020a) Coastal dune restoration vegetation monitoring report. Point Reyes National Seashore, Point Reyes Station, California. <https://irma.nps.gov/DataStore/Reference/Profile/2284461>
- Parsons L, Sayre J, Ender C, Rodrigues JLM, Barberán A (2020b) Soil microbial communities in restored and unrestored coastal dune ecosystems in California. *Restoration Ecology* 28:S311–S321. <https://doi.org/10.1111/rec.13101>
- Pearson DE, Ortega YK, Runyon JB, Butler JL (2016) Secondary invasion: the bane of weed management. *Biological Conservation* 197:8–17. <https://doi.org/10.1016/j.biocon.2016.02.029>
- Pellegrini E, Boscutti F, Alberti G, Casolo V, Contin M, De Nobili M (2021) Stand age, degree of encroachment and soil characteristics modulate changes of C and N cycles in dry grassland soils invaded by the N₂-fixing shrub *Amorpha fruticosa*. *Science of the Total Environment* 792:148295. <https://doi.org/10.1016/j.scitotenv.2021.148295>
- de la Peña E, de Clercq N, Bonte D, Roiloa S, Rodríguez-Echeverría S, Freitas H (2010) Plant-soil feedback as a mechanism of invasion by *Carpobrotus edulis*. *Biological Invasions* 12:3637–3648. <https://doi.org/10.1007/s10530-010-9756-1>
- Peterson RA (2022) bestNormalize: normalizing transformation functions. Version 1.8.3. <https://cran.r-project.org/package=bestNormalize>
- Pickart AJ, Maslach WR, Parsons LS, Jules ES, Reynolds CM, Goldsmith LM (2021) Comparing restoration treatments and time intervals to determine the success of invasive species removal at three coastal dune sites in northern California, U.S.A. *Journal of Coastal Research* 37:557–567. <https://doi.org/10.2112/JCOASTRES-D-20-00085.1>
- Pickett B, Irvine IC, Bullock E, Arogyaswamy K, Aronson E (2019) Legacy effects of invasive grass impact soil microbes and native shrub growth. *Invasive Plant Science and Management* 12:22–35. <https://doi.org/10.1017/imp.2018.32>
- R Core Team (2022) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reid AM, Morin L, Downey PO, French K, Virtue JG (2009) Does invasive plant management aid the restoration of natural ecosystems? *Biological Conservation* 142:2342–2349. <https://doi.org/10.1016/j.biocon.2009.05.011>
- Reynolds PL, Glanz J, Yang S, Hann C, Couture J, Grosholz E (2017) Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer. *Ecosphere* 8:e01711. <https://doi.org/10.1002/ecs2.1711>
- Robichaud CD, Rooney RC (2021) Effective suppression of established invasive *Phragmites australis* leads to secondary invasion in a coastal marsh. *Invasive Plant Science and Management* 14:9–19. <https://doi.org/10.1017/imp.2021.2>

- Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9:912–919. <https://doi.org/10.1111/j.1461-0248.2006.00939.x>
- Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19:46–53. <https://doi.org/10.1016/j.tree.2003.10.005>
- Weber E (2003) *Invasive plant species of the world: a reference guide to environmental weeds*. CAB International Publishing, Wallingford, United Kingdom
- Wheeler RE, Torchio M (2016) Permutation tests for linear models in R. R package version 2.1.0. <https://CRAN.R-project.org/package=lmPerm>
- Wiedemann AM, Pickart A (1996) The *Ammophila* problem on the northwest coast of North America. *Landscape and Urban Planning* 34:287–299. [https://doi.org/10.1016/0169-2046\(95\)00240-5](https://doi.org/10.1016/0169-2046(95)00240-5)
- Winsemius S, Stein C, Parsons L, Minnick S, Ryan A, Suding K (2015) Plant-soil interactions and implications for restoration of coastal sand dunes at Point Reyes National Seashore. Poster. California Native Plant Society Conference, San Jose, California
- Wolfe BE, Klironomos JN (2005) Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55:477–487. [https://doi.org/10.1641/0006-3568\(2005\)055\[0477:BNGSCA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0477:BNGSCA]2.0.CO;2)
- WRCC (Western Regional Climate Center) (2021) Climate data from Point Reyes RCA CA weather station. Western Regional Climate Center, Reno, Nevada.
- Yang B, Fuqua SR, Parsons L, Barberán A (2022) Managing the soil microbiome to overcome legacy effects of beachgrass invasion. Poster. Ecological Society of America Conference, Montreal, Canada
- Zarnetske PL, Seabloom EW, Hacker SD (2010) Non-target effects of invasive species management: beachgrass, birds, and bulldozers in coastal dunes. *Ecosphere* 1:1–20. <https://doi.org/10.1890/ES10-00101.1>

Supporting Information

The following information may be found in the online version of this article:

Table S1. Post hoc comparisons for mechanically treated foredunes and backdunes at Abbotts.

Table S2. Post hoc comparisons for herbicide-treated backdunes at Abbotts and AT&T.

Table S3. Post hoc comparisons for herbicide-treated foredunes at Abbotts and AT&T.

Table S4. Vegetation cover, richness, and diversity variables monitored at Abbotts Coastal Dune Restoration project area and in target native habitats.

Table S5. Vegetation cover, richness, and diversity variables monitored at AT&T North and South dune restoration project areas.

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