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Ammophila arenaria as a Nurse Plant: Implications for Management of an Invasive Species

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Ammophila arenaria (European beachgrass) was initially introduced to California from the coasts of Europe and North Africa to stabilize dunes and has since become a dominant invasive species on dune habitats along the west coast of the United States (Wiedemann and Pickart 1996). *Ammophila arenaria* primarily spreads by a rhizome network that is stimulated by active sand burial, allowing the species to rapidly stabilize shifting sand dunes (Buell et al. 1995). The rapid spread of dense stands of *A. arenaria* has caused a reduction in native plant richness and abundance (Wiedemann and Pickart 1996). However, at lower densities, *A. arenaria* may not have a negative impact on native plant species diversity and could even play a facilitative role (J. Solins, University of California, Davis, unpub. data). Tall vegetative structures such as shrubs often act as nurse species by providing a wind break, shade and soil stabilization for smaller plants and seedlings in dune systems (Shumway 2000, Rudgers and Maron 2003, Castanho et al. 2015). Due to a more favorable microclimate, herbaceous vegetation under shrubs and bunchgrasses are often larger, and have a higher reproductive output, compared to individuals in open areas (Shumway 2000). Given that *A. arenaria* is a tall species relative to most dune plants that stabilize soil, it has potential to act as a nurse plant.

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Although considering the positive impacts of invasive species can make management decisions more complicated, it is necessary to fully understand potential consequences of invasive species removal. If invasive species have positive impacts on native diversity, then additional management may be required to mitigate negative impacts of invasive species removal. For example, if native shrubs or bunchgrasses provide favorable microclimates similar or superior to those created by *A. arenaria* (i.e., Rudgers and Maron 2003), then active planting of these native nurse species may be a beneficial practice. This study examines: 1) whether *A. arenaria* is facilitating a more diverse native community than areas in the absence of a tall vegetative structure; 2) whether understory communities differ under *A. arenaria* and *Baccharis pilularis* (coyote brush), a widespread native shrub; and 3) whether the presence of *A. arenaria* and *B. pilularis* have a similar effect on native plant diversity.

I conducted this study at the UC Davis Bodega Marine Reserve in Bodega Bay, California, US, on sand dunes with low (< 30%) *A. arenaria* cover. *Ammophila arenaria* was introduced to the property in the 1920s–1950s to stabilize naturally shifting sand dunes and has since spread through most of surrounding areas. I visually estimated the percent cover of each species in the 0.5 m^2 area where vegetation grew most densely under 12 *A. arenaria* and 12 *B. pilularis* individuals (hereafter, focal species), and within twelve 0.5 m^2 control plots where no shrubs or bunchgrasses were present. I randomly selected all sampling sites among focal species and open areas that were not within 0.5 m of another shrub or bunchgrass. To provide insight into characteristics of nurse species that may affect their understory communities, I recorded the focal species' height, width at the widest diameter, percent canopy cover over the sampled understory vegetation and the cardinal direction of the sample area relative to the base of the focal species.

I calculated Shannon diversity in each plot using the species percent cover estimates. I then used a linear model and ANOVA to determine if there were differences in diversity among treatment groups, and performed mean comparisons using a Tukey test ($p \leq 0.05$). To examine whether communities differ under different nurse species, I used Non-metric Multidimensional Scaling (NMDS) with the Bray-Curtis dissimilarity index to visualize differences among plant communities, and PERMANOVA to test for significant differences in the community composition among groups. I conducted all analyses using R (v.3.2.3, R Foundation, Vienna Austria), and used the R package "vegan" to calculate Shannon diversity and to perform NMDS and the PERMANOVA.

Comparing focal species characteristics indicated that, on average, *A. arenaria* was taller (height: 0.56 m ± 4.51 SE), narrower (width: 0.82 m ± 11.2 SE), and had a lower canopy cover (canopy cover: 7.42 % ± 3.23 SE) than did *B. pilularis* (height: 0.33 m ± 4.52 SE; width: 1.23 m

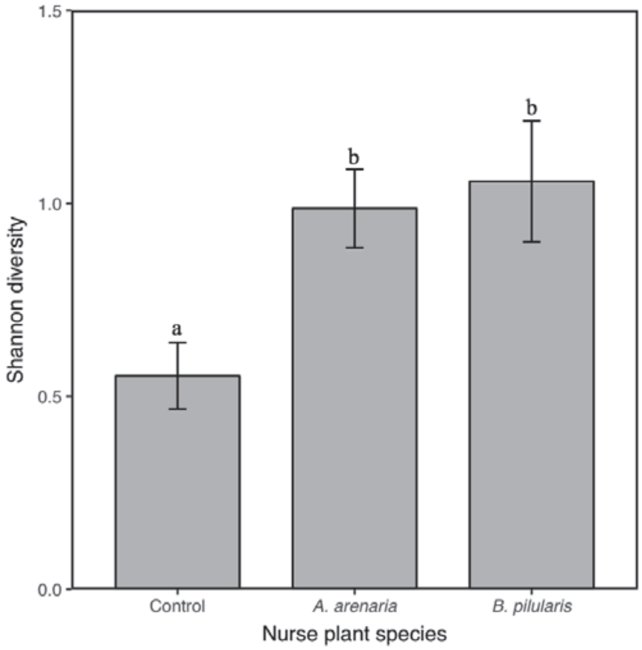

Figure 1. Average Shannon diversity by plot type. Diversity in *Ammophila arenaria* plots and *Baccharis pilularis* plots is significantly higher than in control plots ($p < 0.05$). Different letters denote significant differences in diversity. Error bars indicate ± 1 SE.

± 8.85 SE; canopy cover: 19.6% ± 6.88 SE). The densest understory vegetation was most commonly present on the northwestern, southeastern, or eastern side of both nurse species. However, species height, width, canopy cover, and direction of densest understory community were not significant predictors of diversity (ANOVA; height: $F_{1,13}$ = 1.81, p = 0.20; width: $F_{1,13}$ = 0.52, p = 0.48; canopy: $F_{1,13}$ = 0.10, p = 0.761; direction $F_{6,13}$ = 2.15, p = 0.117) or differences in community composition (PERMANOVA; height: $F_{1,13}$ = 0.97, p = 0.466; width: $F_{1,13}$ = 1.77, p = 0.080; canopy: $F_{1,13}$ = 1.91, p = 0.054; direction $F_{6,13}$ = 0.97, p = 0.541).

A total of 30 species were identified across all plots and categorized as native or exotic (Supplementary Table 1). Two forbs, four grasses, three lichens, and one moss were not identified and therefore were not indicated as native or exotic. Among the 20 remaining species, all but four were native. Total cover of exotic species was < 2%, on average. Average native cover was higher in the open, control plots (58.95 % ± 12.0 SE) compared to plots with *A. arenaria* (31.8% ± 8.4 SE) and *B. pilularis* (19.5% ± 3.5 SE). However, this difference in cover was largely driven by a single species, *Cardionema ramosissimum* (Sand mat). When *C. ramosissimum* was not included, average native cover in control plots was only 6.7% (± 2.0 SE), in *A. arenaria*

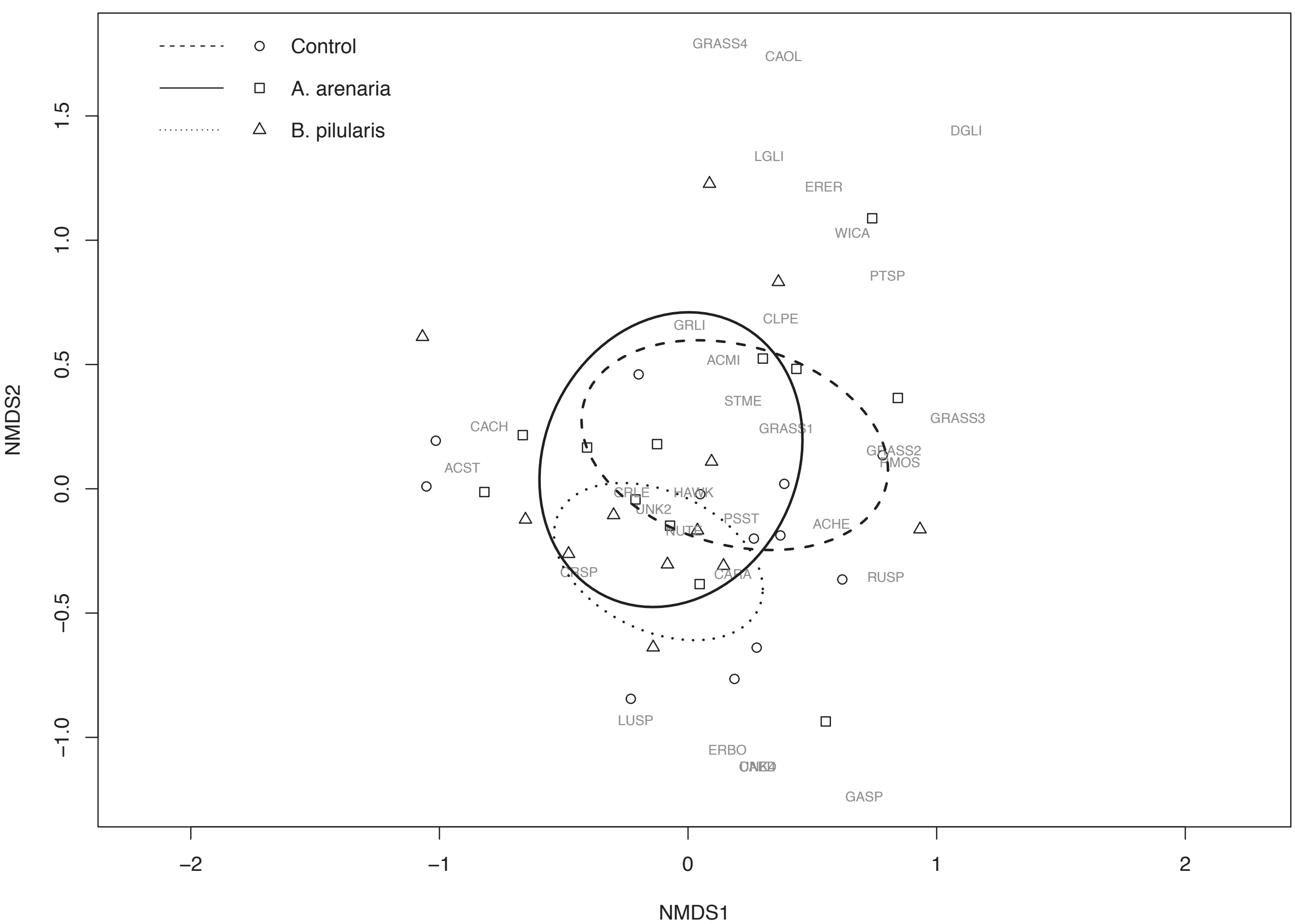

Figure 2. NMDS ordination of plots. Ellipses are 95% confidence intervals around plot type centroid (stress = 0.23).

plots was 11.28% (± 4.3 SE), and in *B. pilularis* plots was 10.21% (± 2.4 SE). Shannon diversity was significantly higher under both focal species than in the control plots (ANOVA; $F_{2,13} = 6.38$, $p = 0.012$; Tukey HSD; control vs. *B. pilularis*: $p = 0.013$; control vs. *A. arenaria*: $p = 0.037$). There was no difference in diversity among communities below *B. pilularis* and *A. arenaria* (Tukey HSD; $p > 0.05$; Figure 1).

There was a significant difference in the community among plot types (PERMANOVA; $F_{2,13} = 2.19$, $p = 0.014$). The NMDS showed low overlap (indicating a low level of similarity) of communities in *B. pilularis* and control plots, indicating that the difference in communities among plot types was likely driven by differences between *B. pilularis* and control plot communities. There was high overlap (indicating a high level of similarity) of communities in *A. arenaria* and *B. pilularis* plots and of communities in *A. arenaria* and control plots (Figure 2).

Consistent with other studies in coastal dune systems, there is evidence that plant communities differ in open areas and under large vegetative structures in terms of diversity (Forey et al. 2009, Monge and Gornish 2015). However, there were similar community compositions and no differences in diversity between plant communities under the two focal species, suggesting that both species are facilitating diverse native plant communities.

Although not directly tested in this study, there were indications of possible mechanisms driving differences below focal species and in open areas. Prevailing winds in Bodega Bay come from the NW (Barbour et al.1973). Therefore, the high concentration of understory plants on the SE and E side of the nurse plants suggests that *A. arenaria* and *B. pilularis* are acting as wind breaks (Dona and Galen 2007, Li 2008). The high concentration of understory plants on the NW side may indicate that *A. arenaria* and *B. pilularis* are also acting as seed traps for wind dispersed species, leading to a higher concentration of propagules on the NW side compared to other areas (Bullock and Moy 2004).

Reduction in invasive plant cover is a common restoration goal, however, removal alone often does not lead to return of native species (Kettenring and Adams 2011). The results of this study indicate that removal of *A. arenaria* in areas where it is at a low density may be harmful to native plant communities because *A. arenaria* may be acting as a nurse plant.

Although the results of this study may initially imply that *A. arenaria* should not be removed when present at low densities, *A. arenaria* strongly reduces native plant diversity when it reaches high densities (Widemann and Pickart 1996). Therefore, controlling *A. arenaria* before it increases in density or spreads to other areas is important for long-term maintenance of a diverse native plant community (Kettenring and Adams 2011). Based on the results of this study, planting *B. pilularis* could mitigate negative impacts on the native plant community resulting from *A. arenaria* removal. This study suggests that planting key native species may encourage retention and recruitment of a diverse native plant community in areas where invasive species are playing a positive role.

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