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The importance of pilot studies and understanding microhabitat requirements when reintroducing endemic plants during coastal dune restoration

Justin C. Luong [1,2] · Madeline P. Nolan [3] · Lisa C. Stratton [2]

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Abstract

In coastal California dune ecosystems protect coastal cities from damaging storms and provide habitat for native wildlife. Despite the economic and ecological importance of coastal dunes, habitat loss has continued and is predicted to accelerate with a changing climate. To combat the effects of climate change and ensure that coastal dunes will persist into the future, they need to be prioritized for conservation and restoration. However, for restoration to be successful, endemic plants, which are plant with specialized habitat requirements, need to be prioritized because they make up a significant portion of the biodiversity in California coastal dunes. Because endemic plants are rare and there is limited stock of plants available for transplant, we need to be more aggressive in using pilot studies. These can be used to evaluate the biotic and abiotic conditions that maximize growth and reproduction and to help guide effective reintroduction. To evaluate how exploratory pilot studies can enhance the restoration of rare and endemic plant species, we conducted a study restoring *Lupinus nipomensis*, a United States federally endangered species, on coastal dunes in San Luis Obispo County, California. We found that *L. nipomensis* had the highest seed production in plots that had a steep, north facing slope and were protected from herbivores. Our results suggest that restoration efforts should be focused on areas with these characteristics to maximize restoration success. Our pilot reintroduction of *L. nipomensis* highlights the importance of using pilot experiments to enhance reintroduction success and to quicken the recovery of coastal dune ecosystems.

Keywords Microhabitat requirements · Rare plant introduction · Dune restoration · *Lupinus nipomensis* · Reintroduction · Endangered species

Introduction

Along the coast of California, dune ecosystems provide numerous economic and ecological benefits to coastal cities despite being significantly fragmented and degraded (Van der Maarel and Usher 1997). They are known to protect coastal cities from damaging storm systems, prevent salt-water intrusion into the water table (Mascarenhas 2004; Giambastiani et al. 2007; Everald et al. 2010), are used recreationally as off-highway vehicle parks, and host a wide variety of native species with a particularly large number of endemic plants (Martinez et al. 2004; Grootjans et al. 2002; Tzatzanis et al. 2003). Unfortunately, despite their importance, habitat loss and degradation due to land use change has continued and is predicted to accelerate as sea levels rise with a changing climate (Van der Maarel and Usher 1997; Doukakis 2005; Hapke et al. 2006; IPCC 2013). Coastal dune habitat needs to be prioritized for conservation and restoration to ameliorate past degradation and to allow coastal dunes to persist into the future. Restoration efforts need to focus on plant species that are restricted to coastal dunes, endemic coastal dune plants, because they are ecologically unique and provide important ecosystem services for human populations. Despite making up a diverse portion of the biodiversity in California's coastal dunes (Myers et al. 2000), endemic coastal dune plants are at an increased risk of extirpation from these ecosystems. In fact, many of the remnant dune systems that

✉ Justin C. Luong
jluong4@ucsc.edu

[1] Environmental Studies, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA

[2] The Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara, CA 93106, USA

[3] Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA

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are present today lack endemic plants that were historically present (Tzatzanis et al. 2003). The loss of these endemic coastal dune plants is problematic because they provide important ecosystem services, such as invertebrate refugia (native pollinator and natural enemies), soil stabilization and improved soil fertility (Cardinale et al. 2012; Gamfeldt et al. 2008). Furthermore, the loss of endemic species from a system removes biological interactions which can allow for the persistence of other species through direct facilitation or facilitative competition (Thompson 1997; Verdú and Valiente-Banuet 2008). Therefore, to address the loss of endemic coastal dune plants they will need to be reestablished during restoration efforts.

Currently, plants are reintroduced into new areas by either planting seedling plugs or direct seeding (Maunder 1992; Rossi et al. 2016; Pavlik et al. 1993; Richardson et al. 2014; Pardini et al. 2015; Maschinski and Haskins 2012). In order to address the loss of endemic plants from coastal dunes, reintroduction and novel establishment during restoration efforts may be necessary (Maschinski and Haskins 2012). Reintroductions are often necessary because natural reestablishment of endemic species is unlikely because their habitat is often fragmented, which increases the physical barriers that plants and their dispersal partners have to cross, often preventing their establishment in areas where they previously occurred (Münzbergová and Herben 2005).

While there are tradeoffs in using both approaches, most notably, there are often higher rates of establishment with seedling plugs, but there is an exponential increase in required budgetary resources (Dunwiddie and Martin 2016). While using seed plugs may be desirable, this method is more effective with perennial species compared to annual species which often are stressed beyond recovery after transplanting due to their short lifecycle and general evolutionary focus on having resilient populations compared to the perennial strategy of becoming more resistant (Cornelissen et al. 2003). As such, reintroduction of annual plants is most commonly practiced through direct seeding which is often unsuccessful, but affordable and often the only option (Dunwiddie and Martin 2016). Therefore, further understanding of the dynamics of restoring rare, endemic annual species by direct seeding though observing the entire lifecycle is imperative (Maschinski and Haskins 2012).

Although being a commonly used "practice", many of these reintroduction efforts fail with little to no establishment of the endemic plant (Godefroid et al. 2011; Maschinski and Haskins 2012). Reintroductions of rare and endemic plants fail for many reasons, but most commonly is caused by poor habitat selection due to a lack of natural history knowledge of the sites of the extant populations (McLeod et al. 2001; Falk et al. 1996; Fiedler 1991; Maschinski and Haskins 2012) resulting in stress caused by a mismatch in abioitic factors and biotic interactions (Godefroid et al. 2011; Griffith et al. 1989; Bevill et al. 1999). The presence of specific microhabitat conditions has been found to maximize plant growth and reproduction has benefited a wide variety of rare plants (Richardson and Hanks 2011). For example, the endangered *Lupinus tidestormii* established most successfully in less stabilized dune habitats which was guided by microhabitat knowledge (Pardini et al. 2015). The endangered *L. aridorum* reproduced more successfully in sites with moderate soil moisture and appropriate microbial symbionts both mediated by litter cover type (Richardson et al. 2014). These case studies highlight the utility of pilot studies to guide reintroduction efforts through identifying microhabitats that will maximize the chance of establishment and perpetuate reproduction. Unfortunately, microhabitats are often difficult to identify cursorily because landscapes are heterogeneous and appropriate sites are rare, small and discontinuous within an area (Vargas et al. 2013; Dunwiddie and Martin 2016). As such, pilot studies will provide data where there is a lack of information to guide habitat selection to increase the success in reintroducing endemic species (Godefroid et al. 2011; Maschinski and Haskins 2012; Davy 2002). To evaluate how such exploratory pilot studies can address these issues and inform the restoration of rare and endemic plant species, we conducted a study to restore and examine the full lifecycle of *Lupinus nipomensis*, a United States federally endangered species, on coastal dunes in San Luis Obispo County, California. *L. nipomensis* is an annual herb found in the Guadalupe-Nipomo Dune complex (Fig. 1; Clark 2000).

From previous field surveys, *L. nipomensis* was found to exist in small clusters (yearly population ranging from 139 to 771). The small, fragmented nature of the population and the fact that much of their likely habitat has been converted to agriculture, makes it ideal for conducting a pilot study to target reintroduction efforts and increase reestablishment success (Hall, LCSLO personal communication). Because the populations persist on private land, the United States Fish and Wildlife Service (USFWS) has prioritized this species for reestablishment into preserves to better protect this species from habitat conversion and climate change. Several suitable sites were previously identified (CCBER, unpublished data 2015) including Guadalupe Dunes National Wildlife Refuge, which is protected and managed by USFWS, and Black Lake Ecological Area, which is protected and managed by the Land Conservancy of San Luis Obispo. Black Lake Ecological Area was chosen for this study because it has active management of *Ehrharta calycina,* an exotic species known to compete with *L. nipomensis* (Bossard et al. 2000; Hall, personal communication 2014).

To determine if *L. nipomensis* has microhabitat preferences within back dunes, we directly sowed seeds in a heterogeneous environment that varied in aspect, slope, and exposure to herbivory. The results of our study will help guide reestablishment efforts of *L. nipomensis* and highlight the importance of using pilot studies to identify microhabitat preferences and increase success of reestablishment efforts for an endemic and endangered plant.

Methods

Species description

Lupinus nipomensis is a United States federally endangered and California State endangered annual species of lupine that is endemic to coastal dunes in San Luis Obispo County, California. It grows as a basal rosette reaching 10–20 cm in height with somewhat succulent leaves and stems (Sholars 2016). *L. nipomensis* produces standard papilinoid flowers which fruits with dehiscent pods as they mature, with an average of 3–5 seeds per pod. Within the dune complex *L. nipomensis* was historically observed in back dunes and occasionally in inter-dune habitat. The loss of coastal back dune habitat has restricted the range of *L. nipomensis* to a 2 mi^2 area along the central California coast in the Guadalupe-Nipomo Dune Complex (Fig. 1; Wilken 2009; Skinner and Pavlik 1994). In 2000 it has been listed as an endangered species and conservation efforts have been ongoing (Clark 2000).

Seed source and area description

Seeds were collected from wild *Lupinus nipomensis* populations on the Nipomo Mesa by the Santa Barbara Botanical Garden in 2005. Seeds from 2005 were collected from a random sample of individuals in all known colonies, limited to 5% take sanctioned by USFWS permitting and stored in cool, dry conditions at the Botanic Garden. In 2012, wild collected seeds were germinated via cold stratification (including scarification) and grown by the Cheadle Center for Biodiversity and Ecological Restoration (CCBER) to increase the seed stock. All individuals collected in 2005 had ten seeds from every individual started in 2012 outdoors in a mix of native dune sand and potting soil. Plants received weekly watering throughout until senescence and seeds were collected as seed pods dehisced. All seeds were handled and stored based on standard protocol from the Center for Plant Conservation adapted by Rancho Santa Ana Botanical Garden for California. Seeds used in this outplanting experiment were from the seed bulking effort in 2012. Seeds were randomly selected by parent using a random number generator from 2012 parents to create seed packets with 20 seeds per pack for the experiment.

The experiment took place in Black Lake Ecological Area (35.056408, −120.604279), a back-dune ecosystem near Nipomo, CA in San Luis Obispo County (Fig. 1). Black Lake is characterized by a Mediterranean climate with wet, cool winters and dry, hot summers that are tempered by coastal fog events (Fayram and Frye 2014). Back dunes are the oldest part of a dune complex where plant establishment has increased dune stability. They are characterized by low relief (25 m or less), sinuous dune ridges, and have higher plant diversity than the other parts of the dune complex (Buckler 1979; Miller et al. 2010). The soil profile of the back-dune area is fine sand (125–250 μm) from 0 to 18 m in the profile and has no hydric soils (Soil Survey Staff 2016). The texture of the soil across the experimental area is sandy loam with a pH, electroconductivity (EC), and nutrient content (pH = 6.12, EC = 31.13, dS, soil organic matter = 3.27 g/100 g of soil, % nitrogen = 0.0402% and % carbon = 0.7005%) characteristic of stabilized dunes (Provoost et al. 2004). There is an ongoing effort to control the exotic veldt grass, *E. calycina,* population using a graminoid specific herbicide, Fusilade DX (fluazifop-p-butyl). To minimize the effects of herbicide on the experiment, herbicide was not used within 25 m of the experimental plots.

Experimental treatments

Aspect and slope treatment

To determine if *Lupinus nipomensis* preferred specific microhabitat conditions, we chose sites that varied in their slope and aspect. We chose slope and aspect because lupine species are known to be sensitive to water and light and both slope and aspect are known to impact the exposure of plants to these environmental variables (Braatne and Bliss 1999; Bennie et al. 2006). We had three slope treatments (steep slope, gentle slope and swale) and three aspect treatments (north facing, south facing, and no aspect). We crossed the aspect treatment with the slope treatment for a total of four different treatments: steep south facing, steep north facing, swale no aspect and gentle south facing. We could not include a north facing gentle slope because one did not exist within the experimental area.

Caging treatment

Herbivory is a common problem in restoration efforts because, when excessive, herbivory can lead to a reduction in seedling survival and population persistence (Rausher and Feeny 1980; Salihi and Norton 1987). To determine if herbivory was negatively impacting *L. nipomensis*, we had three different caging treatments. The caging treatments differed in the size of the top screen with one treatment consisting of a 0.25in^2 mesh size (small cage) and the second treatment consisting of a 2×4 in^2 mesh top (large cage; Fig. 2). The small caging treatment blocked most herbivores except small insects while the large caging treatment only prevented herbivory from large mammals such as deer. All cages were fully enclosed, 90 cm in diameter, and 60 cm tall. The sides of all

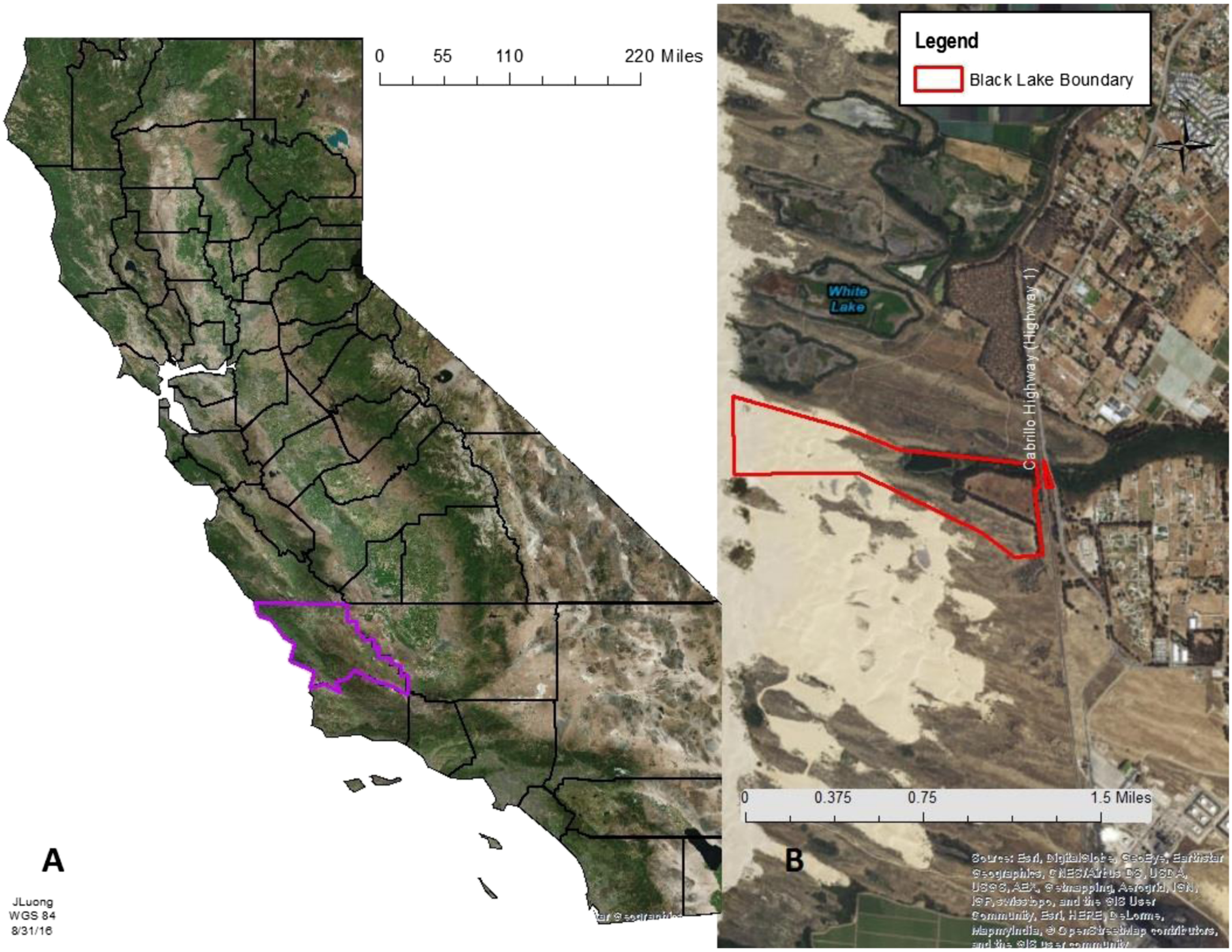

Fig. 1 *Lupinus nipomensis* microhabitat study area. **a** *Lupinus nipomensis* is endemic to San Luis Obispo County (outlined in purple) which is located in Southern California north of Sana Barbara County. **b** The study area is located in Blake Lake Ecological Area which is along the southwest coast of San Luis Obispo County

cages were constructed from 0.25 in^2 mesh hardware cloth wrapped around rebar buried 7.5 cm deep. The third treatment, the control, had rebar present at the four corners but no type of mesh barriers. We replicated each caging treatment six times for a total of 18 plots in each topographical site (Fig. 3).

Seed germination and survivorship

It is known that other species of lupine have hard seed coats that require scarification to promote germination (Hughes 1915). Therefore, to determine if scarification improved *L. nipomensis* field germination and reproduction, we scarified half the seeds by running the wide-edge of the seeds across 400 grit sandpaper one time. The operculum was avoided during the scarification process. Within each plot (72 total), 40 *L. nipomensis* seeds were sown in a grid of individual depressions approximately 5 mm deep and covered in a thin layer of sand. All plots were divided in half in a north-south orientation with one side receiving 20 seeds that were scarified and the other receiving 20 seeds that were not scarified. Prior to sowing, all eucalyptus litter, *Ehrharta calycina* and *Conicosia pugioniflormis* were removed from within all plot areas. In addition, all *E. calycina* and *C. pugioniflormis* were removed if they occurred within 5 m of any plot. No irrigation was provided during the experiment.

Experimental monitoring

In total there were 72 research plots with six replications per treatment type. Each treatment of aspect × slope × caging × scarification received 20 seeds, totaling 40 seeds per plot as each caging treatment was split for pairwise test of scarification on germination. Plots were monitored every two weeks after *Lupinus nipomensis* was sowed on Dec 18th, 2015 and first germinated Jan 25th, 2016. New germinants were

Fig. 2 A picture of the three different types of cages used for the caging treatments. From left to right: the no cage treatment (4 rebar posts), the small cage ($0.25in^2$ hardware cloth wrapped around 4 rebar posts and $0.25in^2$ hardware cloth as a top), and the big cage ($0.25in^2$ hardware cloth wrapped around 4 rebar posts and 2x4in hardware cloth as a top)

monitored biweekly until the plant died. Herbivory was measured using a 4-point scale with 0 = no herbivory, 1 = only leaflets affected, 2 = one whole leaf affected, 3 = multiple whole leaves affected, 4 = entire plant affected. We further classified class 0 as no herbivory, class 1 and 2 as mild herbivory, and class 3 and 4 as severe herbivory. Reproductive

Fig. 3 The location of the four-different aspect/slope treatments and the corresponding replicates in the Black Lake Ecological Area study site. The gentle south facing slope treatment is highlighted in pink, the swale no aspect treatment is highlighted in green, the steep south facing slope treatment is highlighted in blue, and the steep north facing slope is highlighted in orange

output was quantified as soon as seeding phenology set and was determined by the number of seed pods per plant throughout the season.

Data analysis

R statistical software was used to create all figures except maps and used for all statistical analyses (Version 3.40, R Development Core Team 2007). ArcGIS was used to create all maps (Version 10.4, Environmental Systems Research Institute 2012). A multi-way analysis of covariance (ANCOVA) was used to determine if there were significant interactions between aspect, slope, and herbivory on the reproductive output of *Lupinus nipomensis*. These were followed by a Tukey's honest significant difference test (TukeyHSD). Student's T test was used to determine the differential effect of scarification treatments on germination of *L. nipomensis* regardless of aspect, slope or caging.

Results

Seed production and growth rate

A total of 278 individuals of 1440 sown seeds germinated in all plots with 24 of those individuals successfully reproducing. All other individuals died before they could produce seed. Of those that died, the majority died from desiccation (130), with other individuals dying from being washed out (3), natural senescence (24) or undeterminable causes (121). For plants that successfully reproduced, the average number of seed pods was 20.0 ± 5.08 pods per individual plant. However, the number of pods produced varied greatly between individuals, ranging from 2 to 119 pods on a single individual.

Effect of scarification on germination and seed production

We found that scarification had a significant effect on percent germination ($t = 6.93$, $p < 0.0001$) with scarified seeds 945% more likely to germinate than unscarified seeds (208 scarified seeds germinated vs. 22 unscarified seeds; Fig. 4). We also found that scarification positively impacted seed pod production for plants. Plants that came from scarified seeds produced an average of 1.83 seed pods while then plants that came from unscarified seed produced an average of 0.0769 seed pods; however, only one unscarified plant produced seed pods.

Effect of herbivory, slope and aspect on seed production

Across all 278 individuals, we found that aspect was the most important abiotic variable that influenced the reproductive output of *L. nipomensis*. While slope did not have a significant impact on the seed production of *L. nipomensis* (Fig. 5; $F = 0.031$, $p = 0.861$), we found that plants in north facing plots produced significantly more seed (4.47 ± 2.04 seed pods) than south facing aspects (0.519 ± 0.274; Fig. 5; $F = 5.81$, $p < 0.005$). We also found a significant interaction between slope and aspect on the seed production of *Lupinus nipomensis* (Fig. 5; $F = 4.521$, $p < 0.001$ with severity of herbivory as a covariate). Post hoc analyses indicated that the north facing steep sites produced an average of 4.47 ± 2.04 seed pods, compared to south facing steep slopes which on average produced 0.347 ± 0.228 seed pods ($p < 0.05$). No

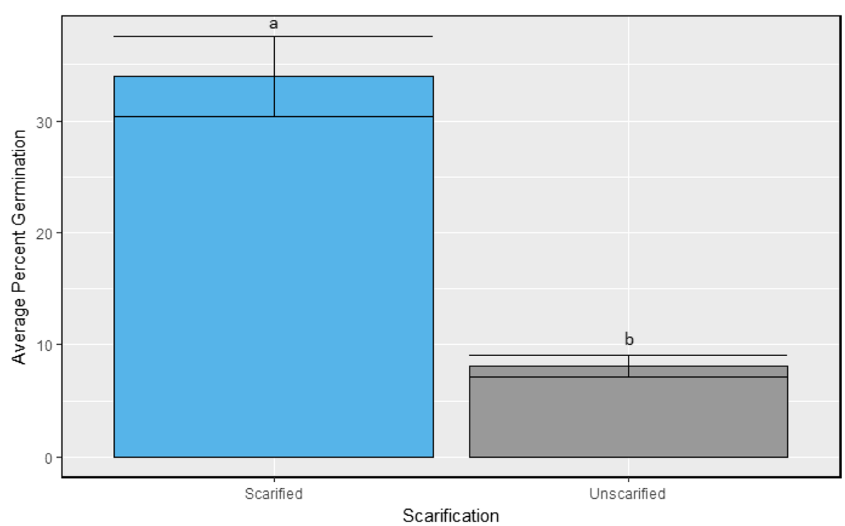

Fig. 4 Scarifying the seeds prior to sowing had a significant effect on germination ($t = 6.93$, $p < 0.0001$). Error bars represent standard error

other differences were found between other topographic treatments.

Effect of caging on the severity of herbivory

The chance of an individual *Lupinus nipomensis* plant experiencing severe herbivory (defined as class 3 and 4 herbivory) was significantly impacted by the presence of caging (Fig. 6; F = 4.52, $p < 0.05$). While we found no difference in severe herbivory between plants in small and big cages ($p = 0.979$), individuals in plots with no cages experienced severe herbivory 32.7% of the time compared to 1.85% in big cages ($p < 0.05$) and 4.09% in small cages ($p = 0.05$). We also found that severity of herbivory had a significant impact on total seed pod production (F = 5.52., $p < 0.005$; Fig. 7). *L. nipomensis* plants that experienced severe herbivory produced 0.0952 ± 0.00952 seed pods while those that experienced mild (class 1 and 2) herbivory produced 5.73 ± 2.95 seed pods ($p < 0.005$).

Discussion

By following the entire lifecycle of *Lupinus nipomensis* we were able to determine that *L. nipomensis* does prefer microhabitats in back dunes, particularly areas with north facing slopes which maximizes reproductive output (Fig. 5). We hypothesize that *L. nipomensis* grows better in these microhabitats because north facing slopes receive less insolation thereby retaining more soil moisture, which could minimize environmental stress between periods of rain (Bennie et al. 2006). However, after separating the interaction we found that slope did not impact seed pod production which implies aspect is more important than slope. Furthermore, since the type of cage did not change the likelihood of severe herbivory, we hypothesize that rabbits or other large mammals (those that were too big to get through either caging size) were the main herbivores at Black Lake Ecological Area (Fig. 6). We also demonstrated that the germination rate and seed production of *L. nipomensis* was significantly higher when scarified seeds were used (Fig. 4). In fact, only one plant that was unscarified was able to produce seed through the span of the experiment, this demonstrates the importance of scarifying seeds if immediate results are desired (Hughes 1915).

Despite strong evidence that north facing slopes maximize the reproductive output of *L. nipomensis*, our study could be complemented with additional reintroductions into other protected back dune habitats and long term monitoring. Because of the influence of precipitation patterns on annual species' life cycles, additional studies in other back dune areas could help confirm the applicability of our study to a broader spectrum of conditions (weather, soils, disturbance, biotic interactions) which will increase the success of large scale ex-situ seeding work with this species and those that share similar life strategies and preferences. Monitoring of the restored population at Black Lake should be continued for multiple generations because it has been found that long term monitoring is a superior indicator for reintroduction success compared to short term monitoring as the effect of interannual precipitation variation on this species is still relatively unexplored and negatively affects the population (Holl and Hayes 2006).

Even with the added benefit of additional pilot reintroductions and long term monitoring, this study demonstrates the importance of using pilot studies prior to reintroduction efforts. Not only did we find that specific site characteristics maximized reproductive output, but that out-planting

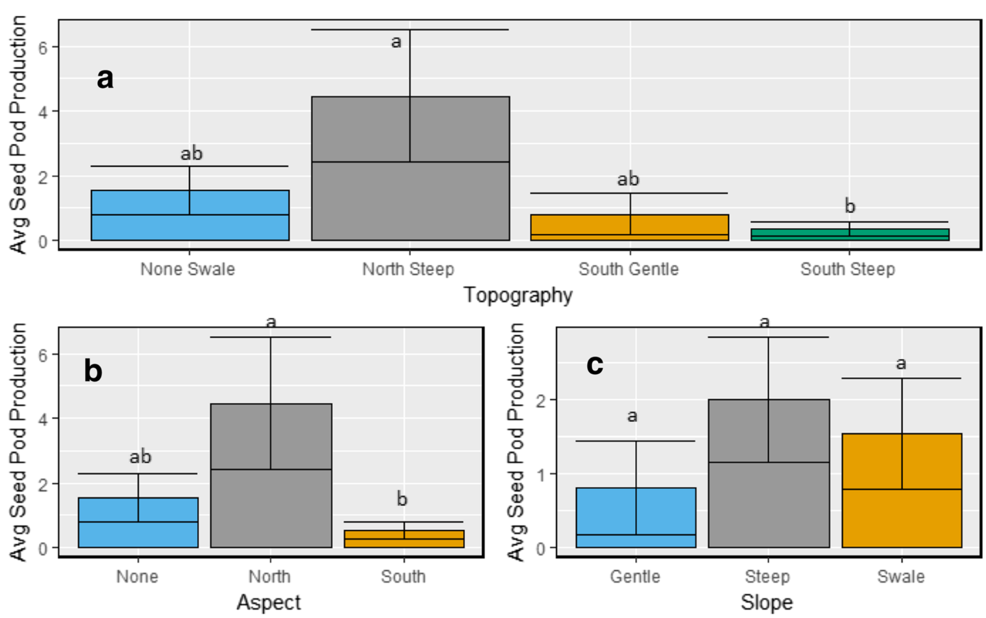

Fig. 5 The total seed pod production across **a**) the four different topography treatments and **b**) the three different aspect treatments and **c**) the three different slope treatments. Panel **a** shows that the north facing steep slope produced more seeds on average compared to the south facing steep slope ($p < 0.05$). Looking at Panel **b** and **c** we can see that slope has no direct effect (F = 0.031, $p = 0.861$) on the impact of topography giving aspect the greatest significance (F = 5.803, $p < 0.005$)

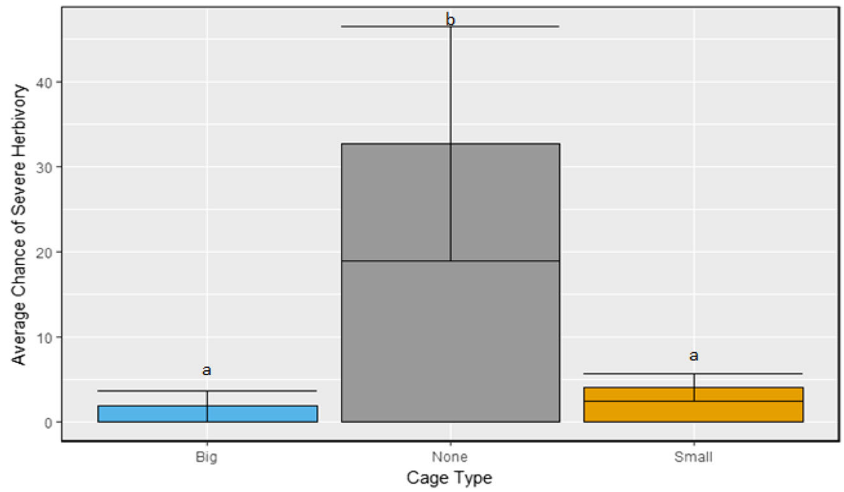

Fig. 6 The chance of severe herbivory (either multiple leaves or the entire plant being consumed) in each of the three different caging treatments. Plants located in the no cage treatment experienced more severe herbivory then plants that were protected by either the big or small cages ($F = 4.52$, $p < 0.05$). Error bars represent standard error

in back dune habitat without these characteristics reduced reproductive and therefore establishment success (Figs. 5, 6 and 7). Pilot studies are therefore useful because they provide information on microhabitat preferences which can be used to guide reintroduction efforts. These concerns are particularly pertinent for microhabitat conditions that only comprise a small portion of the overall habitat. For example, north facing steep slopes comprise less than 10% of the back-dune habitat in Black Lake Ecological Area. Therefore, over 90% of the back-dune habitat within Black Lake Ecological Area would not be ideal for the successful reestablishment of *L. nipomensis*.

Identification of the ideal microhabitats for a rare species is important for reintroduction efforts because having appropriately high lifetime reproductive output is necessary for the persistence of a population. This is particularly true for an annual plant population since there would be no seed produced for next year's generation if a plant cannot reproduce in the initial outplanting due to poor site selection. Even if some individuals are able to reproduce, if this occurs over multiple generations, the seed bank will become depleted and eventually be unable to sustain the next generation; something that is particularly important when there is limited plant material available. Therefore, while searching for microhabitats is often time consuming and costly, it is essential for the success of a rare plant introduction effort (Godefroid et al. 2011; Dunwiddie and Martin 2016) and pilot reintroductions should be utilized broadly to understand which microhabitat conditions are most likely to maximize establishment success.

Conclusion

It is important to prevent losses in rare plants can have unintended consequences through the loss of ecosystem services (Cardinale et al. 2012; Gamfeldt et al. 2008). Characterization of the habitat preferences of rare plants like *Lupinus nipomensis* allows practitioners to focus restoration efforts on areas that are most likely to lead to the successful establishment of a population. This increased understanding will

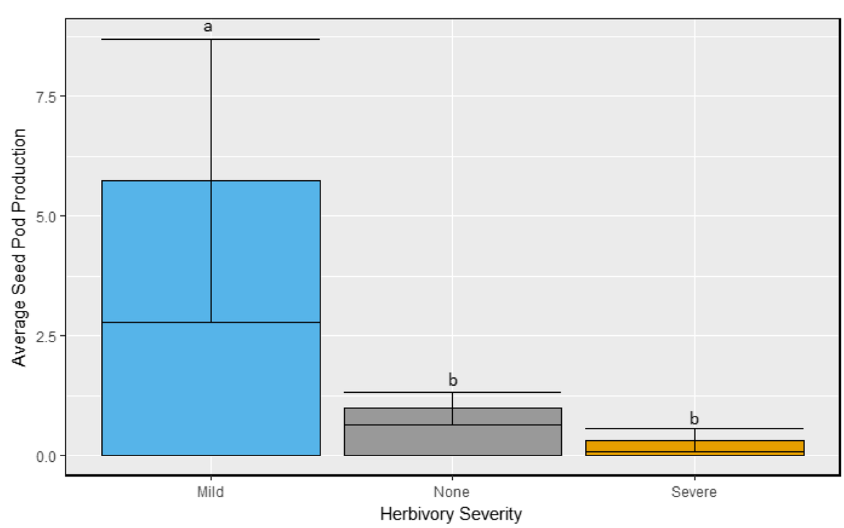

Fig. 7 The effect of severity of herbivory (none – no plant material was consumed, mild – only leaflets or a single leaf was consumed, severe – multiple leaves or the entire plant was consumed) on total seed pod production. Plants that experienced severe herbivory produced less seeds than those that had experienced mild herbivory ($p < 0.01$). There were no differences found between plants that experienced severe herbivory and no herbivory. Error bars represent standard error

allow practitioners to more predictably and successfully conserve and reintroduce new populations of declining rare plants. However, as our study demonstrates, pilot studies can be a small investment that will guide the selection of sites for restoration and reintroduction. Therefore, to ensure that these systems can continue to provide ecosystem services to coastal communities in the future, we need to promote the use of pilot projects in understanding the microhabitat preferences of endemic and endangered plants.

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