



Naval Base Ventura County, San Nicolas Island Terrestrial Flora Program

***Mesembryanthemum crystallinum* experiment 2019 field monitoring**

Final Report

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ABSTRACT

Invasive, non-native species are one of the top threats to biological diversity, which provides critical resilience and stability in an ecosystem. Crystalline iceplant (*Mesembryanthemum crystallinum*; hereafter MECR) decreases native plant richness as well as arthropod richness and functional diversity on San Nicolas Island, and replaces larger insects such as beetles, moths, and flies that are important prey items for the Island Fox with much smaller insects such as springtails. It covers a large portion of San Nicolas Island as well as all of the California and Mexico Channel Islands. The U.S. Navy aims to reduce MECR cover and restore diverse native habitat to benefit the natural resources on San Nicolas Island. We investigated several techniques to regain plant diversity and native plant cover in Fall 2016-Winter 2018 (Knapp et al. 2018); this report details our findings in a third year of vegetation monitoring. At each of three sites (Buckwheat Badlands, Caliche Plateau, and Stilted Dunes), we established 42 plots and applied combinations of Grow-kill, Herbicide, and Control treatments with and without hydroseeding native plant species. Monitoring with visual cover estimates in April of 2019 revealed several useful patterns. First, MECR cover was lowest in the Grow-kill plots at all three sites, as compared to Herbicide plots and no weeding Control plots, which had similar MECR cover to one another. Second, Grow-kill treatments benefitted plant species richness and native cover over Herbicide treatments in most sites and treatments, particularly when combined with hydroseeding, but did not provide additional benefits to these features in most cases when compared with control plots that were not weeded but were hydroseeded. Third, hydroseeding had clear benefits for plant species richness and native plant cover at Stilted Dunes, and for native cover at Buckwheat Badlands. While the three sites started with similar MECR cover in 2016, greater control was achieved at Caliche Plateau and Stilted Dunes right after treatments than at Buckwheat Badlands, which is a more heavily disturbed site with consistently greater MECR density throughout the site. By 2019, MECR cover remained low only at Stilted Dunes. This longer-term control at Stilted Dunes, combined with more open spaces for germination, likely influenced the more pronounced benefit of hydroseeding at that site. An extreme drought year following hydroseeding contributed to MECR control, but also hindered native plant establishment. We suggest that the Navy's goals can be achieved most cost-effectively by adjusting restoration strategies to the level of MECR invasion and native plant status at each site. A grow-kill strategy (or perhaps, repeat weed removal without watering) controls MECR while benefitting native plant richness and diversity, but at more heavily invaded sites, a sustained effort beyond one field season is needed to maintain this control. To increase native plant richness and diversity, hydroseeding is most beneficial where bare soil is available and native plants are sparsest. At sites with lower invasion levels, hydroseeding natives without MECR control may be a cost-effective strategy to regain native cover and diversity. We recommend the use of a biological control agent on the island to assist with MECR control, but native revegetation is also recommended to avoid increasing erosion. Recent intensive restoration plantings will make future seed collection for hydroseeding more efficient. These cumulative efforts will translate

to improved habitat for higher trophic levels, including rare vertebrates such as the Island Night Lizard and Island Fox.

INTRODUCTION

Biological diversity provides resilience and stability in an ecosystem, via the variety of responses that different species have to annual variation and disturbance (Gunderson 2000; Hautier et al. 2015). Invasive, non-native species are one of the top three threats to this biological diversity, and are a major driver of global change (Mack et al. 2000; Millennium Ecosystem Assessment 2005). Invasive plants alter disturbance regimes, nutrient cycles, the physical environment, and fluxes of both materials and energy (Mack and D'Antonio 1998; Liao et al. 2008; Ehrenfeld 2010). Understanding the impacts of plant invasions can help to guide the conservation and restoration of diverse, functional ecosystems (Lodge 1993; McMahon et al. 2006).

Mesembryanthemum crystallinum (hereafter MECR), or crystalline iceplant, is an annual South African plant that is a widespread invader. It was already reported as abundant on San Nicolas Island (SNI) by 1898 (Junak 2008). It accumulates salts and releases them into the soil upon its death, thereby creating a detrimental osmotic environment (Vivrette & Muller 1977). It is able to spread and form high soil cover, and has been associated with a decrease in both native plant species richness (Williams & Williams 1984) and annual pasture production (Kloot 1983). MECR has invaded the California coast from the San Francisco Bay area south to the border with Mexico and beyond (including all eight of the Channel Islands), and effective habitat restoration techniques are needed to regain the biological diversity and ecosystem function that has likely been lost in those areas.

In 2017 and 2018, we investigated the impacts of MECR invasion on arthropod abundance, richness, composition, feeding guilds, and functional diversity via impacts on plant diversity and native plant cover on SNI (Knapp et al. 2018). We found that either arthropod species richness or arthropod functional diversity (or both) was reduced in MECR plots at all three study sites, and that arthropod composition was consistently altered by MECR invasion at all three sites. Flies (Diptera), beetles (Coleoptera), ants (Formicidae: Hymenoptera), moths (Lepidoptera), wasps (Hymenoptera), and true bugs (Hemiptera) characteristic of native-dominated plots were replaced by small detritivores such as springtails (Collembola) and barklice (Psocoptera) in the *Mesembryanthemum*-dominated plots. The larger arthropod taxa found in native-dominated plots are important prey items for the Island Fox (Cypher et al. 2011). These changes have negative implications for ecosystem functions, stability, and resilience to global environmental change on the island, and habitat restoration will be critical.

The U.S. Navy aims to reduce MECR cover and restore diverse native habitat to benefit the natural resources on SNI. Given the large extent of MECR invasion on the island, they require that the methods used be cost-effective at a large scale. We investigated several techniques to regain plant diversity and native plant cover, and thus support higher trophic levels starting with terrestrial arthropods (Knapp et al. 2018). This report details our findings in a third year of vegetation monitoring.

METHODS

At each of three sites across SNI, chosen for a combination of extensive MECR invasion, accessibility, and habitat diversity, Director of Conservation Denise Knapp, Conservation Technician Chris Garoutte, and U.S. Navy Natural Resources Manager William Hoyer set up six 2x2 meter plots each of the following seven treatments (42 plots at each site, 126 plots total):

- Grow-kill MECR with hydroseeding
- Grow-kill MECR, without hydroseeding
- Herbicide MECR with hydroseeding
- Herbicide MECR, without hydroseeding
- No MECR treatment Control, with hydroseeding
- No MECR treatment Control, w/o hydroseeding
- Native-dominated Control

Our three sites are shown in **Figure 1** and their locations are as follows:

- 1) Buckwheat Badlands (BB), 33.221/ -119.449
- 2) Stilted Dunes (SD), 33.261/ -119.554
- 3) Caliche Plateau (CP), 33.247/ -119.544

MECR treatments

Santa Barbara Botanic Garden (SBBG) Director of Conservation & Research Denise Knapp and Conservation Technician Alena Leonatti visited the island each month between October 2016 and January 2017 to perform grow-kill treatments. We used 2-gallon watering cans to apply 8 gallons of water on each visit in October and November, which saturated the soil to a degree at which we thought it would enhance *Mesembryanthemum* germination. Because we saw little germination either inside or outside the plots during those months, we increased our water quantity to 12 gallons per plot in December, applied over two days which resulted in three days of saturation. We used a 60-gallon AquaTank water bladder together with a variety of plastic receptacles to fill the watering cans.

Before January, the few seedlings we observed were easily controlled by hand pulling, which made hoeing or raking unnecessary and allowing us to disturb the soil as little as possible. With the greater than average rain that had fallen earlier in the month, no watering was necessary in January, and there was a thick carpet of *Mesembryanthemum* seedlings. This germination was likely related to both rainfall and temperature cues, and may or may not have been enhanced by our watering treatments. We used a hoe to remove these seedlings, and removed the densest clumps from the plots in order to avoid this barrier inhibiting the germination of other taxa.



Figure 1. The Stilted Dunes (SD), Caliche Plateau (CP), and Buckwheat Badlands (BB) study locations on San Nicolas Island.

Alena Leonatti visited the island on February 2 to direct herbicide treatments performed by Kevin Thompson of Channel Islands Restoration (CIR). Due to the heavy fog and potential diluting effect it may have, Kevin used 2.5% glyphosate, which is slightly higher than the normal rate (2%). The spraying was performed successfully. At the same time, Alena hoed *Mesembryanthemum* in the appropriate plots.

Hydroseeding

Seed was collected from the general vicinity of each of our study sites on three separate visits between May 23 and July 12, 2016. Denise Knapp, Alena Leonatti, and SBBG Gardener Robert Carrillo visited the island from February 14-16, 2017 to perform the hydroseeding, with the help of William Hoyer (U.S. Navy) and Northern Arizona University (NAU) biological soil crust experts Anita Antoninka and Peter Chuckran. Mixes of 8-15 species customized for each site (**Table 1**) were applied at a rate of 0.008 lbs/square meter (=0.55-0.57 lbs/site total) together with paper mulch and tackifier using a Turbo Turf HS-50-M portable hydroseeder (Turbo Technologies Inc., Beaver Falls, PA). M-Binder tackifier was applied at a rate of 100-200 lbs/acre, and Nature's Own paper fiber mulch was applied at a rate of 1,500 lbs/acre. Paper mulch was chosen over wood mulch both because it is required for our portable model, and because it creates a "paper mâché" over the soil which seals in moisture and provides better seed to soil contact.

Vegetation Surveys

Vegetation surveys were performed in April of 2019 by Denise Knapp and Conservation Technician Stephanie Calloway. We visually estimated cover for each plant taxon found within all 42 1x1 m subplots at each of our three sites. Two surveyors worked together, estimating cover independently and then coming to an agreement, in order to provide the most accurate and replicable estimate. Individual species cover estimates were combined to produce an estimate of total relative cover. We also assessed absolute cover (the absolute area covered by vegetation as observed from above) in the field. Using these data, we also calculated plant species richness and native plant cover.

Statistical Analyses

To compare experimental MECR restoration treatments, ANOVA analyses were used for normally distributed data with approximately equal variances, then pairs compared using a Tukey-Kramer HSD test, which presents a familywise error rate (it corrects for the greater probability of getting a significant result when performing multiple tests). When data were not distributed normally, Wilcoxon/Kruskal-Wallis tests were used to compare multiple samples, then pairs were compared using the Steel-Dwass method, which corrects for multiple tests. These corrections result in a conservative interpretation of statistical significance when compared to any given pairwise comparison in isolation. The above analyses were all performed in JMP version 13.0 (Statistical Analysis Software, Cary, North Carolina). Results are considered statistically significant when the probability that there is no difference between the means is five percent ($p=0.05$) or less. In other words, we reject the null hypothesis that there is no difference

Table 1. Native plant seed used for hydroseeding on San Nicolas Island, February 2016

Species	Date collected	Total per species (g)
Stilted Dunes (SD)		
<i>Abronia maritima</i>	June 2016	0.10
<i>Abronia umbellata</i>	June 2016	2.10
<i>Achillea millefolium</i>	June 2016	9.10
<i>Amblyopappus pusillus</i>	June 2016	16.70
<i>Astragalus traskiae</i>	May, June 2016	60.20
<i>Calystegia macrostegia</i>	July 2016	19.90
<i>Daucus pusillus</i>	June 2016	31.00
<i>Isocoma menziesii</i>	May, June, July 2016	67.00
<i>Lepidium lasiocarpum lasiocarpum</i>	June 2016	4.60
<i>Leptosyne gigantea</i>	June 2016	5.60
<i>Lotus argophyllus</i>	June 2016	9.80
<i>Lupinus albifrons douglasii</i>	May, June 2016	17.80
<i>Malacothrix foliosa polycephala</i>	May 2016	0.20
<i>Spergularia macrotheca</i>	June 2016	6.50
	Sum (g)	250.60
	Sum (lb)	0.55
Buckwheat Badlands (BB)		
<i>Achillea millefolium</i>	June, July 2016	35.10
<i>Amblyopappus pusillus</i>	June 2016	27.20
<i>Dudleya virens insularis</i>	July 2016	16.00
<i>Eriogonum grande var. timorum</i>	May, June 2016	93.90
<i>Isocoma menziesii</i>	June, July 2016	49.30
<i>Leptosyne gigantea</i>	May, June 2016	16.80
<i>Lomatium insulare</i>	June 2016	0.20
<i>Plantago ovata</i>	June 2016	9.80
	Sum (g)	248.30
	Sum (lb)	0.55
Caliche Plateau (CP)		
<i>Achillea millefolium</i>	June, July 2016	34.50
<i>Calystegia macrostegia</i>	July 2016	0.20
<i>Deinandra clementina</i>	July 2016	25.00
<i>Dudleya virens insularis</i>	July 2016	11.90
<i>Gnaphalium palustre</i>	July 2016	0.50
<i>Isocoma menziesii</i>	July 2016	75.50
<i>Lepidium lasiocarpum lasiocarpum</i>	June 2016	14.20
<i>Leptosyne gigantea</i>	May 2016	2.80
<i>Lomatium insulare</i>	June 2016	78.80
<i>Oligomeris linifolia</i>	June 2016	15.00
<i>Malacothrix foliosa polycephala</i>	May, June 2016	0.80
	Sum (g)	259.20
	Sum (lb)	0.57

between the means. A statistical trend is indicated when $0.10 \leq p \leq 0.05$. Results are also considered ecologically significant when error bars do not overlap between treatments.

RESULTS

MECR cover

Data for MECR cover in 2019 are presented in **Figure 2**. Residuals by treatment were normally distributed, and Tukey’s tests were used for pairwise comparisons. Comparison data are presented in **Table 2**.

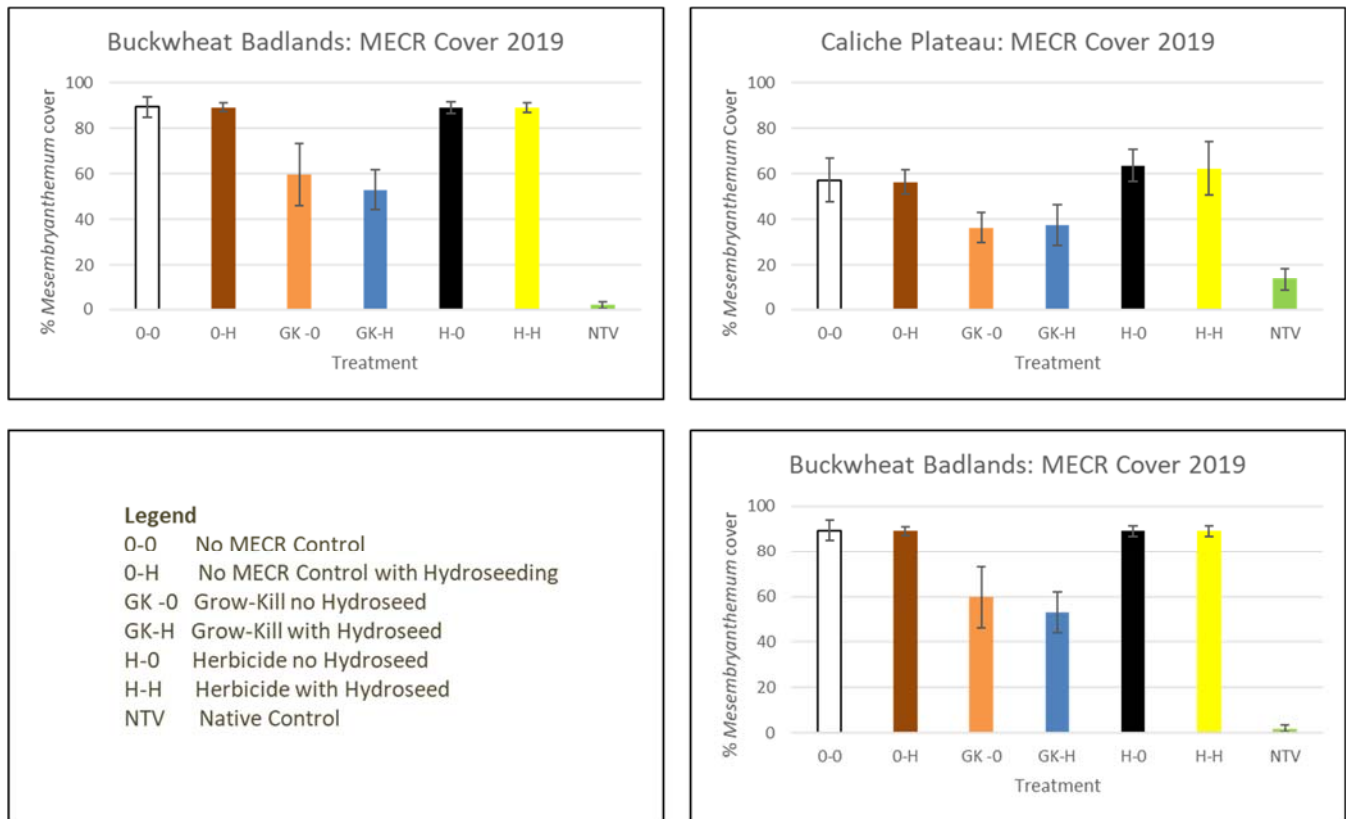


Figure 2. *Mesembryanthemum* cover in 2019 by site and treatment on San Nicolas Island. Comparisons of pairs were made with Tukey’s HSD tests. Statistical differences are discussed in the text.

Patterns were similar at all three sites, and data were analyzed with the site data combined. Grow-kill with hydroseeding treatments, which had a cumulative mean of $36.9\% \pm 5.5$ MECR, had significantly less MECR than both the Herbicide and No MECR control treatments ($64.3\% \pm 5.7$ in Herbicide without hydroseeding plots and $63.9\% \pm 6.2$ in Herbicide with hydroseeding; $56.6\% \pm 7.7$ and $58.5\% \pm 6.6$ in No MECR control plots without and with hydroseeding, respectively). Native control plots had significantly lower MECR than all other treatments (mean $11.0\% \pm 3.4$).

Table 2. *Mesembryanthemum* cover comparison data by treatment, all three sites combined. Significant results are highlighted in orange (highly significant) and red.

Level	- Level	Difference	Std Err Dif	Lower CL	Upper CL	p-Value
H-0	NTV	53.27778	8.468680	27.8768	78.67874	<.0001*
H-H	NTV	52.88889	8.468680	27.4879	78.28985	<.0001*
0-H	NTV	47.50000	8.468680	22.0990	72.90096	<.0001*
0-0	NTV	45.61111	8.468680	20.2102	71.01207	<.0001*
GK-0	NTV	31.44444	8.468680	6.0435	56.84540	0.0057*
H-0	GK-H	27.33333	8.468680	1.9324	52.73429	0.0262*
H-H	GK-H	26.94444	8.468680	1.5435	52.34540	0.0300*
GK-H	NTV	25.94444	8.468680	0.5435	51.34540	0.0419*
H-0	GK-0	21.83333	8.468680	-3.5676	47.23429	0.1422
0-H	GK-H	21.55556	8.468680	-3.8454	46.95651	0.1529
H-H	GK-0	21.44444	8.468680	-3.9565	46.84540	0.1574
0-0	GK-H	19.66667	8.468680	-5.7343	45.06762	0.2422
0-H	GK-0	16.05556	8.468680	-9.3454	41.45651	0.4871
0-0	GK-0	14.16667	8.468680	-11.2343	39.56762	0.6353
H-0	0-0	7.66667	8.468680	-17.7343	33.06762	0.9711
H-H	0-0	7.27778	8.468680	-18.1232	32.67874	0.9777
H-0	0-H	5.77778	8.468680	-19.6232	31.17874	0.9934
GK-0	GK-H	5.50000	8.468680	-19.9010	30.90096	0.9949
H-H	0-H	5.38889	8.468680	-20.0121	30.78985	0.9954
0-H	0-0	1.88889	8.468680	-23.5121	27.28985	1.0000
H-0	H-H	0.38889	8.468680	-25.0121	25.78985	1.0000

Plant Species Richness

Species richness comparison charts for 2019 are presented in **Figure 3**. The statistical penalty when comparing seven different treatments, combined with moderate to high variability, rendered few differences statistically significant. Ecologically significant patterns are recognized when error bars do not overlap.

At Buckwheat Badlands, Native Control plots had much higher plant species richness (mean 11.2 ± 1.2) than all other treatments (all with mean species richness of less than five). Grow-kill treatments had greater species richness (mean 4.3 ± 0.9 and 4.7 ± 0.9 without and with hydroseeding, respectively) than Herbicide treatments, which had the lowest species richness (2.5 ± 0.6 and 2.7 ± 0.4 mean species/plot without and with hydroseeding, respectively) of all treatments.

At Caliche Plateau, species richness was generally similar in all treatments (means range from 7.8 to 11.0), including Native Control plots. Grow-kill without hydroseeding plots had greater species richness (mean 11.0 ± 0.6) than Herbicide and No MECR Control treatments, and had similar richness to Native Controls (mean 10.3 ± 0.6).

At Stilted Dunes, a clear pattern is visible, with hydroseeding treatments all having higher species richness than paired non-hydroseeded treatments. No MECR Control, Grow-kill, and Herbicide treatments lacked significant differences, justifying a combination of these treatments to compare Hydroseeded, Not Hydroseeded, and Native Control plots. Tukey comparisons revealed that hydroseeded plots had significantly greater species richness (mean 9.5 ± 0.3) than both Native Control (mean 7.6 ± 0.9) and non-hydroseeded plots (mean 7.4 ± 0.3) at this site. Statistical comparison data are presented in **Table 3**.

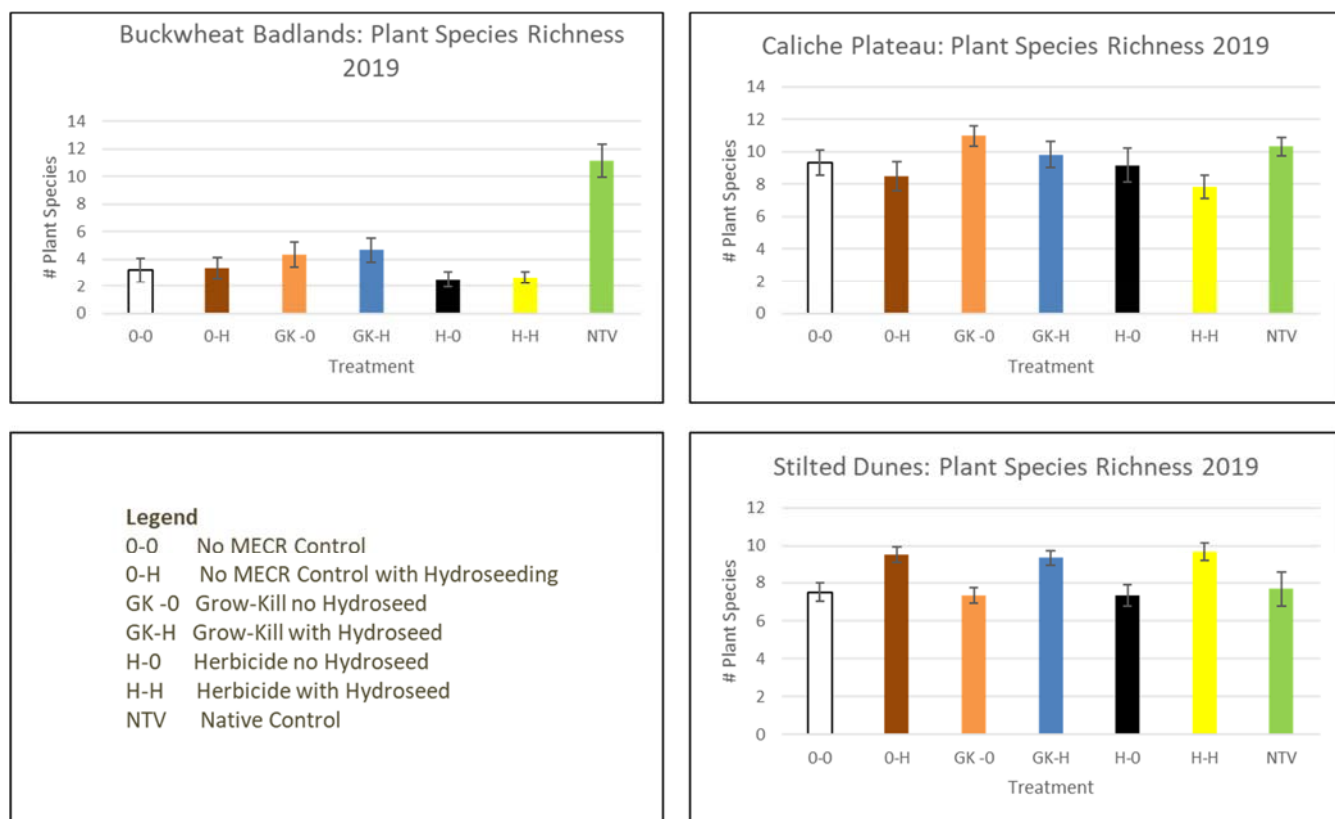


Figure 3. Plant species richness in 2019 by site and treatment on San Nicolas Island. Steel-Dwass non-parametric tests were used to compare all treatments at each site. Statistical differences are discussed in the text.

Table 3. Tukey HSD comparisons of plant species richness by hydroseeding treatments at Stilted Dunes. Yes = hydroseeded, No = not hydroseeded, Native = native dominated Control plots. Significant results are highlighted in orange (highly significant) and red.

Level	- Level	Difference	Std Err Dif	Lower CL	Upper CL	p-Value
Yes	No	2.140523	0.4383790	1.07139	3.209653	<.0001*
Yes	Native	1.862745	0.6155173	0.36161	3.363885	0.0120*
Native	No	0.277778	0.6110407	-1.21244	1.768000	0.8927

Native Plant Cover

Native plant cover data for 2019 are presented in **Figure 4**. Non-parametric Steel-Dwass tests were used for statistical comparisons of pairs. With penalties for multiple comparisons, there were no statistically significant differences between treatments at any of the sites. There was, however, a statistical trend ($0.10 \leq p \leq 0.05$) for Grow-kill plots with hydroseeding to have greater native cover than No MECCR Control treatments with hydroseeding at Buckwheat Badlands. Patterns can also be observed by looking for differences between treatments in mean + standard error (i.e. error bars do not overlap). A clear pattern exists for the Grow-kill with hydroseeding treatment to have greater native cover than all other experimental treatments at Buckwheat Badlands. Native cover was an average of 18 ± 4 SE in these plots, over half that of Native Control plots (30.6 ± 9.1), and much higher than both No MECCR Control plots (mean 3.3 ± 2.5 without hydroseeding, mean 2.6 ± 0.9 with hydroseeding) and Herbicide plots (mean 2.4 ± 1.4 without hydroseeding, mean 5.3 ± 2.2 with hydroseeding).

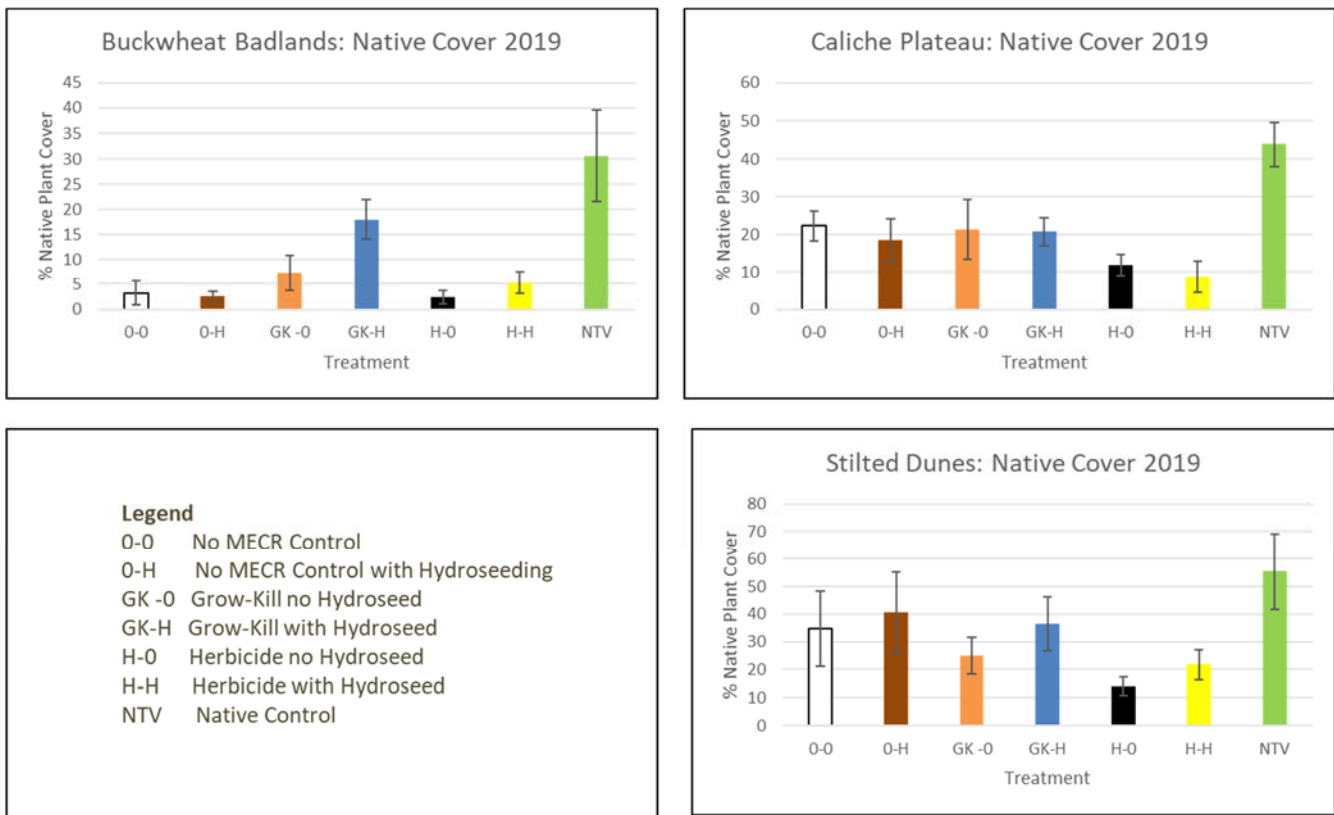


Figure 4. Native plant cover in 2019 by site and treatment on San Nicolas Island. Steel-Dwass non-parametric tests were used to compare all treatments at each site. Statistical differences are discussed in the text.

At Caliche Plateau, both Herbicide treatments had apparently lower native cover (mean $11.9\% \pm 2.8$ and 8.8 ± 4.3 without and with hydroseeding, respectively) than all other treatments (means between 18.4

and 22.3). Statistically, there was a trend for Herbicide without hydroseeding plots to have lower native cover than Native Controls, which had mean cover of $43.8\% \pm 5.8$.

At Stilted Dunes, the lowest native cover was found in Herbicide without hydroseeding plots (mean $14.1\% \pm 3.5$), while the greatest native cover in the experimental treatments was in Grow-kill with hydroseeding ($36.6\% \pm 9.7$) and No MECR Control with hydroseeding ($40.5\% \pm 14.8$) plots. Native cover in the latter plots approached that of the Native Control plots ($55.4\% \pm 13.9$).

DISCUSSION

Several useful patterns have emerged from this research. First, in this third year post-treatment, MECR cover was lowest in the Grow-kill plots, as compared to Herbicide plots and No weeding Controls, which had similar MECR cover to one another. This pattern was significant and consistent at all three sites, and in contrast to our conclusions after the first two years, when Herbicide treatments appeared most beneficial for MECR control (Knapp et al. 2018). Given that we did not see a germination response to our watering treatments until MECR germinated in all plots, this success could be due to the repeat hoeing that those plots received rather than to the water applied to flush the seed bank.

Second, at least one of the Grow-kill treatments also had apparent benefits for species richness over Herbicide treatments at both the Buckwheat Badlands and Caliche Plateau sites, as well as benefits over Herbicide treatments for native cover when utilized with hydroseeding at all three sites. In most cases, however, No MECR Control plots supported similar levels of species richness and native cover to Grow-kill plots, especially when combined with hydroseeding of native plants. This indicates that the primary effect here is the Herbicide treatment depressing species richness and cover, not Grow-kill benefitting it. The exception was at Buckwheat Badlands, where Grow-kill plots supported greater native cover than all other treatments. That site has the densest MECR throughout the site, and has typically supported the lowest species richness and native cover of all three sites, thus has benefitted the most from MECR control and native seed addition.

Third and lastly, hydroseeding had clear benefits for plant species richness and native plant cover at Stilted Dunes, where adding native plant seed was even more beneficial for species richness than MECR control. It also had benefits for native plant cover at Buckwheat Badlands, where Grow-kill plots with hydroseeding had by far the best native cover, reaching over half that of the Native Control plots. This trend was driven by high cover of the native herb *Amblyopappus pusillus* in several plots.

A comparison of MECR cover across sites and years was performed by excluding native plots and combining all treatments. Buckwheat Badlands plots supported 58% MECR cover in 2016 and 55% in 2017 following control. Cover then dropped to 5% in 2018 (a major drought year), but increased to 78% (above baseline levels) in 2019. Clearly, drought has an even more negative effect on MECR success than our control efforts. MECR cover in Caliche Plateau plots dropped from 58% in 2016 to 30% in 2017 after control, then to 7% in the drought year of 2018, but increased to 52% in 2019. Stilted Dunes supported 60% MECR cover in 2016, which dropped to 18% in 2017 following control, and to 8% in 2018 in a drought

year, then increased to 31% in 2019. This shows that while the three sites started with similar MECR cover in 2016, greater control was achieved at Caliche Plateau and Stilted Dunes in the spring following treatments than at Buckwheat Badlands, which is a more heavily disturbed site with consistently greater MECR density throughout the site (vs. just in the plots). After the drought, MECR cover increased at Buckwheat Badlands plots to well past 2016 levels, whereas MECR at Caliche Plateau bounced back to pre-treatment levels, and MECR cover stayed low at Stilted Dunes.

Why was the benefit of hydroseeding most pronounced at the Stilted Dunes site? We hypothesize that it is related to two factors: 1) long-term MECR control was most effective at this site of the three, providing more open soil to receive the seeds with less competition, and 2) Shrubs like *Lupinus arboreus*, *Acmispon argophyllus*, and *Astragalus traskiae* that dominate at this backdune site appear to provide more open spaces for germination underneath and between them than are available at the other two sites. The dense, low-growing *Isocoma menziesii* that dominates at the Caliche Plateau site together with annual herbs does not provide as many open spaces for germination, while MECR is an overwhelming competitor at the Buckwheat Badlands site.

The apparent benefit of hydroseeding is a welcome change from our 2018 report. As of April 2018 (1 year and 2 months following treatment), there was not yet any significant effect (statistical *or* ecological) of hydro-seeding. In April 2017, we saw promising seedling growth, and boosted species richness at Buckwheat Badlands and Stilted Dunes, but the fall 2017-spring 2018 rainfall year was extremely dry, and many of our seedlings perished. It seems that enough of the hydroseeded material persisted and grew, and the 2018-2019 rainfall was sufficient, to support further growth of the native plants at the two sites. Counting on sufficient rainfall is an increasingly risky strategy, however, as droughts grow longer and more frequent. It would be worthwhile to utilize some of the abundant fresh water produced at the island's desalination plant to water seeded areas in the future. Waiting for years when rainfall is looking to be abundant to hydroseed could also be a successful strategy, if contract timelines allow.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The U.S. Navy's goals of reducing *Mesembryanthemum crystallinum* (MECR) cover and restoring diverse native habitat can be achieved most cost-effectively by adjusting restoration strategies to the level of MECR invasion and native plant status at each site. A grow-kill strategy (or perhaps just repeat removal without watering) is more effective than herbicide at controlling MECR while benefitting native plant richness and diversity. At more heavily invaded sites, a sustained effort beyond one field season is needed to maintain this control. To increase native plant richness and diversity, hydroseeding is most beneficial where bare soil is available (either via MECR control or natural conditions, or both) and native plants are sparsest. At sites with less MECR, hydroseeding natives without MECR control may be a cost-effective strategy to regain native cover and diversity.

Even when adjusting restoration strategies to site-specific needs as described above, a major effort will be needed to achieve the goals of reducing MECR cover and restoring native plant cover and diversity at

a large scale on SNI. Successful conversion of the one-acre Scorpion Rock (Santa Cruz Island, CA) from domination by MECR and other invasive plants to majority native plant cover required nearly eight years of effort and hundreds of thousands of dollars (Adams et al. 2014; personal communication with David Mazurkiewicz, National Park Service). Given the vast extent of MECR on the island (iceplant species dominate at least 105 acres; HDR 2014), progress will be slow and expensive.

Biological control, or the introduction of a novel herbivore to control invasive plant populations, is an important tool for conservation management (Caltagirone 1981), and with the extensive testing required in the United States, is now safer than ever (Sheppard et al. 2005). This may be the best option for MECR control on SNI. In this case, the relative taxonomic and genetic isolation of MECR (i.e., there are only two native members of the Aizoaceae family in California) is an advantage, as it will be easier to find a low-risk biological control agent. Further, the island's remoteness would buffer the project from unintended consequences. While MECR offers some protection from erosion, it is an annual plant and does not emerge until the latter portion of the rainy season, which limits this benefit. Still, some revegetation, either prior to or simultaneous with a biocontrol program, would be beneficial to avoid the consequence of extensive MECR control without replacement by native vegetation.

Irrigated container plantings have been installed successfully in recent years on San Nicolas Island in accessible, high-priority locations. These restoration sites will make bulk seed collection for hydroseed application more productive and less time- and resource-intensive going forward. We recommend that restoration efforts continue with seed collection concentrated in these areas, followed by targeted MECR control, native plant hydroseeding, and irrigation when needed.

Our project achieved significant MECR control and native habitat gain for some sites and treatments, with Grow-kill treatments followed by hydroseeding offering the best results. These gains will in all likelihood translate to improved habitat for higher trophic levels, given the negative effects of MECR on arthropod species richness, functional diversity, and composition that we observed early in our study (Knapp et al. 2018). Habitat restoration efforts typically regain lost invertebrate diversity (Knapp 2014), often even after only \leq one year for some insect groups (e.g., Waltz & Covington 2004; Kaiser-Bunbury et al. 2009; Lomov et al. 2010). This will be important for the survival and well-being of rare vertebrates such as the Island Fox (Cypher et al. 2011) and Island Night Lizard (U.S. Fish and Wildlife Service 2012), and for biodiversity at large on the island.

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