San Jose State University
SJSU ScholarWorks

Master's Theses

Master's Theses and Graduate Research

Spring 2013

Restoring native plants following invasive Malephora Crocea (coppery iceplant, Aizoaceae) eradication on Anacapa Island

Nathan William Hale
San Jose State University

Follow this and additional works at: https://scholarworks.sjsu.edu/etd_theses

Recommended Citation

RESTORING NATIVE PLANTS FOLLOWING INVASIVE *MALEPHORA CROCEA* (COPPERY ICEPLANT, AIZOACEAE) ERADICATION ON ANACAPA ISLAND

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Nathan William Hale

May 2013

The Designated Thesis Committee Approves the Thesis Titled

RESTORING NATIVE PLANTS FOLLOWING INVASIVE *MALEPHORA CROCEA* (COPPERY ICEPLANT, AIZOACEAE) ERADICATION ON ANACAPA ISLAND

by

Nathan W. Hale

APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

SAN JOSÉ STATE UNIVERSITY

May 2013

Dr. Susan Lambrecht	Dept. of Biological Sciences
Dr. Shannon Bros-Seemann	Dept. of Biological Sciences
Dr. Lynne Trulio	Dept. of Environmental Studies

ABSTRACT

RESTORING NATIVE PLANTS FOLLOWING INVASIVE *MALEPHORA CROCEA* (COPPERY ICEPLANT, AIZOACEAE) ERADICATION ON ANACAPA ISLAND

by Nathan W. Hale

To avoid unintended complications of invasive species eradication, it is important to understand the potential implications of the techniques used in species eradication efforts. This study aimed to compare how different methods of removing *Malephora crocea* affect the survivorship of planted seedlings of native perennial plants on Anacapa Island. Employing a randomized complete block design in an *M. crocea* stand, three removal treatments were tested: 1) hand-pull; 2) spray with herbicide and leave skeletons; and 3) spray and then remove skeletons after 2.5 months. In each treatment, seedlings of three species (*Leptosyne gigantea*, *Frankenia salina*, and *Grindelia stricta*) and seeds of two species (*L. gigantea* and *G. stricta*) were planted. Survivorship and seed establishment were monitored quarterly between March 2010 and January 2011. For transplanted seedlings, the spray-and-leave treatment resulted in higher survivorship, while no difference was observed between the pull-treatments. Seed establishment was very low overall, but results of seeding of *G. stricta* showed that the spray-and-pull treatment provided for higher establishment than other treatments. *L. gigantea* seed establishment was inconclusive. The spray-and-leave treatment also provided the highest relative soil moisture. My results suggest that the spray-and-leave treatment provided the most suitable conditions for survival of transplanted native perennial vegetation.

ACKNOWLEDGEMENTS

Finally, I'd like to acknowledge my newborn son, Miles Donnan Hale, whose imminent arrival provided me with the impetus to push through the written portion of this project; I love you, Miles.

Table of Contents

List of Figures

List of Tables

Introduction

The human-caused redistribution of the Earth's biological organisms has resulted in dramatic ecosystem disruptions. While species introductions into novel environments can be natural events, humans have accelerated this process by orders of magnitude (Vitousek et al. 1997*b*; Mooney & Cleland 2001). These human-mediated species introductions have resulted in species – here defined as invasive species – establishing and flourishing in novel habitats, causing broad-scale harm to populations of the indigenous species of these habitats, and causing general habitat degradation. Such invasive species have been implicated in perturbations to food webs (Vitousek et al. 1996); nutrient, fire, and water cycles (D'Antonio & Vitousek 1992; Dassonville et al. 2008; Ehrenfeld 2003; Raizada et al. 2008; Ehrenfeld 2010; Young et al. 2010*a*;); ecosystem structure (Saunders et al. 2003; Ehrenfeld 2010; Young et al. 2010*b*); and evolutionary trajectories (Mooney & Cleland 2001), the results of which have impacted global biodiversity and ecosystem stability (D'Antonio & Vitousek 1992; Vitousek et al. 1996; Vitousek et al. 1997*a*; Mooney & Cleland 2001; Sax et al. 2007; Wright 2011). The occurrence of human-caused invasions has contributed to the extinction and extirpation of native species (Vitousek et al. 1996). While mechanisms underlying invasion-related extinctions are primarily observed through impacts of predator and pathogen introductions (Sax et al. 2007), competitive pressure by invasive species to the point of inevitable extinction may be a latent effect that can take hundreds to thousands of years to become realized (Sax et al. 2007). The potential of there being a debt of unrealized destruction from introduced species is supported in the current distribution of

1

invasive species relative to the time of introduction. In a study of 28 European countries, Essl et al. (2011) found that, despite there being an increase in species introductions since 1950 compared to introductions prior to 1950, introduced species richness was predominantly representative of pre-1950s introductions. It is, therefore, possible that more recently introduced species have not yet had time to achieve their maximum level of damage.

Plants represent a significant category of invasive species and can cause dramatic changes to habitats. The total number of non-native plant species in the United States was recently estimated at 25,000 (Pimentel et al. 2005). Many of these species are implicated in a wide range of substantial ecosystem effects (Vitousek et al. 1997*a*; Vitousek and Walker 1989). One example depicting the magnitude of ecosystem disruption possible from a plant invasion is the invasion of *Bromus tectorum* (cheat grass, Poaceae) into the Great Basin of North America. *B. tectorum* was introduced in the late 1800s, and it eventually spread throughout the Great Basin aided, in part, by grazing cattle (Knapp 1996). The dense, fine-textured growth form of this annual grass generated an approximate 20-fold increase in the fire-return interval throughout the basin (Vitousek et al. 1996), which has increased the spread of *B. tectorum*. The ecological effect has been the elimination of native vegetation in large areas, increased erosion, decreased habitat and forage for native animal species, and an overall biological impoverishment (Knapp 1996). Meinke et al. (2009) estimated *B. tectorum* dominates over 28 million ha in the Intermountain West in Idaho, Oregon, Nevada, Utah, and Washington.

The invasion and dominance of *Cocos nucifera* (coconut palm, Arecaceae) within tropical and subtropical islands demonstrates how invasive species can generate radiating impacts across ecosystems (Young et al. 2010*a*; Young et al. 2010*b*; McCauley et al. 2012). *C. nucifera* indirectly reduced the allochthonous bird deposits into the forests of Palmyra Atoll in the Pacific Ocean by providing less-suitable nesting and roosting sites for seabirds compared with native trees (Young et al. 2010*a*). The decrease in habitat for birds has resulted in reduced bird-derived nutrient inputs, which has simultaneously lowered the propagation success of native vegetation, decreased the nutrient content of the remnant native vegetation, decreased diversity and abundance of insects, and decreased body size of native reptiles and spiders (Young et al. 2010*a*). In addition, the surrounding waters experienced significantly reduced nutrient loads, resulting in fewer and smaller-sized zooplankton, which decreased animal occurrences within the aquatic habitats adjacent to *C. nucifera*-dominated forests (McCauley et al. 2012).

Island ecosystems are considered to be inherently susceptible to invasions (Vitousek et al. 1997*a*; Denslow 2003; Kueffer et al. 2010), as invasive species are predicted to establish more easily within islands (Denslow 2003), and island ecosystems are predicted to suffer more impacts from invaders relative to continental areas (D'Antonio & Dudley 1995). This explanation of increased invasibility of islands has been attributed, in part, to a reduced capacity of these systems to withstand invasions as compared to continental systems (Denslow 2003). In general, islands appear to support higher net resource availability for invading species relative to continental systems and, relative to invading species, island-adapted species have a reduced ability to preempt

those resources (Denslow 2003). These characteristics of islands are credited with the lack of invasion resistance observed on islands (Pattison et al. 1998). That islands are inherently more invasible is a topic of some debate (Sol 2000), but the heightened impact from invasions on island-adapted species is well supported (D'Antonio & Dudley 1995; Vitousek et al. 1996). Native island species are generally derived from smaller pools of potential colonizers than are continental species, resulting in a possible vacancy of niches in island communities (D'Antonio & Dudley 1995). In addition, due to their isolation, island species have smaller populations, fewer patches of habitat, and a reduced ability to disperse relative to continental species (D'Antonio & Dudley 1995; Denslow 2003). Reduced dispersal is considered to be an adaptation of island species to concentrate reproductive effort within available niches rather than losing diaspores in the surrounding ocean water (Eliasson 1995). These demographic factors are likely contributors to higher impacts on island species from species invasions (D'Antonio & Dudley 1995). For example, the threat of extinction of terrestrial species as a result of invasive species pressures is among the most pronounced in island species (Vitousek et al. 1996).

The success of species invasions is not solely attributable to relocations and character differences between invaders to native species. Disturbances, such as clear-cutting and agriculture, promote species invasions (Jenkins & Pimm 2003; Eschtruth & Battles 2009; Kueffer et al. 2010) and reduce a system's invasion resistance (D'Antonio et al. 2001). These effects are partly due to the increased resource availability following disturbance (Chakraborty & Li 2010). Satellite image surveys of global disturbances have been used to predict invasive species occurrences, the results of which have been

supported by field observations of major species invasions (Jenkins & Pimm 2003).

These paired anthropogenic mechanisms–the movement of species beyond their native

range and the human-mediated increase in ecosystem disturbances–has resulted in the

ubiquitous presence of invasive species (Vitousek et al. 1997*a*; Vitousek et al. 1997*b*).

In the wake of the destructive consequences to ecosystems and the economic and

social impacts caused by invasive species (see Pimentel et al. 2001 and Pimentel et al.

2005), the tide of invasive species is being countered with the prioritization of species

eradication efforts by governments, conservation organizations, and corporations.

Although the goal of these efforts is the complete eradication of the target species and the

repopulation of native species and ecosystem functions (Myers et al. 2000; Howald et al.

2003), in some cases the eradication itself has resulted in negative ecosystem impacts

such as the replacement of eradicated species with secondary invasive species (Zavaleta

et al. 2001; Allen et al. 2005; Banerjee et al. 2006; Cox & Allen 2008; Crimmins &

McPherson 2008), the elimination of limiting factors in the system, such as removal of

predatory pressure, and the sudden availability of resources (Levine et al. 2002; Hulme &

Bremner 2006; Cox & Allen 2008). The increase of secondary invasive species is

especially characteristic of areas with historic disturbances, such as intense agriculture,

due to long-term impairment of the native seedbank (Banerjee et al. 2006; Crimmins &

McPherson 2008).

The methods used to remove invasive species have, at times, resulted in further

damage to native species. Damaging effects from well-intentioned introductions of

biological control agents have been widely acknowledged (Cory & Myers 2000). For

example, the reduction in both abundance of native tephritid flies and seed production of native thistles have resulted from the introduction of the weevil *Rhinocyllus conicus* for control of invasive thistles in North America (Louda et al. 1997). Additionally, unintended effects of the use of pesticides and herbicides to control non-native species include the mortality of native fauna and other detrimental ecosystem outcomes (Innes & Barker 1999; Howald et al. 2003; Govindarajulu 2008; Eason et al. 2010; Weidenhamer & Ragan 2010).

In some cases, eradication of an invasive species falls short of removing the resulting disturbance. Alteration of abiotic conditions by the target species, such as an increase in soil salinity associated with *Mesembryanthemum crystallinum* (crystalline iceplant, Aizoaceae), has been shown to restrict the return of native species (Vivrette & Muller 1977; El-Ğhareeb 1991). A long-lasting impact has been observed with the invasive *Myrica faya* (fire tree, Myricaceae) on young volcanic soils in Hawaii (Vitousek & Walker 1989). *M. faya* fixes soil nitrogen (N) at levels far exceeding those typical for the native ecosystem. Following removal of *M. faya*, secondary invasive species in these systems seem to be promoted by the legacy of increased soil N (D'Antonio & Meyerson 2002). Therefore, removal alone is not sufficient to restore the impacted habitat. Similarly, if the functional groups and ecosystem services of the native system have been lost due to the presence of invasive species, invasive species can come to serve in a functional capacity for native species (Zavaleta et al. 2001; D'Antonio & Meyerson 2002; Rodriguez 2006). Under these conditions, eradication of invasive species may

cause a system to collapse further, even including threatening the existence of native species (Florens et al. 1998).

Due to the undesirable effects that can accompany invasive species eradication efforts, Zavaleta et al. (2001) argued that species eradications should be addressed within the context of broader ecosystem restoration goals, including focusing on ecosystem-wide interactions and the potential functional roles of exotics, in order to reduce unwanted results. Furthermore, the potential negative effects that eradication methods can have on native species and ecosystem processes should be considered as they relate to restoration goals.

My research addressed questions that stem from a whole-ecosystem approach to removal of non-native plants for restoration. Specifically, I examined how native species responded when planted in areas that experienced different iceplant (*Malephora crocea,* coppery iceplant, Aizoaceae) removal methods. This study occurred on Anacapa Island in California's Channel Islands National Park (CINP). *M. crocea* is a species that was introduced subsequent to a history of disturbances on Anacapa Island and now appears to be having an adverse impact on native species. For example, cover by native plants and abundance of the native common side-blotched lizard (*Uta stansburiana elegans*) were both negatively correlated with the presence of *M. crocea* (S. Lambrecht 2012, San Jose State University [SJSU], CA, unpublished data). As a result of its observed threat to the native community, the National Park Service (NPS) is targeting *M. crocea* for future eradication on Anacapa. Research on how native species recover given different

approaches to iceplant removal is needed to facilitate and expedite restoration of the native plant community.

Anacapa Island and its history of disturbances

Anacapa Island is one of the four northern Channel Islands that are collectively a westward extension of the Santa Monica Mountains of mainland California (Moody 2000). Occurring 19 km from the coast of Ventura, California, Anacapa Island, the second smallest island of the Channel Islands National Park, is comprised of three individual islets—West Anacapa, Middle Anacapa, and East Anacapa—which are separated from each other by low-lying areas that are inundated except at the lowest tides. The islets are arranged in a thin, 8 km-long chain, and their total land-area is approximately 2.9 km² (Moody 2000). While rising approximately 284 m above mean sea level at its highest point on West Anacapa (i.e., Summit Peak), Anacapa Island is characterized as being mesa-like on the eastern end, reflecting a period of being submerged during the Pleistocene (Johnson 1979). In addition, the island has a gradual northward tilt, and all three islets are skirted by steep rugged cliffs. This varied topography has led to a diverse flora.

Plant communities of Anacapa include coastal bluff, coastal sage scrub, annual grassland, island chaparral, and island woodland, the latter two of which only occur on West Anacapa (Junak et al. 1980; Sawyer et al. 2008). In total, 190 native plant species have been identified on Anacapa Island, at least 22 of which are endemic to the Channel Islands (Moody 2000). In addition, Anacapa provides important breeding and roosting

habitat for numerous birds including the ashy storm-petrel (*Oceanodroma homochroa*), brown pelican (*Pelecanus occidentalis*), and Xantus's murrelet (*Synthliboramphus hypoleucus*) (Schoenherr et al. 1999; Whitworth et al. 2005). Anacapa also supports the endemic Channel Islands slender salamander (*Batrachoseps pacificus*), two native lizards, the California alligator lizard (*Elgaria multicarinata multicarinata*) and western side-blotched lizard (*Uta stansburiana elegans*), and a single mammal, an endemic subspecies of the deer mouse, *Peromyscus maniculatus anacapae* (Schoenherr et al. 1999).

Due to its proximity to the mainland and its occurrence along the major shipping lane of the Santa Barbara Channel, Anacapa Island has had a long human presence (Livingston 2006). The accompanying disturbances of human activities on Anacapa Island include the introduction of many non-native plant species. Junak et al. (1997) reported 72 non-native species on Anacapa Island, including the perennial iceplant species, *M. crocea*, which is native to South Africa (Jacobsen 1960).

Anthropogenic disturbances on East Anacapa both preceded and occurred simultaneously with the introduction of *M. crocea* and may have exaggerated its success as an invader. Before it was actively established, sheep ranching occurred on the three islets of Anacapa Island between the late 1800s and the late 1930s (NPS 2005; Livingston 2006). This included an especially intensive period during a ranch-lease program that was started in 1902 by the U.S. Department of Treasury (NPS 2005). The impact of ranching on the island's vegetation was significant given that herd managers would periodically cull the flocks to save those remaining from starvation (Livingston 2006) and

9

resorted to introducing non-native annual grasses, including *Bromus* spp. and *Hordeum* spp. (brome and foxtail, Poaceae), to increase available forage (NPS 2005). In 1912, following construction of a temporary light beacon on East Anacapa, the ranching lease was changed to restrict ranching to Middle and West Anacapa (Livingston 2006). At that point, it is presumed that the grazing pressure on vegetation of East Anacapa was reduced, although the occurrence of some sheep was reported on the islet through the 1960s (Livingston 2006). In the 1930s, the Federal Lighthouse Bureau replaced the beacon with a permanent lighthouse complex, including various buildings, a cement rain-collection pad, and extensive boat landing facilities (Livingston 2006). Construction disturbances, including the building of trails and dirt roads on the island, have resulted in soil erosion and denuding of vegetation (Hochberg et al. 1979). During the time the lighthouse station was initially occupied, *M. crocea* was introduced as a landscaping plant in the front yards of the residential units (Santa Barbara News Press 1951). This succulent vining plant with bright flowers was newly available in California's coastal nurseries around 1933 (Ferren *et al.* 1981) and was documented as observed on the island in 1951, suggesting that it was introduced within that 19-year period. It was likely introduced to serve an aesthetic role around the residences and to reduce erosion and wind-borne dust in light of the effects of construction disturbances and Anacapa Island's characteristically strong winds (Warren Jr. 1958; WRCC 2012). In 1935, at approximately the same time that *M. crocea* was introduced to East Anacapa, a few domestic European rabbits (*Oryctolagus cuniculus*) were introduced on the islet. They

10

quickly increased their numbers to approximately 1,000 by 1941 (SCWP 1941). Rabbits were eliminated by dogs and hunting in the 1950s (Santa Barbara News Press 1951).

The damage by rabbits to the habitats of East Anacapa, while undocumented, is likely to have been comparable to damage recorded within a 14-year period in similar habitats on nearby Santa Barbara Island. Sumner (1953) noted that rabbits had "devastated" Santa Barbara Island's plant communities, and threatened "many of the island's…plants with total destruction." One community type, the giant coreopsis-dominated coastal bluff scrub, was identified as being extremely damaged by rabbits (Sumner 1953). Plant cover growing beneath the canopy of the *Leptosyne gigantea* (giant coreopsis, Asteraceae; formerly *Coreopsis gigantea*) shrubs was reported as being completely denuded, and *L. gigantea* were fatally girdled (Sumner 1953). This community also occurs on East Anacapa, suggesting that rabbits may have reduced its occurrence.

By 2010, *M. crocea* had spread from the few initial plantings to dense monotypic stands covering approximately 7.3 ha, or 11% of East Anacapa Island, and an additional 10.5 ha, or 16% in lower density areas of the islet (S. Chaney 2011, unpublished data). The disturbances described above suggest that *M. crocea* may have easily spread within an especially low-competition environment. In fact, human disturbances on islands, including grazing practices, have been cited as being linked to the success of invading plants (Vitousek et al. 1997*a*; Kueffer et al. 2010). However, the occurrence of many other non-native plant species on Anacapa Island, including those that were there prior to the introduction of *M. crocea* (Hochberg et al. 1979; Halvorson 1992), provides evidence

that *M. crocea* possesses traits that have contributed to its particular success on East

Anacapa in spite of competition from other invasive plants.

***Malephora crocea* on Anacapa Island and challenges to eradication**

A wide variety of dispersal mechanisms has contributed to the success of *M.*

crocea on Anacapa Island. Black rats (*Rattus rattus*) were introduced to Anacapa Island

in approximately 1853 and were present until their eradication in 2003 (McEachern

2004). Both the black rat and the extant Anacapa deer mouse (*Peromyscus maniculatus*

anacapae) are known seed eaters (Clark 1982; Jameson 1952). Given its large seed

production (Bleck 2012), *M. crocea* may have benefited from seed dispersal by these

rodents. Another perennial iceplant species, *Carpobrotus edulis* (freeway iceplant,

Aizoaceae) that is also a non-native invader in coastal communities of California, is

predominantly zoochorous with its germination enhanced following seed ingestion by

deer, rabbits and jackrabbits (D'Antonio 1990). This may also be the case with *M.*

crocea. Another trait conferring successful dispersal is that of the rain-operated,

hygrochastic seed capsule of *M. crocea* (Bittrich & Hartmann 1988), which is found in

98% of species in the Aizoaceae. Triggered by heavy rain and thorough wetting, the

hygrochastic capsule uses the kinetic energy of raindrops to jet-propel seeds from the

capsule (Parolin 2006). This mechanism achieves dispersal of up to approximately 2 m

while allowing the disperser plant to maintain a low stature (Parolin 2006), which is

important in areas with strong winds. In addition, this mechanism allows the plant to

exploit critical rain events in dry environments (Parolin 2006), as is the case on Anacapa,

with an average annual rainfall of approximately 29 cm (WRCC 2012). *M. crocea* also employs vegetative spreading by rooting at leaf nodes (Ferren et al. 1981), enabling an individual that has established in even poor quality patches to spread. *M. crocea* has been observed being dispersed by Western gulls (*Larus occidentalis*), which breed in the thousands on East Anacapa. Gulls have been seen plucking fragments of *M. crocea* during courtship displays and utilizing *M. crocea* in their nests.

Once established, *M. crocea* is well adapted for surviving within the windy, Mediterranean, and haline conditions found on Anacapa (Johnson 1979). Succulent tissue, which was found to be correlated with invasive species success in disturbed habitats (Lloret et al. 2005), allows *M. crocea* to survive periods of drought through water storage in leaf tissues. In addition, *M. crocea* employs CAM photosynthesis to reduce evapotranspiration and accumulates generally high levels of sodium in its tissues, which may be adaptive to reduce internal water potentials so as to balance those of the surrounding environment during periods of water and salt stress (von Willert et al. 1977). The growth form of *M. crocea* also creates a heavy, dense mat that blankets the available substrate, including neighboring plants, effectively eliminating competition (Junak et al. 1980).

The 1985 General Management Plan for the CINP specified goals for restoring Anacapa Island to the potential ecosystem conditions that would likely have been present prior to human disturbances or as near to such conditions as possible (NPS 2000). Under that charter, the CINP resource managers have moved forward to complete species eradication efforts, including an island-wide eradication of introduced *R. rattus*, which

were threatening nesting seabird colonies (NPS 2000). Resource managers have set a goal to eradicate *M. crocea* by 2016, a date that corresponds to the centennial anniversary of the NPS (NPS 2012).

Given that *M. crocea* has covered such large areas over long periods of time and that other non-native invasive species occur on Anacapa, including *C. edulis*, *M. crystallinum*, *Mesembryanthemum nodiflorum* (slender-leaved iceplant, Aizoaceae), *Centaurea melitensis* (tocalote, Asteraceae), *Atriplex semibaccata* (Australian saltbush, Chenopodiaceae), *Erodium cicutarium* (redstem filaree, Geraniaceae), *Avena* spp. (wild oat, Poaceae), and *Bromus* spp., resource managers may need to employ additional measures beyond eradication of *M. crocea* to restore native ecosystems on East Anacapa. In a 4-year study on East Anacapa, researchers found that non-native grass cover increased following removal of iceplant species (primarily *M. crocea*) in contrast to native species that had little response (S. Lambrecht 2012, SJSU, CA, unpublished data). However, in other areas of East Anacapa, the native species *Frankenia salina* (alkali heath, Frankeniaceae) has been observed in abundance where iceplant has been cleared (S. Chaney 2010, personal communication). In this case, *F. salina* was likely coexisting amongst the *M. crocea,* resulting in a perceived repopulation although the increased growth of the plant was more likely a result of being released from competitive suppression by *M. crocea*. Botanists who contributed to the 1978 *Natural Resource Study of the Channel Islands National Monument* (Hochberg et al. 1979) were cautiously aware of the potential threat of secondary invasive species damage when they stated that the replacement of *M. crocea* on Anacapa "by *M. nodiflorum* or *M. crystallinum* would

be a step in the wrong direction…" They went on to recommend that "any intentional modification of areas covered by *Malephora* [*crocea*] should be carefully planned and carried out." Large areas of Santa Barbara Island as well as smaller areas on Anacapa and San Miguel Islands are dominated by *M. crystallinum* (D'Antonio et al. 1992; Halvorson 1992), which has presented a difficult challenge in restoring native species due to its effect on soil salinity (D'Antonio et al. 1992). In contrast, Allen and her colleagues (2005) found that native forbs responded positively to removal of non-native grasses in spite of colonization by secondary invasive species. This suggests that the removal of the most dominant invasive plant species may allow for a high level of autogenic restoration, even if secondary invasive species remain in the system. However, if the goal is to restore native ecological conditions, relying on the ability of native island species to recreate the native conditions on their own in the presence of many invasive species may be very risky.

Native species on Anacapa Island may not be capable of autogenic rehabilitation. For example, *L. gigantea*, which is a foundation species on Anacapa, appears to have adapted a reduced capacity to disperse within island populations. Individuals located on Bird Rock near Catalina Island had significantly narrower and longer seeds and significantly narrower achene wings (pappus) compared to mainland populations on the southern California coast (Schiffman 1997). These traits would result in the island population having a reduced ability to disperse. The reduced dispersal capacity identified in *L. gigantea* populations on Bird Rock and small achene wings indicative of populations on San Miguel Island, which is a larger than Anacapa and within the same

15

group of islands in the CINP (Schwemm 2008), suggest that Anacapa populations of this species would also be less able to colonize areas where *M. crocea* had been eradicated than would invasive species. Furthermore, other invaders may be able to exclude *L. gigantea* and other native species altogether (Schwemm 2008), as was seen in *M. crystallinum* stands on Santa Barbara Island (D'Antonio et al. 1992).

The ability of native species to naturally repopulate areas following *M. crocea* eradication may be a forgone conclusion in the short term on Anacapa. Bare ground comprised a large component of area following *M. crocea* removal even 3 years after removal (S. Lambrecht 2012, SJSU, CA, unpublished data), indicating that iceplant removal was not followed with quick recovery of vegetation, let alone native vegetation. This may be due to several factors, including limited soil moisture, possible abiotic impacts to the soil from *M. crocea*, and depletion of the soil seedbank from long-term residency of *M. crocea*. Invasive species have been shown to significantly affect the composition of soil seedbanks, including in the form of native species depletion; furthermore, these changes are generally greater with increased residence time (Gioria & Moravcova 2012). The impact of long-term *M. crocea* occurrence on the seedbank of Anacapa has not yet been examined. If *M. crocea* occurrence and eradication represent a severe enough disturbance, the ecosystem may never recover unaided. Severely disturbed habitats have been shown to support invasive species-dominated, highly-stable systems that perpetually exclude native species (Stylinsky & Allen 1999).

Even if some native species and functions could occur as an autogenic system response to *M. crocea* eradication on Anacapa, these processes are likely to be quite

slow. Active restoration of functional groups and key native species would accelerate the

restoration process, potentially preempting secondary invasions, degradation of

ecosystem functions, and soil erosion (Whisenant 2002). Establishment of native

perennial species, which can act as nurse plants, can greatly improve conditions for

establishment of seedlings (Whisenant et al. 1995; Carrillo-Garcia et al. 1999; Whisenant

2002; Zahawi & Augspurger 2006). Native perennial species have also been

demonstrated to limit competition by other invasive plants (Cione et al. 2002; Corbin &

D'Antonio 2004), although invasion resistance is not always achieved in restored systems

(Questad et al. 2012). Active establishment of native vegetation has been shown to

facilitate recruitment of native vegetation through increases in local seed availability

from reproduction and from seed rain by volant species (Holl et al. 2000; Zahawi &

Augspurger 2006). These results suggest that use of active planting can be an important

tool in triggering an autogenic restoration response.

A key limiting factor affecting the establishment of vegetation in restoration

within dry habitats is inter-annual climate variation (Cione et al. 2002; Cox & Allen

2008). Anacapa Island is a water-limited environment; as such, vegetation growth and

survival have been shown to be negatively affected by drought (S. Lambrecht 2012,

SJSU, CA, unpublished data). Restoration efforts in water-limited habitats need to

account for this factor. Whisenant and colleagues (1995) utilized catchment basins in a

Larrea tridentata (creosote bush, Zygophyllaceae) shrubland in Texas to increase water

availability during precipitation events. They demonstrated that the treatment resulted in

a five to ten-fold increase in biomass of planted native shrubs compared to the control.

Additional techniques have been shown to benefit the restoration of native plants in semi-arid habitats. For example, a variety of mulches may increase survivorship and productivity of planted native perennial species (D'Antonio et al. 1992; Zink & Allen 1998; Holmes 2008). Identification of a feasible method to provide for the establishment of native perennial species following *M. crocea* removal, given the potential impact of limited soil moisture on habitat restoration on Anacapa, may be an important consideration in the eradication effort.

Pilot efforts by the NPS have focused mostly on *M. crocea* eradication treatments. These include hand-pulling *M. crocea* and disposing of the remains in large piles, solarization or tarping, trampling *M. crocea* by foot, use of different herbicides, leaving *M. crocea* skeletons in place following herbicide application, pulling dead *M. crocea* skeletons following herbicide application, and using a tractor to clear swaths of *M. crocea*. Most of these trials were not conducted in a controlled analysis; therefore, limited quantitative evidence of their efficacy is available. However, researchers working on Anacapa found that three treatments—spraying the *M. crocea* with herbicide and leaving the dead skeletons in place, spraying and removing it by hand-pulling (several months after spraying), and hand-pulling untreated *M. crocea*—while significantly different in effort to accomplish (low to high, correspondingly), were equally effective at removal (S. Lambrecht 2012, SJSU, CA, unpublished data). Due to the lack of observed differences in the occurrence of native vegetation within these treatments, the study provided no evidence to infer which of the methods provided habitat

more conducive for survival of native plantings. It is also currently unknown what effects these treatments have on soil moisture.

The purpose of this research was to identify treatments that would help resource managers actively restore native plants in *M. crocea* removal areas. To accomplish this, I compared *M. crocea* removal methods known to be effective (S. Lambrecht 2012, SJSU, CA, unpublished data) with respect to the ability of the post-removal conditions to support establishment of native vegetation. I hypothesized that potential differences in soil moisture between treatments would be an important factor affecting native plant establishment and survival and that treatments with higher organic material would retain soil moisture better and maintain higher levels of native plant survival. In addition, due to the generally short persistence of the herbicides used in this study (see Methods), I hypothesized that herbicide use would not impact survival of seedlings.

I examined the effect of three iceplant removal methods on seedlings of three species of native perennial plants to address the following questions:

1) Are there differences in soil moisture between *M. crocea* removal treatments? If so, is soil moisture an important factor on seedling survival and/or establishment between treatments?

2) Are there differences between removal treatments in the survival of seedlings of native perennial species transplanted into the treatment areas during the initial year following eradication?

3) Are there differences between removal treatments in the establishment of seeded native plants transplanted into the treatment areas during the initial year following eradication?

4) Given the range of sizes in transplanted seedlings (resulting from the range of time that seedlings were propagated for this study), does the size of the seedling at the time of planting have an effect on its potential to survive?

Methods

Study site

The experimental site (lat 34 ° 00' 49.5"N; long 119° 22' 19.5"W; Fig. 1) was located within the northwest quadrant of East Anacapa, on a relatively flat mesa characteristic of Middle and East Anacapa, approximately 20 m north from a maintained hiking trail. Elevations of the study area ranged between 57.5 and 62.0 masl (USGS 1973). Soils of East Anacapa are considered to be well-drained and relatively shallow (NRDC 2012); however, soils of the study area are among the deeper soils of the island (Junak et al. 1980) at 80-100 cm (NRDC 2012). Parent materials are comprised of volcanic breccia, andesite, and/or basalt (NRDC 2012; Scholl 1960). I used the soil texture analysis of Thien (1979) to characterize soils of the study area. Thein's (1979) method, known as the texture by feel method, entails adding water to a hand-held sample of soil, then manipulating the soil and examining the texture and ribbon-holding ability of the sample in order to classify the soil texture. With this method, I characterized soils of the study area as ranging from clay to silty clay loams within the top 15 cm of the soil profile.

I characterized the vegetation of the study site prior to research-related *M. crocea* removal treatments (discussed below) as a monotypic stand of *M. crocea* (>95% relative cover) with minor occurrences of other species. Other species that I observed included native perennial plants, such as *Distichlis spicata* (salt grass, Poaceae)*, Dudleya*
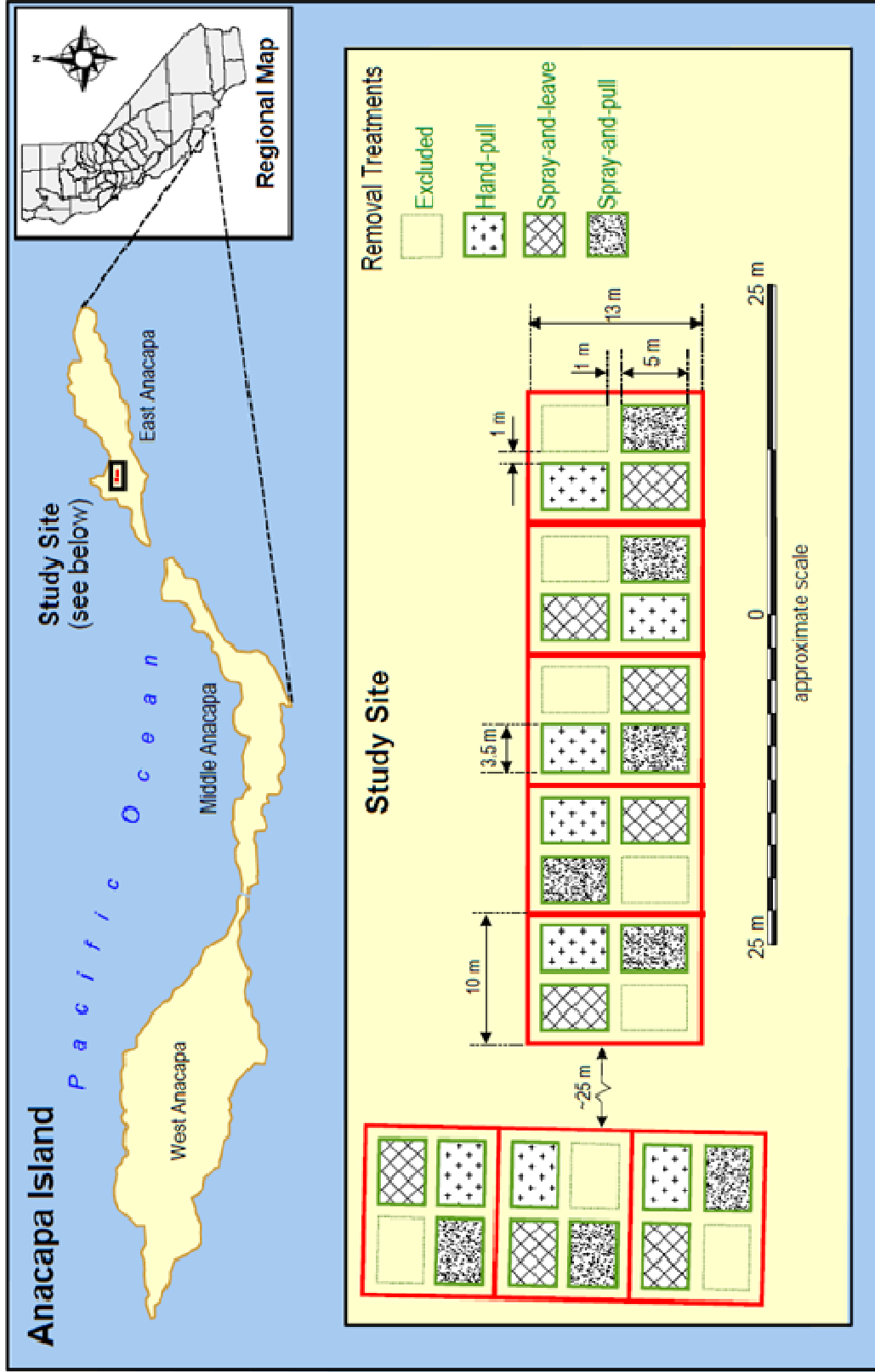
Figure 1. Study site and *M. crocea* removal treatments. The experimental site was located on East Anacapa Island in the Channel Islands National Park, Ventura County, California. Enlargement depicts *M. crocea* removal treatments applied in a randomized complete block layout.

caespitosa (coast dudleya, Crassulaceae), *F. salina*, and *Grindelia stricta* (coast

gumplant, Asteraceae), annual species including unidentified grasses, *Lasthenia*

californica (California goldfields, Asteraceae), *Phacelia distans* (common phacelia,

Boraginaceae), and non-native perennials *M. crystallinum*, *M. nodiflorum*, and *Sonchus*

oleraceus (common sow thistle, Asteraceae) (nomenclature as in Baldwin et al. 2012).

Using the classification system of Sawyer et al. (2008), the vegetation of the study area

was characterized as being an *M. crocea*-dominated iceplant semi-natural herbaceous

stand. A 1979 botanical survey of Anacapa Island conducted by botanists from the Santa

Barbara Botanical Gardens characterized this habitat type on East Anacapa as stands of

M. crocea, and they defined the area of the study site as supporting both island grassland

and solid carpets of *M. crocea* (Junak et al. 1980). They noted that the island grasslands

occurring on East Anacapa were degraded relative to those occurring on the west and

middle islets and that they were predominantly covered with introduced annual grasses

(Hochberg et al. 1979; Junak et al. 1980). They also speculated that the disturbed

grasslands and *M. crocea* dominated areas were likely covered by a mosaic of native

perennial grasses, *L. gigantea*, and *D. caespitosa* (Hochberg et al. 1979). However, the

vegetation community of the experimental site prior to anthropogenic impacts is not

precisely known. The spread of *M. crocea* into the study area likely occurred around

1979, assuming that the habitat transition from mapping done by the SBBG in 1979

(Junak et al. 1980) and the present conditions represents a direct transition of *M. crocea*

encroachment into the grassland.

In order to describe and compare the weather conditions of the study year relative to normal, I obtained climate data from the Western Regional Climate Center (WRCC) website (WRCC 2012). These data were collected at an automated weather station located on East Anacapa, approximately 1.1 km to the east of the study site.

Field study design

To examine effects of *M. crocea* removal (hereafter referenced as either *M. crocea* removal or iceplant removal) on planted native seedlings, I established 24 5 × 3.5-m removal treatment plots in a randomized complete block (RCB) design, where each of eight replicate blocks contained three treatment plots, and each treatment plot contained five planting treatments (Fig. 1; Fig. 2). Replicate blocks were established in two separate groupings with three adjoining blocks tending north to south in one grouping and five adjoining blocks tending east to west in another band approximately 25 m to the east of the former (Fig. 1). This design and placement of replicates was established to minimize the mortality to extant pockets of native plant species, such as areas of *D. caespitosa*, throughout the study area during iceplant removal and to reduce treatment error and adverse researcher-related effects through simplification of layout.

Treatment plots contained within each replicate block were comprised of three iceplant removal treatments. My three treatments were: (1) Hand-pull: iceplant manually pulled on 18 and 19 February 2010, (2) Spray-and-pull: iceplant was sprayed with herbicide on 1 December 2009 and left to die, and then skeletons were hand-pulled on 18 and 19 February 2010, and (3) Spray-and-leave: iceplant was sprayed with

herbicide on 1 December 2009, then left within the plot. These treatments had been

previously tested in their efficacy of removing *M. crocea* on East Anacapa and were

found to be equally effective (S. Lambrecht 2012, SJSU, CA, unpublished data).

Treatment plots were randomly assigned to one of four quadrants of each replicate block.

Meter-wide buffer strips were maintained between quadrants to reduce over-spray

effects. The remaining untreated plot area was used for onsite disposal of pulled iceplant

material from treatments 1 and 2 (Fig. 1).

Within each treatment plot, five 1 × 1-m subplots were randomly assigned to

different planting treatments comprised of indigenous perennial species (Fig. 2). Species

planted included *Coreopsis gigantea, Frankenia salina*, and *Grindelia stricta*. These

species were chosen based on their proximity to the study area (i.e., they occur within 50

m of the study area) and their commonness on East Anacapa. Also, it was presumed that

their perennial life histories and relative structural heterogeneity may provide a range of

facilitative effects to other native species, such as by being nurse plants. Planting

treatments consisted of: (1) 20 *L. gigantea* seedlings, (2) 23 *F. salina* seedlings, (3) 27

G. stricta seedlings, (4) 132 *L. gigantea* seeds, and (5) 132 *G. stricta* seeds. The numbers

of seedlings in each of the transplant treatments (1-3) reflected the number of seedlings

that were grown at the time of planting divided by the number of treatment plots (i.e.,

24).

For seeding treatments, seed numbers reflected generally high germination rates

observed in the greenhouse. The number of seeds was determined by attempting to

reduce potential competitive effects while also providing for the possibility of low field

germination. Moderate to high seed germination rates observed in the lab were assumed

to be only slightly higher than field germination. A seeding template was built to

increase the uniformity of seed placement and the number 132 was determined to be a

reasonable number of seeds, given these criteria. The number 132 was used as a 1×1-m

seeding template with >8 cm spacing between holes was drilled with 11 rows of 12

columns. Subplots were separated from each other and the outer edge of the treatment

plot by 0.5-m buffer strips.
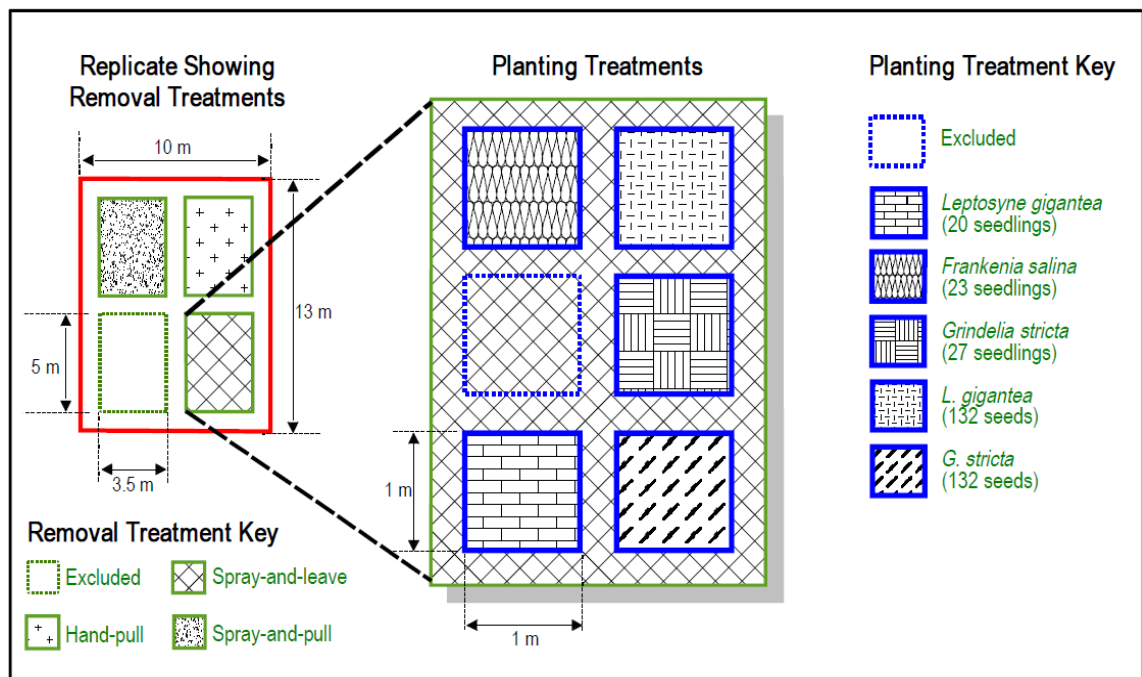
Figure 2. Setup for experimental treatments. *M. crocea* removal treatments were
randomized within each replicate block (general example shown). Within each removal
treatment plot (spray-and-leave treatment shown) five planting treatments were installed,
consisting of three seedling installation treatments and two seeding treatments.

The herbicide that we applied to spray treatment plots was a mixture that had been

previously shown to be effective on perennial iceplant species on Anacapa Island (S.

Lambrecht 2012, SJSU, CA, unpublished data). This mixture was also actively used by the Channel Islands National Park Service (CINPS) for perennial iceplant control and at Point Dume, California State Park in *Carpobrotus* spp. control efforts prior to project planning (S. Chaney 2011, personal communication). Its composition was approximately 0.8% (~89 mL) Garlon 4 (Dow AgroSciences, Indianapolis, Indiana), the active ingredient in which is triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid, butoxyethyl ester), approximately 1.5% (~133 mL) RoundUp Pro (Monsanto Company, St. Louis, MO) the active ingredient in which is glyphosate (N-(phosphonomethyl)glycine), approximately 0.2% (~22 mL) ProSpreader/Activator surfactant (Target Specialty Products, Inc., Fresno, CA), less than 0.1% ammonium sulfate, and approximately 0.7% (~74 mL) dye, with the remaining 98.2% of the mixture comprised of water. Approximately 53.0 L of this mixture was applied within the study area at a quantity of approximately 0.17 L per m² for a total area of 315 m². Herbicide treatments were applied by Sarah Chaney, CINPS restoration biologist and California qualified pesticide applicator (QAL 104844).

Seed collection and seedling production

Seeds for the planting treatments described below were collected throughout East Anacapa during the periods that the seeds were mature for each species. Mature capitula for the *L. gigantea* were collected in late May 2009 and for *G. stricta* in late September 2009. Mature inflorescences of *F. salina* were collected in November 2009. All collected seed were gathered by species into paper bags. Following collection, seed

material was treated to protect the seed from insects and fungal infection. *L. gigantea* and *G. stricta* seed stock was dried for approximately 2 h on a baking sheet in a standard gas-powered oven at approximately 75°C before being left to cool to field station temperature. Seed material was then placed into clean paper bags and into a standard, unlit freezer at approximately 0°C where they remained for approximately10 h (adapted from Lippitt et al. 1994) prior to transport back to San Jose, California. Then seed material was stored at laboratory temperature for several weeks until it was cleaned and sorted. *F. salina* seed material was collected by Sarah Chaney in November 2009. These seeds were then sent by US mail to San Jose where the seed material was similarly oven-dried, placed into a freezer at approximately 0°C for 12 h, and then stored at room temperature.

Seeds were sorted from non-seed plant material by placing seed material on a dry lab surface that had been sterilized with a solution of deionized (DI) water and Physan 20 (Maril Products, Inc., Tustin, CA), per label instructions. Seed material was manually separated from the remaining plant material using sterilized forceps, micro spatulas, and/or dissection needles while wearing latex gloves. Seeds that showed signs of damage (i.e., partial, infected by fungal invasion, damaged by insects, or deformed) were discarded. The remaining seeds were stored by species in sterilized and sealed petri dishes at lab temperature in an unlit drawer prior to germination. *F. salina* seed-bearing plant material was gently crushed with a sterilized kitchen rolling pin. Loosened seeds were then separated by using a clean paper card to push plant material up a tilted piece of paper and releasing the suspended plant material, the effect of which allowed the round

seeds to roll out further from the rest of the material where they could be more easily collected.

In order to provide seedlings for the transplant treatment and to identify methods with high germination rates for these species, I conducted propagation trials for *L. gigantea* and *G. stricta* between October 2009 and January 2010, following seed collection. Germination methods included placing seed in sterile plastic petri dishes with DI-saturated germination substrate comprised of either #1 filter paper (Whatman International, Ltd., Maidstone, England), Kimwipes Ex-L (Kimberly-Clark Corporation, Roswell, GA), or approximately 0.06 g/cm^2 (dry weight) of Sunshine Mix #3 growing medium (Sun GroHortuculture Canada, LLT., Vancouver, BC, Canada). Pre-treatments varied but included combinations of the following: 24 h pre-soak inundation at different temperature regimes (laboratory temperature (22°C - 25°C) or refrigerator temperature [1°C - 4°C]); pre-rinsing seed in a solution of 5% chlorine bleach, 1% surfactant (Coco-Wet, Spray-N-Grow, Inc., Rockport, TX), and DI water for 30 seconds before repeated flushing with DI water; or no pre-rinse or pre-soak treatment prior to placement on the germination medium. Seeds were placed in a uniform grid of 25, 80, or 100 seeds (depending upon petri dish size) within the germinating mediums of the petri dishes, and all petri dishes were sealed with Parafilm (American National Can, Greenwich, CT). After sealing, seed dishes were placed into either a standard refrigerator for 7, 12, or 14 d prior to being placed into a Conviron E7 plant growth chamber (Conviron, Pembira, ND), or they were placed into the Conviron directly. Plants were grown under a regime of 20°C light, 12°C dark, and an 11 h photoperiod. Due to high germination rates observed

with *G. stricta* and initial trials of *F. salina* using no pre-soak or pre-rinse treatment and placing seeds on Sunshine soil mix in a sealed petri dish in a refrigerator for 12 d before moving into the germination chamber, 80% of *F. salina* seedlings were grown using this protocol. Germination means of the seed trials varied across treatments and species. Across trials, *L. gigantea* had a mean germination of 51.5%; *G. stricta* had a mean germination of 86.1%, and *F. salina* had a mean germination of 85.8%.

Germinated seedlings were transplanted following hypocotyl emergence, when cotyledons had fully deployed or, in some cases, when the first true leaves had emerged. Seedlings were then placed into 16.5 cm tall (115 mL) single-cell cones in 98 cone trays (Ray Leach Cone-tainer Single-cell system, Stuewe & Sons, Inc., Tangent, OR). Cones were filled with Sunshine Mix #3 growing medium which was tamped down and saturated with DI water prior to transplanting. Sunshine Mix #3 consists of Sphagnum peat moss, vermiculite, gypsum, and dolomitic limestone. This mix was approved by the National Park Service for use in seedling production for in-park installation. For each seedling, a small hole was made in the growing medium with either sterilized forceps or a micro spatula, and the root was guided into the hole. Growing medium was then backfilled and seedlings were watered in. Cone-filled trays with live seedlings were returned to the germination chamber for 1 to 4 weeks before being transferred to an insect-resistant, open-air structure located on the seventh floor courtyard of the SJSU (SJSU) Duncan Hall building.

The structure, which I designed in collaboration with Sarah Chaney to reduce the chance of insect infestation within the seedlings, was composed of a wood frame, clear

plastic sheeting, and insect-proof screen material. The screen material (No-Thrips Insect Screen, BioQuip, Rancho Dominguez, CA) is a polyethylene monofilament material with 0.15 mm screen holes. Sheeting and screen material were connected to the frame with epoxy and staples, and access to the interior was through a pair of 2.1 m long zippers that were taped over when closed. The interior of the structure was sanitized with Physan 20 solution prior to use.

For transport from SJSU to Anacapa Island, seedlings were placed in new 227 L (61 × 61 × 61 cm) cardboard boxes 18 h prior to arrival at Anacapa. Immediately after boxes were filled with the seedling trays that had been removed from the greenhouse structure, all flap seams were taped to reduce the chance of introducing non-indigenous insects to Anacapa Island. On 16 February 2010, boxed seedlings were loaded into the bed of a campus pickup truck, covered with a new plastic tarp, and driven to Ventura, CA where they sat covered overnight. On the morning of 17 February 2010, boxes were loaded onto a National Park Service boat (Ocean Ranger II) and transported to Anacapa. Once there, boxes were crane-lifted onto the island where the seedlings were watered and placed under bird-proof net-covered PVC frames for 7 d for hardening. Water available

Seedlings were watered with DI water as needed, and a 4 L to 5 mL solution of DI water and a kelp-based fertilizer (Seaweed Extract, Grow More, Gardena, CA) was applied to the soil of all seedlings. Cones were haphazardly rearranged within the trays, and trays were haphazardly rearranged within the greenhouse on a weekly to biweekly basis. Seedlings that died were replaced with germinated seedlings once cones were cleaned, sterilized, and filled with unused growing medium.

on Anacapa during this study came from two 189.3 kL redwood storage tanks located on East Anacapa. At the time of the study, water in these tanks was most recently sourced from Long Beach public drinking water that was shipped to Anacapa and pumped into the tanks. Tanks are refilled approximately annually.

Treatment effects on soil moisture

To measure the effects of removal treatment on soil moisture, I attempted to measure volumetric water content (VWC) within the treatment areas. VWC was collected with a time-domain reflectometry (TDR) probe (Field Scout TDR 200, Spectrum Technologies, Inc., Plainfield, IL) with 120 mm probe lengths. When sampled, VWC readings for all replicates were collected between 1130 h PST and 1300 h PST on a single day per 2010 sampling assessment (March, June, and October 2010). During each sampling event 15 VWC samples were taken within each plot (three independent samples collected immediately adjacent to each of the five planting treatment subplots).

The TDR instrument often overestimated VWC readings (e.g., 107% VWC), which was likely caused by attenuation of the electromagnetic wave due to high levels of soil salinity within the study area (Wyseure et al. 1997). Because soils with electrical conductivity (EC) greater than 2 dS/m will result in inaccurate VWC readings (STI 2010), I attempted to identify a relationship between the probe readings and actual VWC of sampled soil. To do this, I collected ten soil samples with a range of probe readings similar to those observed within the plots from locations immediately adjacent to the study area (within approximately 10 m of the study area). Soil samples were collected

with an 89.8 mm diameter length of round steel pipe, 90.5 mm long, the volume of which

(574 cm³) was calculated to collect approximately the content of the TDR probed soils.

To collect soils, the pipe was gently hammered into the soil until the top edge was flush

with the soil surface, capturing the probe sample locations. The pipe and sample were

then excavated and the soil edges were leveled flush with the pipe edge using a knife to

ensure that sample volumes were uniform. Samples were immediately weighed, then

oven-dried for approximately 12 h prior to transport to the lab at SJSU, where the drying

was completed in a drying oven set at 75°C for approximately 5 d. Actual volumetric

water content was calculated as the volume of moisture lost divided by the sample

volume.

The results of a regression analysis showed that in spite of inaccuracy of the TDR

probe, readings were related to actual volumetric water content samples (n = 10; R =

0.882, $p = 0.001$, after log-log transformation). Therefore, actual probe readings were

retained to be examined for differences in soil VWC between treatments.

Transplanting

In order to test the effects of iceplant removal treatment on survival of

transplanted seedling, the following methods were utilized. Seedlings of each species

were grouped into size classes (small, medium, or large) due to the fact that, immediately

prior to planting, seedlings ranged in age from 4 weeks to approximately 3.5 months, and

therefore showed a broad range in sizes. Sizes were characterized and grouped through

visual estimation of standing biomass. Within each seedling size class, seedlings were

randomly assigned to a plot (numbered 1 through 24). This ensured that each plot received the same number of seedlings of each size class for each species and corrected for unidentified growing condition biases.

Seedlings were transplanted into the study plots from 25 February – 28 February 2010. Seedlings were planted in the following order: *F. salina*, *L. gigantea,* and *G. stricta*. Following installation of *G. stricta* seedlings on 2 March 2010, 100 mL of water were poured around the root zone for each *G. stricta* seedling due to an absence of precipitation since planting. Light precipitation events during and immediately following planting of *L. gigantea* and *F. salina* seedlings allowed for planting without supplemental water. Seedlings were placed in uniform grids with no less than 20 cm spacing between neighbors. The few seedlings for all species that had died since transplanting were replaced with remaining unplanted seedlings of the same size class on 2 March 2010.

To be able to address the question of the effect of plant size on survival, measurements of seedling size were taken for all individuals (collected 28 February and 1-2 March 2010, following planting). For *L. gigantea*, stem diameter, measured with digital calipers at approximately half-way between the ground and the lowest leaves of individual seedlings, and above ground plant height were measured. Leaf number and aboveground plant height were measured for *F. salina*, and leaf number and maximum leaf spread (a measure of the distance between the tips of the two longest leaves growing from opposing sides of the basal rosette that were manually spread into a horizontal plane) were measured for *G. stricta*. No relationship was detected between size metrics

and survival for *L. gigantean* or *G. stricta*; therefore, these data were excluded from further analyses.

Seedling survival was sampled on four occasions over 1 year. Sampling events were 28-29 March 2010, 2-3 June 2010, 20-22 October 2010, and 16-17 January 2011. *F. salina* seedling survival was recorded through the June 2010 sampling event; however, natural resprouting that appeared to be from extant *F. salina* rootstock in the study area made differentiating planted seedlings impossible. During the October and January sampling events, dormant *L. gigantea* seedlings were distinguished from dead seedlings through differences in stems. Stems that were smooth and turgid were recorded as live and those that were partially collapsed, wrinkled, and/or mushy, were noted as dead. Survival data were collected in a spatial diagram corresponding to the relative location of seedlings within the subplots. This was to ensure that initial size data could be associated with the fate of each seedling.

Seeding

To test the effectiveness of seeding as a restoration treatment and the effects of iceplant removal treatments on seeding establishment, the following methods were utilized. Collected seed, as discussed above, were stirred gently, and sets of 132 seeds were drawn from chance locations within the seed containers (adapted from Stein et al. 1986). Samples were drawn into 24 sets per species. Species included in seeding treatments were *L. gigantea* and *G. stricta*. Seed sets were stored in coin envelopes for

transport to Anacapa Island, and they were haphazardly assigned to plots prior to planting.

Following completion of the iceplant removal treatments, seeds were planted in randomly assigned subplots within the study plots in a 1 × 1-m grid using a pre-fabricated template for uniform seed placement. Seeding for *G. stricta* occurred on 18-19 February 2010 and seeding for *L. gigantea* occurred on 20-21 February 2010. The template used to place seeds was made of high-density polyethylene that had been drilled with 6.4-mm holes. In total, the template contained 132 holes that were placed in eleven rows spaced 8.9 cm apart and twelve columns spaced 8.3 cm apart. The template was placed on the subplot and secured in place while one seed was dropped through each hole of the template to replicate broadcasting of seed. In total, 3,168 seeds of each species were placed in the study area using this method.

Seedling establishment from seed treatments was recorded during the same sampling events as transplant survival, excluding the January 2011 sampling event. However, seed establishment in the spray-and-leave treatment was measured only during the October 2010 sampling event due to concerns that probing for seedlings within the dead iceplant mat would damage the seedlings; therefore, only seed treatment establishment of spray-and-pull and hand-pull treatments were collected during the March and June 2010 sampling surveys. Seedlings of *G. stricta* at the cotyledon stage could not be confidently differentiated from cotyledons of *S. oleraceus* in the seed treatments resulting in poor sampling data for *G. stricta* from the late March 2010

sampling. Seeding trials of *L. gigantea* resulted in extremely low numbers of surviving seedlings and, therefore, were excluded from statistical analyses.

Emergent, surviving seedlings of both *L. gigantea* and *G. stricta* seeded trials were also counted. As these trials were installed spatially distant from each other, seedlings of both species were counted within both seeded subplots to provide a proxy for non-treatment seedling occurrences within the study area. To account for "natural" seedling numbers within seeded subplots, an area mean of natural seedlings per seeded subplot was calculated for each replicate block and subtracted from the number of surviving seedlings of the seeded subplots in that replicate block. Area means were calculated as the mean number of seedlings of the non-seeded species (i.e., seedlings of *G. stricta* observed within the *L. gigantea* seeded subplots and *vice versa*) per subplot for both the replicate block and the contiguous block(s).

Potential correlates

Abiotic variables were collected immediately prior to planting to enable identification of potential relationships with seedling survival and soil moisture. Slope was measured with an inclinometer per iceplant removal treatment plot. Aspect was determined for each replicate using the inclinometer and a compass, and these data were converted to Cartesian coordinates for analysis. VWC means (described above) were also analyzed as potential correlates. During the October 2010 assessment, percent cover of all dominant (cover) plant species encroaching into the study plots was visually estimated due to observed heterogeneity of cover between treatment plots. Species

37

measured included *D. spicata, F. salina, M. crocea*, and both *M. crystallinum* and *M. nodiflorum* (combined as *Mesmbryanthemum* spp.). Of these, only *F. salina* cover was found to be important to native plant survival; the others were excluded from further analysis.

Statistical analyses

To test for differences in seedling responses among iceplant treatments, I used a repeated measures randomized complete block (RCB) analysis of variance (ANOVA) or analysis of covariance (ANCOVA) when response variables were significantly correlated with covariates ($R \geq 0.6$ and $p \leq 0.05$). These analyses were conducted using the number of surviving (transplant treatment) or established (seeding treatment) seedlings per planting treatment, per species, for the dependent variables. Prior to conducting these tests, I used a partial multiple correlations analysis to identify relationships between dependent variables and several measured variables (slope, aspect, VWC, seedling size, and percent cover of naturally occurring vegetation by species as measured in October 2010) to identify potential correlates; four variables required ANCOVA analysis (Table 1). Iceplant removal treatment was included as the fixed factor, and replicate block was included as the random factor. Two planned comparisons were tested, one between both pull-treatments and the no-pull treatment and, within the pull treatments, another between the herbicide spray treatment and the no-spray treatment. An exception to these planned comparisons was in the analysis of survival of seeded *G. stricta* in June 2010 because

survival was not assessed within the spray-and-leave treatment areas; therefore, only pull

treatments were compared.

Table 1. Analyses conducted for treatment effect on seedling, seed, and VWC.
Dates (in parentheses) indicate data collection period(s) used in analyses. All
analyses account for the blocking factor due to the RCB study design.

Measured Variable	ANOVA	ANCOVA
G. stricta seedling survival (†RM: 03/10, 06/10, 10/10, & 01/11)	X	--
G. stricta seedling survival (01/11)	--	% *F. salina* (10/10)
F. salina seedling survival (†RM: 03/10 & 06/10)	--	*F. salina* height
G. stricta seed establishment (03/10)	X	--
G. stricta seed establishment (10/10)	--	VWC (03/10)
VWC (RM†: 03/10, 06/10, & 10/10)	--	Slope

† RM: Repeated measure analyses utilized.

<center>**Results**</center>

East Anacapa weather conditions during the study period

My study was conducted during a period of relatively variable weather. Cumulative precipitation on Anacapa during the study period (December 2009 – January 2011) was 575 mm, which is 30% higher than the historical mean for the equivalent period (Fig. 3; WRCC 2012).
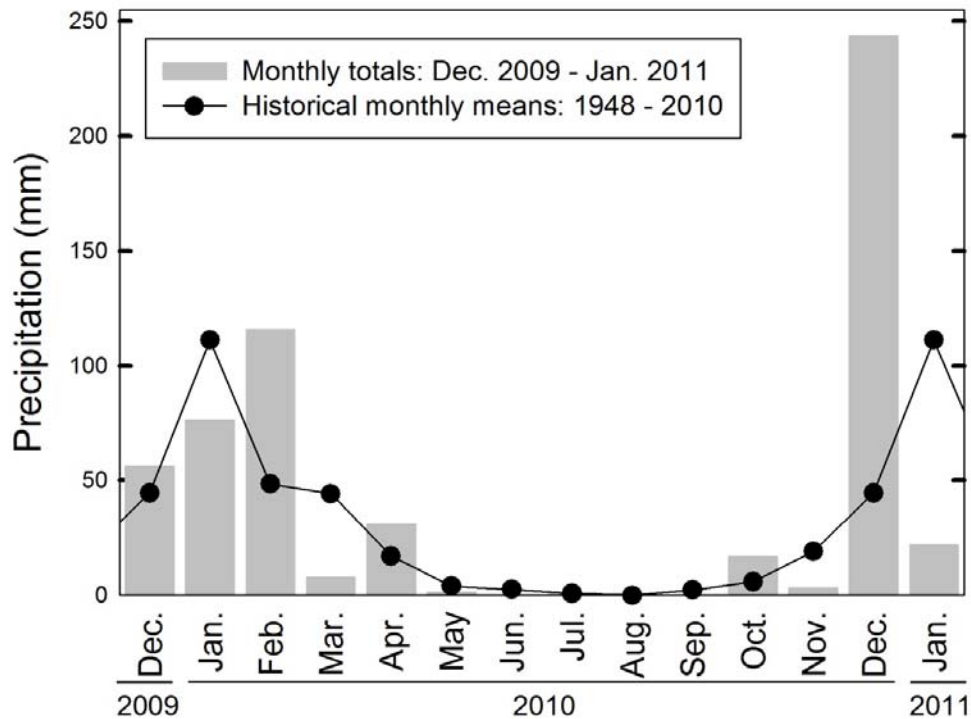
Figure 3. Rainfall on East Anacapa Island during the study period. The historical trend line is limited to available precipitation records from the Western Regional Climate Center (2012).

Application of herbicide for the spray treatments (1 December 2009) was followed by a period of typical precipitation for that time of year. Pull treatments and installation of planting treatments were conducted during a relatively wet February,

<center>40</center>

which was followed by abnormally dry weather in March 2010. Between planting and the first sampling event (2 March - 28 March 2010), approximately 7.9 mm of precipitation was recorded (WRCC 2012), which is 18% of the historical mean for the equivalent period. Average wind speed through the study period was 6.1 m/s with gusts reaching 42.5 m/s (WRCC 2012), all of which had originated predominantly from the north or north west ($\bar{x}$ = 339.5°). Air temperature was fairly stable through the study period ($\bar{x}$ = 16.2° C, range 6.7 – 27.2° C).

Recorded precipitation on East Anacapa between September 2008 and September 2009 was 59 mm, which is less than 20% of the historical mean for the equivalent period (WRCC 2012). This indicates that seed stock collected and utilized in this project was created during an extremely dry growing season by drought-stressed parent plants.

Existing conditions of the study area

Measurements of the study area showed little topographical variation. Aspects of the study area were generally northward-facing and ranged between 312 - 350° ($\bar{x}$ = 329.3° ± 2.4°). Slopes of the study plots ranged from 2.5 - 9.5° with a mean slope of 5.3° (± 0.4°). However, slope was found to be significantly different between *M. crocea* removal treatment areas ($F_{2,14}$= 5.56, p=0.02). Planned comparisons showed that slope was steeper in the spray-and-leave treatment areas ($\bar{x}$ = 6.9 ± 0.8) compared to pull treatment areas ($\bar{x}$ = 4.5 ±0.39; $F_{1,14}$= 10.57, p = 0.01). Slopes of the hand pull versus spray and pull treatment areas did not differ ($F_{1,14}$= 0.55, p = 0.47). Measured differences

in slopes between treatments did not appear to account for differences in plant survival or soil moisture (see below for soil moisture, seed treatment, and seedling treatment results).

Dominant plant cover of plants naturally colonizing or reoccurring within the treatment plots showed high variation between treatment plots. Only those species that were occurring at generally high density were recorded. Of the dominant species within the treatment plots in October 2010, *F. salina* showed a wide range of cover ($\bar{x}$ = 16%; ±0.80; range = 0-95%). Density averaged 2.8 ±0.80 m²/17.5 m². *M. crocea* also reoccurred and accounted for a high amount of vegetative cover in October following removal ($\bar{x}$ = 21%; ±.61; range = 0-60%). Density averaged 3.7 ±0.61 m²/17.5 m². The reoccurrence of *M. crocea* was primarily due to seed germination and not resprouting. Other species were identified colonizing the iceplant removal areas; however, a significant effect was not identified as a result of their estimated cover. A small number of natural *G. stricta* and *L. gigantea* seedlings were detected in the treatment plots; as a result, seed trial data were adjusted based on an estimate of natural germination (see Methods). Surveys for these seedlings were completed in the seeding treatment subplots of the contrasting species. A total of 19 *G. stricta* seedlings were noted in the *L. gigantea* seeded subplots by October 2010, and one short-lived *L. gigantea* seedling was noted in the *G. stricta* seeded subplots in March 2010.

Soil moisture

As expected, soil VWC readings were significantly higher in the spray-and-leave treatment compared with the pull treatments (Table 2). No difference was identified

between the pull treatments. Across treatments, VWC decreased between March and

June 2010. However, between June and October 2010, VWC decreased the most in

spray-and-leave, decreased to a lesser amount in spray-and-pull, and did not change in

hand-pull.

Table 2. Repeated-measures RCB ANCOVA and planned contrasts for VWC
(volumetric water content) collected in iceplant removal treatments† on 29
March, 3 June, and 22 October 2010 on East Anacapa. Significant results are
in bold.

Source	df	F	P
Between-subjects effects			
Block	7	0.99	0.48
Treatment	2	17.55	**<0.001**
Error			
Treatment Contrasts			
Pull vs. Leave	1	35.05	**<0.001**
Spray-and-pull vs. hand-pull	1	0.05	0.84
Error	14		
Within-subjects effects			
Time	2	241.33	**<0.001**
Time × Block	14	2.92	**<0.001**
Time × Treatment	4	1.10	**0.02**
Error(Time)	13		

† Treatments: Hand-pull, spray-and-leave, or spray-and-pull of *M. crocea* (iceplant).

This pattern may be a result of some maximal drying capacity of the soils of East

Anacapa that was already approached in the hand-pull treatment by June 2010 but not in

the spray treatments. Across time, a significant time × block interaction was observed.

VWC decreased in all blocks between March 2010 and June 2010 sampling events, but

between June 2010 and October 2010, two blocks showed a slight increase in VWC

compared with the other six blocks that showed a slight decrease in VWC. This

difference in block response over time was not enough to have an effect on treatment differences in VWC or on seedling survival except in seeding trials of *G. stricta*.

Seed treatment

Few of the planted seeds established during the period of study. Three *L. gigantea* and 50 *G. stricta* seedlings were found within all treatment areas in October 2010. A total of 10 *L. gigantea* seedlings had established within the pull treatment plots by March 2010, but all of these died by June 2010. All three seedlings observed in October were located in the spray-and-leave treatment in a single plot. Due to low numbers, *L. gigantea* seed data were excluded from analyses.

Iceplant treatments affected establishment of seeded *G. stricta*. Differences observed between the *G. stricta* seed establishment in the pull treatment plots, prior to adjusting the data for estimated natural seedling establishment (see Methods), were marginally insignificant in June 2010 ($F_{1,7} = 4.17$, $p = 0.08$); however, by October 2010, differences were more pronounced (Table 3, Fig. 4). October 2010 data allowed for analysis of differences between pull treatments and the spray-and-leave treatment (Table 3). After subtracting naturally-occurring *G. stricta* seedlings from the October dataset, the difference between pull treatments remained significant; however, the difference between spray-and-leave and spray-and-pull became marginally non-significant.
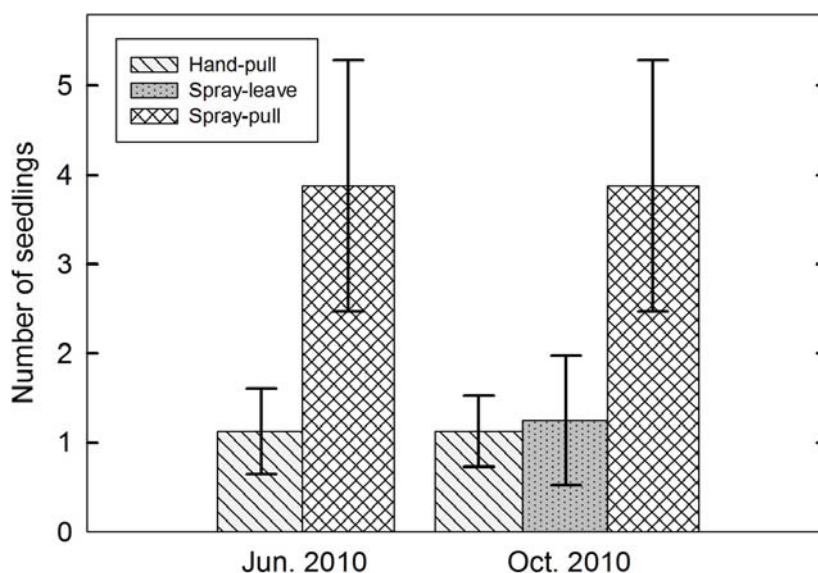
Figure 4. Differences in mean seedling establishment (n = 24 with n = 8 per treatment) in *G. stricta* seeded treatments between iceplant removal treatment areas. No data were collected in the spray-and-leave treatment area in June 2010. Error bars = ± 1 SE.

Table 3. RCB ANOVAs and unplanned contrasts for *G. stricta* seed establishment measured in iceplant removal treatments† on 22 October 2010 on East Anacapa. This analysis was duplicated with an adjusted data set which included subtraction of an estimate of seedlings from naturally-occurring seed. Treatment contrasts reported are with alpha set at 0.017 after Dunn-Sidak correction. Significant results are in bold.

Source	df	*G. stricta* establishment		*G. stricta* establishment adjusted	
		F	*P*	*F*	*P*
Between-subjects effects					
Block	7	3.73	**0.02**	2.29	0.09
Treatment	2	5.19	**0.02**	4.65	**0.03**
Error	14				
Treatment Contrasts					
Hand-pull vs. spray-and-leave	1	0.02	0.90	0.06	0.81
Hand-pull vs. spray-and-pull	1	8.13	**0.013**	7.61	**0.015**
Spray-and-leave vs. spray-and-pull	1	7.41	**0.017**	6.29	0.03
Error	14				

† Treatments: Hand-pull, spray-and-leave, or spray-and-pull of *M. crocea*.

Also, a significant block effect was identified before the adjustment due to the fact that the three eastern-most replicate blocks accounted for 78% of *G. stricta* seed establishment. This block effect was not retained following the adjustment, indicating that there were differences in natural seeding across the study area.

Seedling treatments

For all species of planted seedlings, iceplant removal treatment was an important factor for survival through the study period. The spray-and-leave treatment strongly increased survival of seedlings compared with planting within areas where *M. crocea* material (alive or dead from prior herbicide treatment) had been pulled. The following sections present the details for each planted species.

Leptosyne gigantea **seedlings**

The spray-and-leave treatment was the only treatment to support *L. gigantea* survival beyond the March 2010 survey, and the survival in this treatment decreased then stabilized. Of the 160 *L. gigantea* seedlings planted, only 2 *L. gigantea* seedlings survived within the two pull treatments (1 seedling in each) on 28 March. By 3 June 2010, no *L. gigantea* seedlings were alive in the pull treatment areas. In striking contrast, 88 individuals were alive within the spray-and-leave treatment areas in March 2010 ($\bar{x}$ = 11.0 $\pm$ 0.9), and 64 individuals were alive in June 2010 ($\bar{x}$ = 8.0 $\pm$1.1). Within the spray-and-leave treatment, *L. gigantea* survival decreased through the first three surveys (Fig.

46

4); however, survival leveled-off, remaining relatively stable between October 2010 ($\bar{x}$ = 3.4±1.1) and January 2011 ($\bar{x}$ = 3.3 ±1.0).
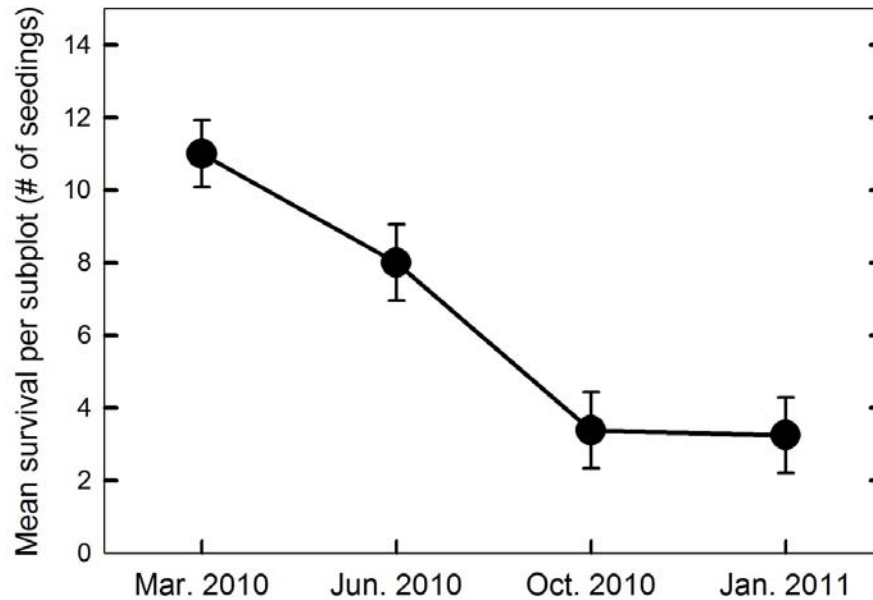
Figure 5. Survival of planted *L. gigantea* seedlings (n = 8) in the spray-and-leave treatment over time. Twenty seedlings were planted per subplot in February 2010. Error bars = ± 1 SE.

Grindelia stricta seedlings

The spray-and-leave treatment increased survival of *G. stricta* seedlings in comparison with the two pull treatments (Table 4; Fig. 6). Planned comparisons revealed that the spray-and-leave treatment resulted in significantly higher survival than either of the pull treatments. Between the pull treatments, the herbicide treatment and hand-pull treatment had similar effects on survival. The repeated measures RCB ANCOVA showed that these results were stable throughout the year.

Partial multiple correlation analyses indicated that *G. stricta* survival in January 2011 was negatively correlated with cover of naturally occurring *F. salina* that had

resprouted or colonized in the treatment plots (R = 0.62, p = 0.001). However, this correlation was mostly attributed to a single outlier. In one replicate plot, *F. salina* cover reached 95% as measured in October 2010. In this plot, only 2 out of 27 *G. stricta* seedlings were alive in January 2011. In the other seven plots, mean survival was 25.9 ± 0.4 seedlings, and mean *F. salina* cover was less than 13%. When this outlier was removed, the correlation between naturally occurring *F. salina* and survival of transplanted *G. stricta* was not significant (R = 0.39, p = 0.08, n = 7).

Table 4. Repeated measures RCB ANOVA and planned contrasts for *G. stricta* seedling treatment measured in iceplant removal treatments† on 28 March, 2 June, and 21 October 2010 and 16 January 2011 on East Anacapa. Significant results are in bold.

Source	df	F	P
Between-subjects effects			
Block	7	1. 24	0.34
Treatment	2	169.50	**<0.001**
Error	14		
Treatment Contrasts			
Pull vs. Leave	1	338.63	**<0.001**
Hand-pull vs. spray-and-pull	1	0.38	0.55
Error	14		
Within-subjects effects			
Time	3	5.82	**0.002**
Time × Block	21	1.33	0.21
Time × Treatment	6	0.57	0.75
Error(Time)	42		

† Treatments: Hand-pull, spray-and- leave, or spray-and-pull of *M. crocea* (iceplant).

Figure 6. Differences in mean seedling survival of *G. stricta* seedling transplants between iceplant removal treatments (n = 24 with n = 8 per treatment). Twenty-seven *G. stricta* seedlings were planted per subplot in February 2010. Error bars = ± 1 SE.

Frankenia salina seedlings

F. salina seedling survival within the spray-and-leave treatment was significantly higher than within the pull treatments, and there were no differences between the pull treatments (Table 5; Fig. 7). The tests of assumptions for the repeated measures RCB ANCOVA indicated that the size of the *F. salina* plants at the time of planting, measured as the above ground height at the time seedlings were planted, had differing effects on *F. salina* seedling survival among the treatments (Fig. 8). In the spray-and-leave treatment and in the hand-pull treatment, there was a positive relationship with height. No significant relationship was identified between height and survival in the spray-and-pull treatment areas (R = 0.53, p = 0.18, n = 8). The time × treatment × height interaction

identified that the relationship between seedling survival and height was more

pronounced in the spray-and-leave treatment in June compared with March 2010, while

the relationship between height and treatment had not changed in the hand-pull treatment

between time periods.

Table 5. Repeated measures RCB ANCOVA and planned comparisons for *F. salina* seedling treatment measured in iceplant removal treatment areas† on 28 March and 2 June 2010 on East Anacapa. Mean *F. salina* seedling height at the time of planting was included as a covariate. Significant results are in bold.

Source	df	F	P
Between-subjects effects			
Block	7	1.61	0.21
Treatment	2	28.20	**<0.001**
Error	14		
Treatment × height	3	34.82	**<0.001**
Error	13		
Treatment Contrasts			
Pull vs. Leave	1	56.35	**<0.001**
Hand-pull vs. spray-and-pull	1	0.06	0.81
Error	14		
Within-subjects effects			
Time	1	0.08	0.78
Time × block	7	0.61	0.76
Time × treatment × height	3	4.90	**0.02**
Error(Time)	42		

† Treatments: Hand-pull, spray-and-leave, or spray-and-pull of *M. crocea* (iceplant).

Decreases in *F. salina* survival between the two time periods were greater for plants that

were shorter during planting than those that were taller during planting in the spray-and-

leave treatment. Height and leaf number of *F. salina* at the time of planting were

strongly correlated ($R = 0.72$, $p < 0.001$, n = 24), so only height was analyzed.
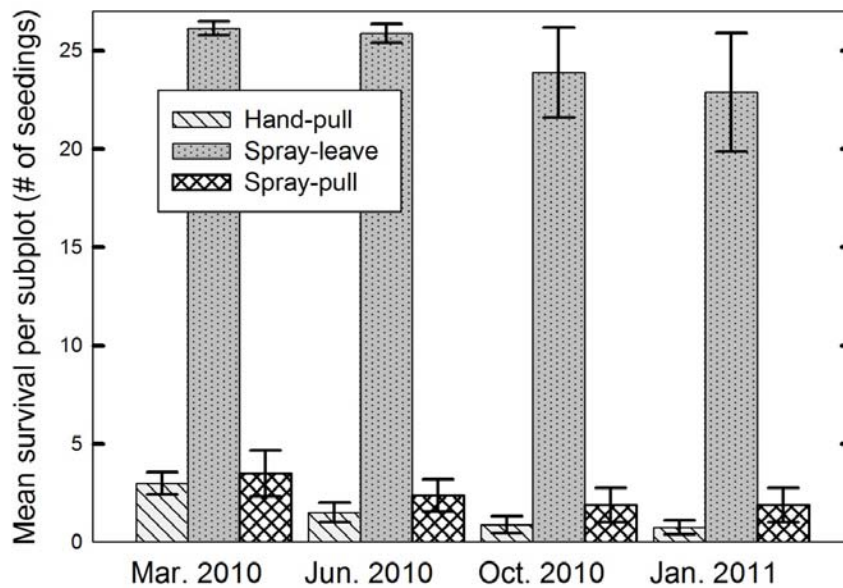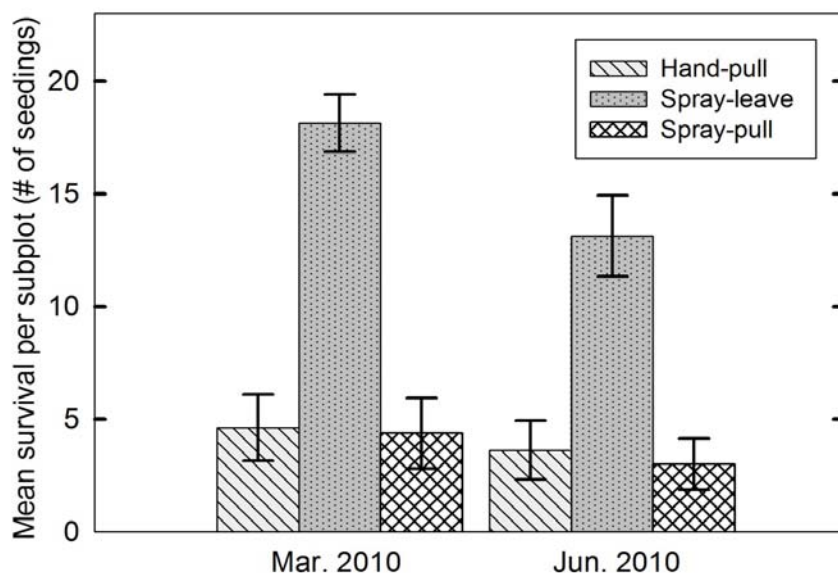
Figure 7. Differences in mean seedling survival of *F. salina* seedling transplant treatments between iceplant removal treatments (n = 24 with n = 8 per treatment). Twenty-three *F. salina* seedlings were planted per subplot in February 2010. Error bars = ± 1 SE.
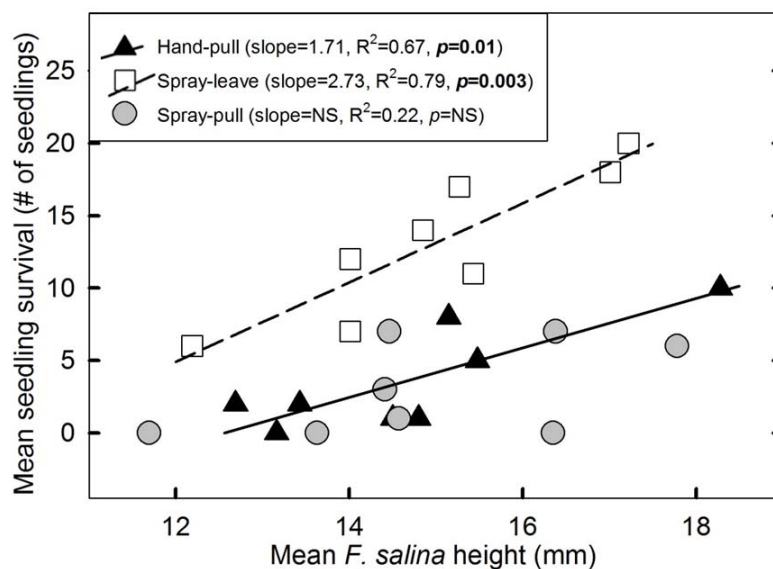
Figure 8. Relationship between *F. salina* seedling height at planting (25-26 Feb. 2010) and survival on 2 June 2010. Survival is per treatment subplot out of 23 planted seedlings (n = 24 with n = 8 per treatment). Significant results are in bold.

Discussion

The search for successful techniques to restore habitat following invasive species eradication is a common challenge for resource managers. Ideally, eradication and habitat restoration can be achieved with a minimum of effort and resources. This means that if there are several techniques available for eradication, each should be assessed for the potential benefits and disadvantages to habitat restoration.

This research was built on the following ideas: 1) several eradication methods (hand-pull, spray-and-leave, and spray-and-pull) have been shown to be useful in removal of the invasive iceplant, *M. crocea* on Anacapa Island (S. Lambrecht 2012, SJSU, CA, unpublished data); 2) autogenic restoration on Anacapa Island is expected to be slow, at best, if not entirely impeded by secondary invasive species (D'Antonio et al. 1992; Stylinsky & Allen 1999; Yelenik & Levine 2010); and 3) following application of these eradication methods, resultant site conditions may differ in the suitability for habitat restoration. Specifically, I hypothesized that the spray-and-leave eradication method would lead to higher survival of native seedlings due in part to the conservation of soil moisture. In addition, I hypothesized that there would be no impact on seedling survival of using herbicides to treat *M. crocea* compared with not using herbicide due to the limited residency of the herbicides used in this study.

While the results of this study addressed only a few questions arising from the effects of different *M. crocea* removal treatments, and there is more information that should be obtained before adopting a large-scale program for iceplant eradication (see

below), the study's findings provide some practical direction for eradication and habitat restoration on Anacapa Island.

Soil moisture

Iceplant removal treatments in this study affected soil moisture differently, specifically the spray-and-leave treatment was associated with higher soil moisture levels than the pull treatments. The fact that treatment differences in VWC meter readings were maintained across time further indicated that the relationships were generally valid. However, the VWC meter readings showed only a relative relationship between treatments since the probe readings were overestimated. The results did not confirm the importance of soil moisture to seedling survival. This result was in spite of the fact that VWC and transplanted seedling survival were both significantly higher in spray-and-leave than in the pull treatment areas. This inconsistency may be an outcome of high variation in readings as a result of equipment inaccuracy or sampling error.

Despite the absence of data to support a relationship between soil moisture and seedling dynamics, several additional indicators suggest that moisture was critical to seedling survival. Seedling mortality in the first month following transplanting indicated that soil moisture was probably a critical factor for seedling survival. By the first sampling event, 66% of all transplanted seedlings died, the majority of which were planted in the pull treatment plots. The month between planting and sampling was marked by unusually dry conditions for that time of year on Anacapa, which points to the possibility that limited moisture played a part in the high mortality. In addition, dead

seedlings were most often dessicated and attached to the substrate where they had been growing as opposed to showing signs of herbivory or obvious symptoms of infection.

It is well established that soil moisture can be a critical factor in survival for plants in similar habitats, including coastal sage scrub communities (Cione et al. 2002; Cox & Allen 2008) and island communities (Donlan et al. 2003; Yelenik & Levine 2010). Research on San Miguel Island identified low rainfall as a factor in *L. gigantea* seedling mortality (Schwemm 2008). The use of a moisture meter suited to the soil conditions (Sevostianova & Leinauer 2008) and a more robust sampling design for soil moisture may have resulted in evidence supporting a correlation between soil moisture and seedling survival. However, the differences in soil moisture may not have been sufficient to affect seedling survival between treatments, and the observed differences in survival may have been associated with other factors. Further research is warranted to investigate the importance of precipitation on establishment of Anacapa's native flora, as this can be a critical factor for native vegetation within the islands of California (Levin et al. 2008; Yelenik & Levine 2010) and an important consideration to include in restoration planning (Schwemm 2008; Yelenik & Levine 2010).

Effect of eradication treatment on seed establishment

My results identified that removal treatments appear to have affected seedling establishment in seeded treatments in spite of low observed germination numbers. This conclusion was drawn from analyses of *G. stricta* seeding treatment, as only 3 *L. gigantea* seedlings persisted through the monitoring period. It should be noted, however,

that seeded *L. gigantea* seedlings survived only within the spray-and-leave treatment and only in one treatment subplot. *L. gigantea* germination and establishment may be facilitated by the presence of debris or cover, and other unidentified conditions important for this species may be unevenly distributed within the study area. This result is consistent with results of a study of *L. gigantea* seed establishment on San Miguel Island. Catherin Schwemm (2008) found that *L. gigantea* seed establshiment was positively correlated with the presence of ground cover in the form of native annual plants, low-growing perennial plants, and litter, while establishment was negatively related to non-native grass cover. Her results show that cover is important for *L. gigantea* establishment but that the type of cover matters. Regardless, my results provide scant evidence from which to draw a conclusion regarding any effect that removal treatments had on seeding of *L. gigantea*. Alternatively, seed establishment results for *G. stricta* demonstrated that iceplant removal treaments affected conditions differently in ways that were important to seed establishment.

In contrast with my hypothesis, the spray-and-pull treatment provided for the highest *G. stricta* establishment over hand-pull and spray-and-leave. The lower seedling establishment identified in the spray-and-leave treatment, which was only significant prior to adjustment of the data set for natural seeding, may have been due to factors associated with the thick skeletal mat of herbicide-treated iceplant. Treatment seeds were dropped into the subplots through a grid placed on top of the dead vegetation. Along with natural seed rain, these seeds may have been caught in the vegetation rather than traveling to the soil below. Seeds would have either not germinated or experienced

arrested development due to the unsuitability of conditions within the suspended mat. Seeds that did find suitable substrate and moisture to germinate may have died in part due to low levels of sunlight. I assume that most *G. stricta* seeds that made it to the soil surface and found suitable conditions, aside from sunlight, did germinate because light exposure did not appear to affect germination in laboratory trials, and laboratory germination rates for *G. stricta* showed very high viability (i.e., 86% across all trials). Another possibility is that the cover of iceplant skeletons provided more suitable habitat for mice (Orrock et al. 2004), which may have led to higher seed predation in the spray-and-leave treatment. This conclusion seems unlikely as island deer mice have been shown to concentrate their foraging on *L. gigantea* inflorescences and mature seed capitatum where the foraging effort is most highly rewarded (Schwemm 2008). The probability that seed numbers per treatment subplot would be much more sparse in comparison to intact *L. gigantea* areas suggests that these seeds may not have attracted these preditors. Conversely, mouse populations were reported as being high during the study (J. Savage 2010, personal communication), which may have resulted in some pressure on treatment seeds.

Differences in seed germination between hand-pull and spray-and-pull, both before and after adjusting the data-set for natural seeding, suggest that the herbicide treatment unexpectedly provided some benefit to *G. stricta* seed establishment. One possibility for this result is that this treatment, by treating the *M. crocea* with herbicide and removing the vegetation 2.5 months later, allowed the skeletal mat to partially decompose. When the mat was subsequently pulled, small bits of partially decomposed

56

M. crocea may have remained on the soil surface, increasing the micro-site suitability for

G. stricta germination. Hand-pulling better enabled complete removal of *M. crocea* plant

material. Further investigation into the effects of a spray-and-pull treatment on seed

establishment could be useful 1) to understand the mechanism that supports higher

germination, 2) to determine if certain species benefit more or less from this treatment,

and 3) to understand if this effect is maintained despite the type of herbicide used (e.g.,

Aquamaster compared with Roundup Pro and Garlon 4).

Efficacy of seeding for restoration

Two species of perennial plants that are common and conspicuous on Anacapa

were used to investigate the efficacy of seeding as a method to restore native vegetation

following iceplant eradication. Of the two, 3 *L. gigantea* individuals and 50 *G. stricta*

individuals established by the final survey. After adjusting these data to estimate

seedling numbers from treatment seeds, *L. gigantea* establishment remained unchanged,

and 32 of the 50 *G. stricta* seedlings were estimated to have been established from

treatment seeds. These numbers do not clearly indicate whether seeding was an effective

restoration method. If seeding is used, broadcasting *L. gigantea* seed following pull

treatments is not advised, and broadcasting *G. stricta* seed following spray-and-pull

treatments is likely to yield higher densities of established vegetation compared with the

hand-pull and spray-and-leave treatments.

While the establishment numbers look quite low, especially considering high

coverage of other native vegetation within many of the plots and, thus, the potential for

future competitive exclusion (Banerjee et al. 2006), it is important to consider the context of seed numbers planted, timing, and weather conditions. The effort invested in seed collection and broadcasting was generally low and would be much lower with traditional broadcasting methods. As such, increased seeding per unit area may dramatically increase germination. Research conducted on San Miguel Island by Schwemm (2008) found that *L. gigantea* seedbank abundance was an important factor in population growth dynamics, indicating that broadcasting high seed numbers would increase establishment. Schwemm's (2008) research also found that under a natural seeding scenario, *L. gigantea* seedlings were cued to germinate with initial fall precipitation and that high *L. gigantea* seedling mortality was linked with low winter precipitation. By the time seeds were planted for my study (20-21 Feb. 2012) winter was two-thirds finished for the year and most of the winter precipitation had already fallen (WRCC 2012). Therefore, *L. gigantea* seedlings may have been planted at an unsuitable time to achieve high germination and survival. This may also be the case for *G. stricta* since seeds used in this study were mature by September 2009 and needed no pretreatments other than water to germinate. Further investigations should include an assessment of optimal timing for seeding.

Several additional considerations of seeding may be useful to managers planning future island restoration efforts. As exemplified between the two species included in seeding, some species appear to be better suited to broadcasting than others, and different species may respond to different conditions. Therefore, further investigations should focus on a range of species to gain a better understanding of which may be more effectively used in broadcasting and under what conditions. For example, some species

may require specific pretreatments for effective germination and establishment (see Emery 1988). Also, in areas where *M. crocea* removal is followed by recolonization of non-native grasses (S. Lambrecht 2012, SJSU, CA, unpublished data), seeding may be of limited benefit (Schwemm 2008; Yelenik & Levine 2010).

Effect of eradication treatment on transplanted seedlings

The differences in the effect of iceplant removal treatments on transplanted seedling survival were dramatic. The spray-and-leave treatment of *M. crocea* removal, while predicted to confer an advantage to planted seedlings, provided significantly higher quality habitat for first-year seedlings across all planted species than did either pull treatment. This result was particularly noteworthy as the effect was apparent by the first survey on 28 March 2010 after a month with low precipitation and with wind gusts reaching 32.2 m/s. While this method may provide for a range of benefits to seedlings, the foremost drivers of this response may be the retention of soil moisture by the dead iceplant mulch (Nyamai et al. 2011) and the protection to seedlings that was likely provided by the surrounding dead iceplant structure from the high winds. This effect may be naturally provided when seedlings grow at some optimal distance near each other (Bhattacharjee et al. 2010) or in the presence of mature conspecific vegetation (Schwemm 2008; Yelenik & Levine 2010).

While it is unknown if the herbicides used in the spray-and-leave treatment supported seed establishment directly through some form of growth stimulation (Weidenhamer & Callaway 2010), it is suspected that the benefit to seedlings was a result

of the organic matter of the dead *M. crocea* and not a direct effect of either the triclopyr or glyphosate. The absence of any difference observed in transplanted seedling survival between the spray-and-pull and hand-pull treatments suggests that the herbicides did not provide a direct benefit. While heribicide residues may have accumulated differently between the spray-and-pull and spray-and-leave treatments, any direct effects were unlikely given that neither the herbicide nor its metabolites were likely to have persisted at meaningful levels after the 79 d-period between spraying and seeding (Norris et al. 1987; Stephenson et al. 1990; Petty et al. 2003; Perez et al. 2007). Therefore, the high survival of seedlings in the spray-and-leave treatment was primarily attributed to the presence of dead plant material.

An important difference between the spray-and-leave treatment and the pull treatments that is useful for resource managers is the difference in the need to dispose of the remnant vegetation. Prior to this study, NPS efforts to remove *M. crocea* were largely focused on pulling live *M. crocea* and either leaving large piles to decompose or transporting the remains to an area of East Anacapa known as Trash Cove (NPS 2005). Allowing the dead vegetion to remain in place dismisses the problem of disposal and possibly reduces other adverse consequences of the eradication effort, such as wind-borne erosion, trampling of desirable vegetation, impacts to soil microbial communities, and/or loss of nutrients stored within the vegetation.

A possible drawback of the spray-and-leave treatment is the limitation the dead iceplant mats may impose on future colonization by native species. Conser and Conner (2009) found that the perennial iceplant *C. edulis* had a strong negative impact on the

success of a native annual dune species, *Gilia millefoliata* (dark-eyed gilia,

Polemoniaceae). Specifically, soils that had been occupied by *C. edulis* reduced the

germination, survival, growth, and reproduction of *G. millefoliata* compared with soils

previously occupied by native plants. *C. edulis*-affected soils were found to be lower in

pH and higher in recalcitrant organic content. While it is unknown whether *M. crocea*

causes similar effects, it may utilize similar mechanisms of soil alteration to confer

dominance once established, thus preventing native species from colonizing. The effects

of *M. crocea* on soil conditions are virtually unstudied and need more work before

specific recommendations can be made.

   While the results of this study indicate that the pull treatments were equal with

regard to seedling survival, there may be further implications to ecosystems from the use

of herbicide in *M. crocea* eradication. Herbicides, including those used in this study, can

impact plants and ecosystems at the community level. For instance, herbicides that were

used in this study have previously been shown to increase soil fungal and actinomycete

populations, decrease the functional diversity of soil bacteria, and reduce rhizobium

nodulation and mycorrhizal formation (Weidenhamer & Callaway 2010), though these

effects appear to be limited, especially when herbicides are applied at the recommended

concentrations. The potential effects of herbicides on other desirable species, including

amphibians (see Govindarajulu 2008) such as the native slender salamander, should be

carefully considered before any large scale herbicide program is adopted. During

iceplant pulling for this study, several individual salamanders were observed. Also, large

salamander congregations have been reported within live *M. crocea* mats on Anacapa

Island (H. Fitting 2012, personal communication). Further research should be conducted

to understand more broadly the potential risks of herbicide use on the ecosystems of

Anacapa. This research should include analysis of the effect of alternative herbicides on

restoration of native plants.

All three species responded to the removal treatments similarly in that they all

showed higher survival in the spray-and-leave treatment compared with the pull

treatments; however, overall, each species had differing levels of survivorship. As

indicated above, *G. stricta* survival was especially high in the spray-and-leave treatment

and very low in the pull treatments. In contrast, *L. gigantea* was especially low overall,

though all surviving individuals were in the spray-and-leave treatment area from the

second through final surveys. The inter-specific differences suggest that the

characteristics of the study site and the conditions of the year are more suited to some

species than to others and that some species respond better to transplanting. Since the

beginning of this project, the NPS has established a shadehouse for seedling production

on Anacapa. Future planting efforts could be conducted in a controlled manner to enable

effective monitoring and evaluation of these treatments with regard to establishment of

other species and species assemblages. These efforts could also investigate the

importance of abiotic conditions, weather, and annual timing of planting.

While the spray-and-leave treatment is significantly less labor-intensive than the

pull treatments (S. Lambrecht 2012, SJSU, CA, unpublished data), the use of herbicides

may be generally undesireable. Public opinion of herbicide use in natural lands is

generally low (Shindler et al. 2011; Toman et al. 2011), which can elicit public conflict,

especially given the function of the National Park System and the perception of the pristine wildlands that are embodied therein. For example, during field work conducted for this study, I descibed the purpose of the effort to a woman who was visiting Anacapa. Subsequently, she submitted a letter to the CINP superintendent expressing disaproval of the use of herbicides on Anacapa Island. In addition, having grade-school students participate as volunteers in *M. crocea* eradication and native plant restoration by the CINP may present additional public saftey concerns about the use of herbicides to treat vegetation in the presence of school children. In public lands, addressing or avoiding additional public concerns may be required elements of any restoration program. Under these conditions, utilization of an alternative method that mitigates public concern may be advantageous.

Comparisons of alternative methods to eradicate *M. crocea* that retain the dead vegetation without the use of herbicides is an important area for future study. During the time of this study, as a pilot investigation, I pulled a 17.5 m² patch of *M. crocea* by hand, inverted it, and left it in place. This treatment was conducted in October 2010, and by January 2011, approximately 90% of the *M. crocea* had died, and much of the remaining 10% appeared to be stressed, indicating that this method might serve as an effective alternative to the spray-and-leave treatement. Another effective alternative method could include solarization, which has been shown to effectively eliminate invasive species in coastal climates (Lambrecht & D'Amore 2010).

Transplanted seedling size

Seedling size was important to seedling survival for one of the three transplanted species. The taller *F. salina* individuals showed higher survival than shorter individuals. Differences in size were likely related to difference in age due to the span of time that seedlings were reared; however, seedling age was not recorded, so this potential correlation was not examined. That this size effect was not observed in the other species may indicate that the size differences were not sufficiently distinctive to make a difference on survival or that benefits experienced by being larger were offset in some way (e.g., through increased wind-related stress).

For *F. salina*, the effect of size (i.e., height) was significant in two of the treatments, hand-pull and spray-and-leave. In the spray-and-leave treatment the effect was particularly well-pronounced. This result suggests that the plants needed to be taller to succeed in the presence of the mat of dead *M. crocea*, which may have partly shaded the plants. Also, there may have been increased survival of *F. salina* from more developed roots, assuming that the taller plants also had larger roots. The effect of height in the hand-pull treatment may have been similar except that there would not have been an issue with being overshadowed. It is not clear why this effect was not identified in the spray-and-pull.

In general, this study provides some evidence that planting larger plants may provide for greater survival. This effect was secondary to the differences found between iceplant removal treatments, but the increased benefit to being larger for *F. salina* in the spray-and-leave treatment compared with being larger in the other treatments identifies a

synergistic effect that translates directly into management recommendations: For

increased survival, plant taller plants, and plant them in spray-and-leave areas.

Conclusion

This study shows that the effects of eradication treatments can be critical to

subsequent planting efforts. The success of both seeding and transplanting methods for

restoring native perennial plants are affected by the resultant conditions of different

eradication treatments, but the highest benefit per planting method was from different

eradication treatments. Seeding of *G. stricta* experienced the highest establishment in the

spray-and-pull treatment compared to the other treatments, while only a few plants

established from seeding of *L. gigantea* and only in the spray-and-leave treatment. In

contrast, spray-and-leave treated areas supported transplanted seedling survival far better

than either pull treatment. The hand-pull treatment was the least effective for plant

survival and establishment. This is particularly noteworthy, as hand pulling was a

commonly-used method for *M. crocea* eradication on Anacapa Island prior to this study.

Given the results, the use of a spray-and-leave treatment may be the best method

for iceplant eradication and survival of native plantings on Anacapa. This is particularly

true if there will continue to be widespread use of transplanting. If seeding is the only

method that can be employed due to resource constraints, an understanding of the

germination and establishment requirements for individual species would be important

for management to ensure that species can be seeded according to site conditions

following removal treatment(s). An herbicide treatment could be used both with and

without removal of the dead iceplant so that seeding of a broader mix of species may be supported. As indicated above, herbicide use can negatively impact other elements of an ecosystem and can elicit public controversy. Therefore, a thorough impact analysis of risks and benefits needs to be conducted before broad-scale use of herbicide is adopted.

Finally, existing site conditions are important to both the survival of planted seedlings, as was seen in the mortality of *G. stricta* as a result of the presence of densely occurring *F. salina*, and the establishment of seeded species, as was seen in the spatial concentrations of established seedlings of both *L. gigantea* and *G. stricta*. This indicates that the methods used to remove invasive species are by no means the only important factors to consider for restoration of native species.

Further research that would be helpful to support restoration of Anacapa Island should focus on establishment limitations of native species, identification of the abiotic and biotic makeup of potential reference sites for restoring *M. crocea* stands, and methods to reduce the colonization of other non-native species, including non-native grasses and iceplant species, into *M. crocea* removal areas. In addition, a careful examination should be undertaken to evaluate the potential functional roles and ecosystem processes that *M. crocea* may provide on Anacapa to insure that unintended consequences to native species are not promoted as a result of the eradication.

Implications for practice

- Treating the invasive iceplant, *Malephora crocea*, with herbicide (a glyphosate and triclopyr mix) and leaving the skeletal mat prior to planting native perennial seedlings resulted in remarkable seedling survival compared with planting in areas where live or herbicide-treated iceplant had been removed.

- Herbicide-treated iceplant left in place provided for higher soil moisture compared with removed iceplant areas.

- Existing conditions were important to native perennial plant restoration. The presence of numerous extent *Frankenia salina* stems resulted in high cover of *F. salina* and low survivorship of planted *Grindelia stricta* seedlings.

- Seeding native perennial species showed mixed success in iceplant removal treatments, highlighting the importance of understanding species-specific requirements for germination and establishment before adopting a restoration method.

- Seedling size can be an important factor in restoration success. In this study, taller *F. salina* seedlings survived better than shorter seedlings, and this effect was greater in spray-and-leave treatment areas compared with pull areas. This effect was not seen in the other species.

LITERATURE CITED

Allen, E. B., R. D. Cox, T. Tennant, S. N. Kee, and D. H. Deutschman. 2005. Landscape restoration in southern California forblands: Response of abandoned farmland to invasive annual grass control. Israel Journal of Plant Sciences **53**:237-245.

Baldwin, B. G., D. H. Golman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken, editors. 2012. The Jepson manual: vascular plants of California, 2nd edition. University of California Press, Berkeley.

Banerjee, M. J., V. J. Gerhard, and E. P. Glenn. 2006. Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. Restoration Ecology **14**:339-249.

Bhattacharjee, J., J. P. Taylor Jr., and L. M. Smith. 2010. Optimum seedling productivity in cottonwoods: a function of neighbor distance. Journal of Arid Environments **74**:1018-1023

Bittrich, V. and H. Hartmann. 1988. The Aizoaceae – a new approach. Botanical Journal of the Linnean Society **97**:239-254.

Bleck, J. 2012.*Malephora crocea* (Jacq.) Schwantes. Page 163 in B. G. Baldwin, D. H. Golman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken, editors. The Jepson manual: vascular plants of California, 2nd edition. University of California Press, Berkeley.

Buisson, E., K. D. Holl, S. Anderson, E. Corcket, G. F. Hayes, F. Torre, A. Peteers, and T. Dutoit. 2006. Effect of seed source, topsoil removal, and plant neighbor removal on restoring California coastal prairies. Restoration Ecology **14**:569-577.

Carrillo-Garcia, A., J. L. Leon de la Luz, Y. Bashanl, and G. J. Bethlenfalvay. 1999. Nurse plants, *Mycorrhizae*, and plant establishment in a disturbed area of the Sonoran Desert. Restoration Ecology **7**:321-335.

Chakraborty, A. and B. Li. 2010. Departure from naturalized to invasive stage: a disturbance induced mechanism and associated interacting factors. Journal of Plant Ecology **3**:231-242.

Cione, N. K., P. E. Padgett, and E. B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. Restoration Ecology **2**:376-384.

Clark, D. A. 1982. Foraging behavior of a vertebrate omnivore (*Rattus rattus*): meal structure, sampling, and diet breadth. Ecology **63**:763-772.

Conser, C. and E. F. Connor. 2009. Assessing the residual effect of *Carpobrotus edulis* invasion, implications for restoration. Biological Invasions **11**:349-358.

Corbin, J. D., and C. M. D'Antonio. 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. Restoration Ecology **12**:36-43.

Cory, J. S., and J. H. Myers. 2000. Direct and indirect ecological effects of biological control. Trends in Ecology & Evolution **15**:137-139.

Cox, R. and E. B. Allen. 2008. Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. Journal of Applied Ecology **45**:495-504.

Crimmins, T. M, and G. R. McPherson. 2008. Vegetation and seedbank response to *Eragrostis lehmanniana* removal in semi-desert communities. European Weed Research Society Weed Research **48**:542-551.

D'Antonio, C. M. 1990.Seed production and dispersal in the non-native succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. Journal of Applied Ecology **27**:693-702.

D'Antonio, C. M., W. L. Halvorson, and D. B. Fenn. 1992. Restoration of denuded areas and iceplant areas on Santa Barbara Island, Channel Islands National Park. NPS-WRUC/NRTR-92/46. Cooperative National Park Resources Studies Unit, University of California, Davis.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.

D'Antonio, C. M., and T. L. Dudley. 1995. Biological invasions as agents of change on islands versus mainlands. Pages 103-121 in P. M. Vitousek, L. L. Loope and H. Adsersen, editors. Islands: biological diversity and ecosystem function. Springer-Verlag, New York, New York.

D'Antonio, C. M., J. Levine, and M. Thomsen. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. Journal of Mediterranean Ecology **2**:233-245.

D'Antonio, C. M. and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology **10**:703-713.

D'Antonio, C. M. and J. D. Corbin. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology **85**:1273-1283.

Dassonville, N., S. Vanderhoeven, V. Vanparys, M. Hayez, W. Gruber, and P. Meerts. 2008. Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia **157**:131-140.

Denslow, J. S. 2003. Weeds in Paradise: thoughts on the invasibility of tropical islands. Annals of the Missouri Botanical Garden **90**:119-127.

Donlan, C. J., D. A. Croll, and B. R. Tershy. 2003. Islands, exotic herbivores, and invasive plants: their role in coastal California restoration. Restoration Ecology **11**:524-530.

Eason, C., R. Henderson, S. Hix, D. MacMorran, A. Miller, E. Murphy, J. Ross, and S. Ogilvie. 2010. Alternatives to brodifacoum and 1080 for possum and rodent control-how and why? New Zealand Journal of Zoology **37**:175-183.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics **41**:59-80.

El-Ğhareeb, R. 1991.Vegetation and soil changes induced by *Mesembryanthemum crystallinum* L. in a Mediterranean desert ecosystem. Journal of Arid Environments **20**:321-330.

Eliasson, U. 1995. Patterns of diversity in island plants. Pages 35–50 in P. M. Vitousek, L. L. Loupe, and H. Andersen, editors. Islands: biological diversity and ecosystem function. Springer-Verlag, New York, New York.

Emery, D. E. 1988. Seed propagation of native California plants. Santa Barbara Botanic Garden, Santa Barbara, California.

Eschtruth, A. K. and J. J. Battles. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecological Monographs **79**:265-280.

Essl, F., S. Dullinger, W. Rabitsch, P. E. Hulme, K. Hülber, V. Jarošík, I. Kleinbauer, F. Krausmann, I. Kühn, W. Nentwig, M. Vilà, P. Genovesi, F. Gherardi, M. Desprez-Loustau, A. Roques, and P. Pyšek. 2011. Socioeconomic legacy yields an invasion debt. Proceedings of the National Academy of Sciences **108**:203-207.

Ferren Jr., W. R., J. Bleck, and N. Vivrette. 1981. *Malephora crocea* (Aizoaceae) naturalized in California. Madroño **28**:80-85.

Florens, F. B. V., D. Daby, and R. Jones. 1998. The impact of controlling alien plants and animals on the snail fauna of forests on Mauritius. Journal of Conchology Special Publication **2**:87-88.

Gioria, M., P. Pysek, and L. Moravcova. 2012. Soil seedbanks in plant invasions: promoting species invasiveness and long-term impact on plant community dynamics. Preslia **84**:327-350.

Govindarajulu, P. P. 2008. Literature review of impacts of glyphosate herbicide on amphibians: what risks can the silvicultural use of this herbicide pose for amphibians in B.C.? Ministry of Environment Wildlife Report **28**:1-79.

Halvorson, W. L. 1992. Alien plants at Channel Islands National Park. Pages 64-96 in C. P. Stone, C. W. Smith, and J. T. Tunison, editors. Alien plant invasions in native ecosystems of Hawai'i: management and research. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu.

Hochberg, M., S. A. Junak, R. Philbrick, and S. Timbrook. 1979. Botany. Pages 5.1–5.85 in D. M. Power, editor. Natural resources study of the Channel Islands National Monument. Santa Barbara Museum of Natural History, Santa Barbara, California.

Holl, K. D., M. E. Loik, E. H. V. Lin, I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology **8**:339-349.

Howald, G. R., K. R. Faulkner, B. Tershy, B. Keitt, H. Gellerman, E. M. Creel, M. Grinnell, S. T. Prtega, and D. A. Croll. 2003. Eradication of black rats from Anacapa Island: biological and social considerations. Pages 299-312 in D. K. Garcelon and C. A. Schwemm, editors. Proceedings of the sixth California Islands Symposium, Ventura, California. Institute for Wildlife Studies, Arcata, California.

Hulme, P. E., and E. T. Bremner. 2006. Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. Journal of Applied Ecology **43**:43-50.

Innes, J., and G. Barker. 1999. Ecological consequences of toxin use for mammalian pest control in New Zealand – an overview. New Zealand Journal of Ecology **23**:111-127.

Jameson, E. W. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada, California. Journal of Mammalogy **33**:50–60.

Jacobsen, H. 1960. A handbook of succulent plants, vol. III. Mesembryanthemums (Ficoidacea). Blandford Press, London, England.

Jenkins, C. N., and S. L. Pimm. 2003. How big is the global weed patch? Missouri Botanical Garden **90**:172-178.

Johnson, D. L. 1979. Geology, soils, and erosion. Pages 3.1–3.71 in D. M. Power, editor. Natural resources study of the Channel Islands National Monument. Santa Barbara Museum of Natural History, Santa Barbara, California.

Junak, S. A., M. Hochberg, R. Philbrick, and S. Timbrook. 1980. Plant communities of Anacapa Island, California. Pages 222-231 in R. Linn, editor. Proceedings of the 2nd conference on scientific research in the National Parks: Volume 4 - resource analysis and mapping. National Park Service, Washington, D.C.

Junak, S., R. Philbrick, S. Chaney, and R. Clark. 1997. A checklist of vascular plants of Channel Islands National Park.2nd edition. Southwest Parks and Monuments Association, Tucson, Arizona.

Kueffer, C., C. Daehler, C. W. Torres-Santana, C. Lavergne, J. Meyer, R. Otto, and L. Silva. 2010. A global comparison of plant invasions on oceanic islands. Perspectives in Plant Ecology, Evolution and Systematics **12**:145-161.

Knapp, P.A. 1996. Cheatgrass (*Bromus tectorum* [L.]) dominance in the Great Basin Desert. Global Environmental Change **6**:37-52.

Lambrecht, S. C. and A. D'Amore. 2010. Solarization for non-native plant control in cool, coastal California. Ecological Restoration **28**:424-426.

Levine J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2002. Mechanisms underlying the impacts of exotic plant invasions. The Royal Society Review **270**:775-781.

Levine, J. M., A. K. McEachern, and C. Cowan. 2008. Rainfall effects on rare annual plants. Journal of Ecology **96**:795-806.

Lippitt, L., M. W. Fidelibus, and D. A. Bainbridge. 1994. Native seed collection, processing, and storage for revegetation projects in the western United States. Restoration Ecology **2**:120-131.

Livingston, D. S. 2006. Historic resource study: Anacapa Island. National Park Service, Channel Islands, Department of the Interior, Ventura, California.

Lloret, F., R. Medail, G. Brundu, I. Camarda, E. Moragues, J. Rita, P. Lambdon, and P. E. Hulme. 2005. Species attributes and invasion success by alien plants on Mediterranean islands. Journal of Ecology **93**:512-520.

Louda, S. M., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science, New Series **277**:1088-1090.

McCauley, D. J., P. A. DeSalles, H. S. Young, R. B. Dunbar, R. Dirzo, M. M. Mills, and F. Micheli. 2012. From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. Scientific Reports **2**:doi:10.1038/srep00409.

McEachern, K. 2004. Ecological effects of animal introductions at Channel Islands National Park. Park Science **22**:1-9.

Meinke, C. W., S. T. Knick, and D. A. Pyke. 2009. A special model to prioritize sagebrush landscapes in the Intermountain West (U.S.A.) for restoration. Restoration Ecology, **17**:652-659.

Moody, A. 2000.Analysis of plant species diversity with respect to island characteristics on the Channel Islands, California. Journal of Biogeography **27**:711-723.

Mooney, H. A. and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences **98**:5446-5451.

Myers, J. H. Myers, D. Simberloff, A. M. Kuris and J. R. Carey. 2000. Eradication revisited: dealing with exotic species. Trends in Ecology & Evolution **15**:316-320.

NPS (National Park Service). 2000. Channel Islands National Park final environmental impact statement: Anacapa Island restoration project. National Park Service, Channel Islands, Department of the Interior, Ventura, California.

NPS (National Park Service). 2005. Cultural landscape inventory: Anacapa Island Light Station. National Park Service, Channel Islands, Department of the Interior, Ventura, California.

NPS (National Park Service). 2012. Restoring Anacapa Island: native plants. National Park Service, Channel Islands, Department of the Interior, Ventura, California. URL http://www.nps.gov/chis/naturescience/restoring-anacapa-island-native-plants.htm. [accessed on 5 July 2012].

NRCS (Natural Resources Conservation Service), 2009. Channel Islands area, California, parts of Santa Barbara and Los Angeles Counties (CA688). Web Soil Survey, Natural Resource Conservation Service, United States Department of Agriculture.URL http://websoilsurvey.nrcs.usda.gov/. [accessed on 10 March 2012].

Norris, L. A., M. L. Montgomery, and L. E. Warren. 1987. Triclopyr persistence in western Oregon hill pastures. Bulletin of Environmental Contamination and Toxicology **39**:134-141.

Nyamai, P. A., T. S. Prather, and J. M. Wallace. 2011. Evaluating restoration methods across a range of plant communities dominated by invasive annual grassland to native perennial grasses. Plant Science and Management **4**:306-316.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not direct, cues of predation risk. Behavioral Ecology **15**:433-437.

Parolin, P. 2006.Ombrohydrochory: Rain-operated seed dispersal in plants – with special regard to jet-action dispersal in Aizoaceae. Flora **201**:511-518.

Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia **117**:449-459.

Perez, G. L., A. Torremorell, H. Mugni, P. Rodriquez, M. Solange Vera, M. do Nascimento, L. Allende, J. Bustingorry, R. Escaray, M. Ferraro, I. Izaguirre, H. Pizarro, C. Bonetto, D. P. Morris, and H. Zagarese. 2007. Effects of the herbicide roundup on freshwater microbial communities: a mesocosm study. Ecological Applications **17**:2310-2322.

Petty, D. G., K. D. Getsinger, and K. B. Woodburn. 2003. A review of the aquatic environmental fate of triclopyr and its major metabolites. Journal of Aquatic Plant Management **41**:69-75.

Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E. Wong, L. Russel, J. Zern, T. Aquino, T. Tsomondo. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems and Environment **84**:1-20.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273-288.

Questad, E. J., J. M. Thaxton, and S. Cordell. 2012. Patterns and consequences of re-invasion into a Hawaiian dry forest restoration. Biological Invasions DOI: 10.1007/s10530-012-0253-6.

Raizada, P., A. S. Raghubanshi, and J. S. Singh. 2008. Impact of invasive alien plant species on soil processes: a review. Proceedings of the National Academy of Sciences, India. Section B **78**:288-298.

Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions **8**:927-939.

Santa Barbara News Press. 1951. Television replaces poker in popularity among coast guardsmen at lonely Anacapa Island Station. July 16, 1951, Evening Edition, Santa Barbara New Press, California.

Saunders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences **100**:2474-2477.

Sawyer, J. O., T. Keeler-Wolf, and J. M. Evens. 2008. A manual of California vegetation. 2nd edition. California Native Plant Society Press, Sacramento.

Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, A. Hastings, R. D. Holt, M. M. Mayfield, M. I. O'Connor and W. R. Rice. 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution **22**:465-471.

Schiffman, P. M. 1997. Wing reduction in island *Coreopsis gigantea* achenes. Madroño **44**:394-396.

Schoenherr, A. A., C. R. Feldmeth, and M. J. Emerson. 1999. Natural history of the islands of California. University of California Press, Berkeley.

Scholl, D. 1960. Relationship of the insular shelf sediments to the sedimentary environments and geology of Anacapa Island, California. Journal of Sedimentary Petrology **30**:123-139.

Schwemm, C. A. 2008. Establishment limitations and population recovery of giant coreopsis (*Coreopsis gigantea*) on the California Channel Islands. Dissertation. University of California, Santa Barbara.

Sevostianova, E. and B. Leinauer. 2008. Accuracy of moisture sensors in saline soils. Report for the Water Resources Research Institute, New Mexico State University, Las Cruces.

Shindler, B., R. Gordon, M. W. Brunson, and C. Olsen. 2011. Public perceptions of sagebrush ecosystem management in the Great Basin. Rangeland Ecology & Management **64**:335-343.

Sol, D. 2000. Are islands more susceptible to be invaded than continents? Birds say no. Ecography **23**:687-692.

SCWP (Southern California Writers' Project). 1941. Sierras in the sea. Pages 65-78 in Santa Barbara: a guide to the channel city and its environs. Hastings House, New York, New York.

STI (Spectrum Technologies, Inc.). 2010. Fieldscout TDR 100 / 200 Soil Moisture Meter Product Guide: Item #6435FS & 6440FS. Spectrum Technologies, Inc., Plainsfield, Illinois.

Stein, W. I., R. Danielson, N. Shaw, S. Wolff, and D. Gerdes. 1986. Users guide for seeds of western trees and shrubs. USDA-Forest Service Pacific Northwest Research Station PNW-193.

Stephenson, G. R., K. R. Solomon, C. S. Bowhey, and K. Liber. 1990. Persistence, leachability, and lateral movement of triclopyr (Garlon) in selected Canadian forestry soils. Journal of Agricultural and Food Chemistry **38**:584-588.

Stylinsky, C. D. and E. B. Allen. 1999. Lack of native species recovery following severe exotic disturbance in southern Californian shrublands. Journal of Applied Ecology **36**:544-554.

Sumner, L. 1953. The 1953 Channel Islands National Monument inspection: story in pictures, with summary and recommendations. Report for the National Park Service, Sequoia and Kings Canyon National Park, California.

Thein, S. J. 1979. A flow diagram for teaching texture by feel analysis. Journal of Agronomic Education **8**:54-55.

Toman, E., M. Stidham, B. Shindler, and S. McCaffrey. 2011. Reducing fuels in the wildland-urban interface: community perceptions of agency fuels treatments. International Journal of Wildland Fire **20**:340-349.

USGS (Unites States Geological Survey). 1973. Anacapa Island. Map. 1:24,000. 7.5 minute quadrangle. USGS, Menlo Park, California.

Vitousek, P. M. and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs **59**:247-265.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84**:468-478.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997*a*. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology **21**:1-16.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997*b*. Human domination of Earth's ecosystems. Science **277**:494-499.

Vivrette, N. J. and C. H. Muller. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. Ecological Monographs **47**:301-318.

vonWillert, D. J., D. A. Thomas, W. Lobin and E. Curdts.1977. Ecophysiologic investigations in the family of the Mesembryanthemaceae. Occurrence of a CAM and ion content. Oecologia **29**:67-76.

Warren Jr., E. 1958. Off Santa Barbara: California's ranches in the sea. The National Geographic Magazine **116**:256-283.

Weidenhamer, J. D. and R. M. Callaway. 2010. Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. Journal of Chemical Ecology **36**:59-69.

WRCC (Western Regional Climate Center). 2012. Anacapa Island California. National Oceanic and Atmospheric Administration. URL http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca0188+sca. [accessed on 24 April 2012].

Whisenant, S. 2002. Terrestrial systems. Pages 97–107 in M. R. Perrow and A. J. Davy, editors. Handbook of Ecological Restoration, Volume 1: Principles of Restoration. Cambridge University Press, New York, New York.

Whisenant, S. G., T. L. Thurow, and S. J. Maranz. 1995. Initiating autogenic restoration on shallow semiarid sites. Restoration Ecology **3**:61-67.

Whitworth, D. L., H. R. Carter, R. J. Young, J. S. Koepke, F. Gress, and S. Fangman. 2005. Initial recovery of Xantus's Murrelets following rat eradication of Anacapa Island, California. Marine Ornithology **33**:131-137.

Wyseure, G. C. L., M. A. Mojid, and M. A. Malik. 1997. Measurement of volumetric water content by TDR in saline soils. European Journal of Soil Science **48**:347-354.

Yelenik, S. G. and J. M. Levine. 2010. Process limiting native shrub recovery in exotic grasslands after non-native herbivore removal. Restoration Ecology **18**:418-425.

Young, H. S., D. L. McCauley, R. B. Dunbar, and R. Dirzo. 2010*a*. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsides. Proceedings of the National Academy of Sciences **107**:2072–2077.

Young, H. S., T. K. Raab, D. J. McCauley, A. A. Briggs, and R. Dirzo. 2010*b*. The coconut palm, *Cocos nucifera*, impacts forest composition and soil characteristics at Palmyra Atoll, Central Pacific. Journal of Vegetation Science **21**:1058-1068.

Zahawi, R. A. and C. K. Augspurger. 2006. Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. Ecological Applications **16**:464-478.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution **16**:454-459.

Zink, T. A. and M. F. Allen. 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. Restoration Ecology **6**:52-58.