

SOUTHEAST FARALLON ISLAND SEED BANK CHARACTERIZATION

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In

Geography: Resource Management and Environmental Planning

by

Richard Adam Chasey

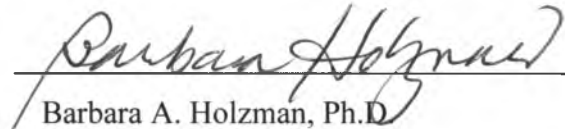
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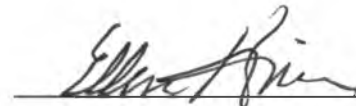
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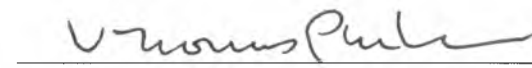
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CERTIFICATION OF APPROVAL

I certify that I have read *Southeast Farallon Island Seed Bank Characterization* by Richard Adam Chasey, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirement for the degree Master of Arts in Geography: Resource Management and Environmental Planning at San Francisco State University.

  
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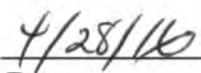
## SOUTHEAST FARALLON ISLAND SEED BANK CHARACTERIZATION

Richard Adam Chasey  
San Francisco, California  
2016

Characterization of soil seed banks ('seed banks' hereafter) are important to increased understanding of vegetation communities and can shed light on their true diversity as well as their response to and recovery from disturbance. These factors help guide effective environmental management, especially in disturbed ecosystems. We performed the first characterization of the seed banks on Southeast Farallon Island, assessing species richness, density, distribution, and temporal variation, and through these the status of native and non-native seed banks on the island. These were compared with the aboveground vegetation in order to reveal patterns within and between the above- and belowground communities. Results show that the seed banks and aboveground vegetation were heavily impacted by non-native species in richness, density, and cover, although native species remain present and widespread in both systems. Seasonal variation characteristic of Mediterranean annual vegetation communities was exhibited in both the seed banks and aboveground vegetation, although no yearly variation was detected. Results suggest the existence of a largely homogenous seed bank across the island, of which the annual expression in the aboveground vegetation is dependent upon numerous factors including disturbance, environmental factors, germination cues, and seed input from previous seasons. By revealing a widespread and robust presence of native seeds in the seed banks, this study can help guide effective restoration of native vegetation on SEFI and provide a baseline dataset that future studies can use to assess impacts of ongoing and proposed management actions on Southeast Farallon Island and other temperate island ecosystems.

I certify that the Abstract is a correct representation of the content of this thesis.

  
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## **INTRODUCTION**

Soil seed banks ('seed banks' hereafter) are aggregations of ungerminated seeds in or on the soil and associated litter, that are potentially capable of replacing adult plants following death (Baker 1989). A thorough understanding of seed banks is important to ecological knowledge and proper management of ecosystems throughout the world (Keddy et al. 1989; van der Valk & Pederson 1989). As anthropogenic disturbances increase in both scale and severity throughout the world, understanding the role of seed banks and their responses to introduction or removal of disturbance becomes increasingly important to effective environmental management and decision making. More specifically, the role of disturbance and seed banks on insular ecosystems – those isolated from mainland systems and with unique species assemblages and often high rates of endemism – are relatively unknown and hold implications for their proper management. The study presented here aims to address these knowledge gaps in our understanding of vegetation systems on disturbed insular ecosystems and our understanding of seed banks in general.

The ecological importance of seed banks has been noted since Darwin (1859) discussed the presence of seeds in the soil of riparian ecosystems and their role in plant recruitment. Seed bank science has progressed rapidly and the primacy of seed banks as sources of reproduction is now generally acknowledged (Simpson et al. 1989). Seed banks represent

a type of ecological memory of conditions that have historically prevailed in a given landscape, and play crucial roles in maintenance of ecological and genetic diversity in vegetation populations and communities (Baker 1989; Gross 1990). Seed banks are also important components of an ecosystem's resilience and ability to respond to disturbance (Coffin & Lauenroth 1989; Merou et al. 2013).

A general lack of correlation between aboveground vegetation and seed banks has been recognized in the literature for many vegetation communities (Thompson & Grime 1979; Coffin & Lauenroth 1989; Warr et al. 1994; Cline et al. 2008). While a certain species may be well represented or dominant in the seed bank, it may be scarce or absent from the aboveground vegetation (Coffin & Lauenroth 1989; Cline et al. 2008). The opposite can also be true, with species well represented in the aboveground vegetation scarce or even absent in the seed bank (Warr et al. 1994). True overall site diversity and future vegetation community makeup are thus difficult to assess via measurement of aboveground vegetation alone and are best done in concert with seed bank characterizations (Warr et al. 1994; Cline et al. 2008).

Principal characteristics of seed banks include species richness, seed density, vertical and horizontal distribution, germination cues, temporal variation, and viability (Simpson et al.

1989). Seed banks are divided into two broad strategy types; transient, in which seeds remain viable for  $\leq 1$  year, and persistent, in which seeds remain viable for  $>1$  year (Simpson et al. 1989). Transient seed banks are adapted to utilize gaps created by seasonally predictable damage and mortality in the aboveground vegetation, while persistent seed banks are more adapted to reestablishment following temporally and/or spatially unpredictable disturbances in aboveground vegetation (Cline et al. 2008). Seed banks associated with annual plants disproportionately represent genotypes that were successful in good years, while those associated with perennial plants represent those that have persisted through both good and bad years (Baker 1989).

As many seeds will remain dormant in the soil until specific germination conditions are met (e.g., soil moisture, scarification, or soil temperature), an understanding of the temporal variation in seed banks is an important aspect of seed bank characterization (Thompson & Grime 1979; Coffin & Lauenroth 1989; Simpson et al. 1989). Due to the transient nature of many seed banks, temporal variability has been shown to occur at both yearly and seasonal timescales (Thompson & Grime 1979; Coffin & Lauenroth 1989). Due to the importance of interaction between the variability of disturbances and the spatial and temporal variability of seed banks, temporal variation in seed banks is crucial to post-disturbance recolonization or restoration (Coffin & Lauenroth 1989).

The impacts of invasive plants on diversity and abundance of aboveground native vegetation is well established (Mooney & Hobbs 2000), although the effects on native seed banks are less well-known. Invasive plant species tend to produce seed banks that are both large and persistent, and which increase in density as aboveground abundance and seed production of invasive plants increase (Cline et al. 2008). Responses of native seed banks to aboveground invasion varies depending on community type, with some studies showing a lower abundance and diversity of native seeds in invaded ecosystems (Robertson & Hickman 2012), and others showing large, viable native seed banks persisting in invaded ecosystems (Cline et al. 2008). Establishment and increase of invasive species following natural and anthropogenic soil disturbance has been documented in California coastal systems (Vivrette & Muller 1977), a process that can lead to encroachment on native vegetation and eventual landscape dominance given proper environmental cues and seed bank presence.

Knowledge of seed bank dynamics and responses to disturbance regimes is important to vegetation management at all scales. The success of management plans or treatments may depend on understanding a given ecosystem's seed bank responses (Parker et al. 1989). Understanding the species composition of a seed bank, the specific germination cues of these species, and the extent to which these cues can be manipulated, better enables environmental managers to exploit seed banks to either increase germination of desirable

species or reduce germination of undesirable species (van der Valk & Pederson 1989).

Knowing seed bank responses can inform more effective manipulation of environmental factors capable of altering species germination and thus vegetation

composition, knowledge especially useful in recovery of post-disturbance ecosystems (Kalamees & Zobel 2002; Keddy et al. 1989; van der Valk & Pederson 1989).



**Figure 1:** Map of study area, Southeast Farallon Island. Map credit: Jamie Hawk (2015).

Here we present the first comprehensive characterization of the seed banks of SEFI including species richness, density, distribution, and temporal variation, with the specific aim of assessing the current state of native and non-native seed banks on the island. Comparisons will be made with the aboveground vegetation in order to reveal general patterns both within and between the above- and belowground communities. This will provide greater insight into the true nature of the vegetation communities on SEFI and can then be used to guide proper management of these communities. Similarly, this will shed light on the potential role of seed banks in the restoration of native vegetation communities on SEFI.

## **METHODS**

### ***Study area and vegetation***

We conducted this study on Southeast Farallon Island (SEFI) in the Farallon National Wildlife Refuge, California (Figure 1). SEFI is located 48 km west of the San Francisco Bay (37°72' N latitude, 123°0' W longitude) and harbors a typical Mediterranean climate with moderate temperatures year round, wet winters, and dry summers (USFWS 2013). Temperatures are at their highest in October with an average of



16.1°C, and their lowest in January with an average of 11.4°C (USFWS 2013). The site receives an average of 50.8cm of rainfall per year, 89% of which occurs between November and April (USFWS 2013). SEFI is approximately 49 ha in area, ranges in elevation from 0 – 109 m above mean sea level, and has a generally rocky and uneven topography covered largely in bare rock with little soil coverage, although portions are covered with rich brown soil up to ~20 cm deep (USFWS 2013). Soil is composed primarily of decomposing guano and granitic sand with small amounts of animal fragments, vegetation, and human detritus (USFWS 2013).

Due in large part to the harsh marine environment and limited habitat types, vegetation assemblages on SEFI are simple and include just 46 species (Table 1). Of these, 12 are considered native to California, and of the other 34, at least 12 are listed as invasive by the California Invasive Plant Council (Cal-IPC) (Cal-IPC 2006). Herbaceous annuals dominate the landscape, accounting for 33 (71.74%) species, four of which can function as biennials or perennials (*Erodium moschatum*, *Malva neglecta*, *Malva pseudolavatera*, and *Tetragonia tetragonioides*) given proper conditions. Four species on SEFI are considered functional waifs that do not reproduce in this vegetation community (*Coprosma repens*, *Hesperocyparis macrocarpa*, *Pinus radiata*, and *Zantedeschia aethiopica*).

**Table 1.** Terrestrial plant species list of Southeast Farallon Island as detected by San Francisco State University aboveground vegetation transect surveys during spring 2013, fall 2013, spring 2014, fall 2014, and spring 2015 (Vegetation Survey), seed bank assay described here (Seed Bank), and incidental observations by the author made during spring 2014, fall 2014, and spring 2015 site visits (Incidental).

Scientific Name [Family + aceae] <sup>a</sup>	Common Name	Life <sup>b</sup>	Origin <sup>c</sup>	Vegetation Survey	Seed Bank	Incidental
<i>Amsinckia spectabilis</i> Fisch. & C.A. Mey. [Borag-]	Fiddleneck	A	N	•	•	
<i>Avena barbata</i> Link [Po-]	Slender wild oat	A	I*		•	
<i>Bromus carinatus</i> Hook. & Arn. [Po-]	California brome	P	N	•	•	
<i>Bromus diandrus</i> Roth. [Po-]	Ripgut grass	A	I*	•	•	
<i>Calandrinia menziesii</i> (Hook.) Torr. & A. Gray [Monti-]	Red maids	A	N		•	
<i>Chenopodium murale</i> L. [Chenopodi-]	Nettle leaf goosefoot	A	I	•	•	
<i>Claytonia perfoliata</i> Willd. [Monti-]	Miner's lettuce	A	N	•	•	
<i>Coprosma repens</i> A. Rich. [Rubi-]	Mirror plant	P	I			•
<i>Cotula australis</i> (Spreng.) Hook. f. [Aster-]	Australian cotula	A	I	•	•	
<i>Cotula coronopifolia</i> L. [Aster-]	Brass-buttons	P	I*	•		
<i>Crassula connata</i> (Ruiz & Pav.) A. Berger [Crassul-]	Pygmy weed	A	N			•
<i>Ehrharta erecta</i> Lam. [Po-]	Panic veldt grass	P	I*	•	•	
<i>Erigeron glaucus</i> Ker Gawl. [Aster-]	Seaside daisy	P	N			•
<i>Erodium</i> sp. [Gerani-]	Filaree	-	I		•	
<i>Erodium cicutarium</i> (L.) Aiton [Gerani-]	Redstem filaree	A	I*	•		
<i>Erodium moschatum</i> (L.) Aiton [Gerani-]	Greenstem filaree	A,B	I	•		
<i>Festuca bromoides</i> L. [Po-]	Brome fescue	A	I	•	•	

<i>Hesperocyparis macrocarpa</i> (Hartw.) Bartel [Cupress-]	Monterey cypress	P	N			•
<b>Table 1</b> continued.						
Scientific Name [Family + aceae] <sup>a</sup>	Common Name	Life <sup>b</sup>	Origin <sup>c</sup>	Vegetation Survey	Seed Bank	Incidental
<i>Hordeum murinum</i> subsp. <i>leporinum</i> (Link) Arcang. [Po-]	Hare barley	A	I*	•	•	
<i>Juncus bufonius</i> L. [Junc-]	Toad rush	A	N		•	
<i>Lasthenia maritima</i> (A. Gray) M.C. Vasey [Aster-]	Maritime goldfields	A	N	•	•	
<i>Lepidium didymum</i> L. [Brassic-]	Lesser swine cress	A	I	•	•	
<i>Lupinus</i> sp. [Fab-]	Lupine	-	N		•	
<i>Lysimachia arvensis</i> (L.) U. Manns & Anderb. [Myrsin-]	Scarlet pimpernel	A	I		•	
<i>Malva</i> sp. [Malv-]	Mallow	-	I		•	
<i>Malva arborea</i> (L.) Webb & Berthel [Malv-]	Tree mallow	B,P	I	•		
<i>Malva neglecta</i> Wallr. [Malv-]	Common mallow	A,B	I	•		
<i>Malva parviflora</i> L. [Malv-]	Cheeseweed	A	I	•		
<i>Malva pseudotolavatera</i> Webb & Berthel. [Malv-]	Cretin mallow	A,B, P	I	•		
<i>Mollugo verticillata</i> L. [Mollugin-]	Carpet-weed	A	I		•	
<i>Oxalis pes-caprae</i> L. [Oxalid-]	Bermuda buttercup	P	I*			•
<i>Pinus radiata</i> D. Don [Pin-]	Monterey pine	P	N			•
<i>Plantago coronopus</i> L. [Plantagin-]	-	A	I	•	•	
<i>Poa annua</i> L. [Po-]	Annual blue grass	A	I		•	
<i>Poaceae</i> sp. [Po-]	Unknown grass	-	-	•		
<i>Poaceae</i> sp. 2 [Po-]	Unknown grass 2	-	-	•		

<i>Polycarpon tetraphyllum</i> (L.) L. [Caryophyll-]	Four leaved all seed	A	I	•	•	
<i>Polygonum monspeliensis</i> (L.) Desf. [Po-]	Rabbitfoot grass	A	I*		•	
<i>Rubus</i> sp. [Ros-]	-	-	-			•
<b>Table 1</b> continued.						
Scientific Name [Family + aceae] <sup>a</sup>	Common Name	Life <sup>b</sup>	Origin <sup>c</sup>	Vegetation Survey	Seed Bank	Incidental
<i>Rumex acetosella</i> L. [Polygon-]	Sheep sorrel	P	I*			•
<i>Rumex crispus</i> L. [Polygon-]	Curly dock	P(B)	I*	•		
<i>Senecio vulgaris</i> L. [Aster-]	Common groundsel	A	I	•	•	
<i>Sisymbrium orientale</i> L. [Brassic-]	-	A	I			•
<i>Sonchus asper</i> subsp. <i>asper</i> (L.) Hill [Aster-]	Prickly sow thistle	A	I	•	•	
<i>Sonchus oleraceus</i> L. [Aster-]	Common sow thistle	A	I	•	•	
<i>Spergularia macrotheca</i> (Cham. & Schldl.) Heynh. [Caryophyll-]	Sticky sand-spurrey	P	N	•	•	
<i>Spergularia media</i> var. <i>media</i> (L.) C. Presl [Caryophyll-]	Greater sea-spurrey	A	I	•	•	
<i>Stellaria media</i> (L.) Vill. [Caryophyll-]	Common chickweed	A	I	•	•	
<i>Tetragonia tetragonioides</i> (Pall.) Kuntze [Aizo-]	New Zealand spinach	A(P)	I*	•	•	
<i>Trifolium</i> sp. [Fab-]	Clover	-	-			•
<i>Urtica urens</i> L. [Urtic-]	Dwarf nettle	A	I	•	•	
<i>Zantedeschia aethiopica</i> (L.) Spreng. [Ara-]	Calla-lily	P	I*			•
<b>TOTAL</b>				<b>31</b>	<b>32</b>	<b>10</b>

<sup>a</sup> Scientific nomenclature follows the Jepson Flora Project (eds.) [2015] Jepson eFlora, <http://ucjeps.berkeley.edu/IJM.html> [accessed on October, 13, 2015].

<sup>b</sup> Life cycle: A = Annual; B = Biennial; P = Perennial

<sup>c</sup> Origin: N = Native to California, I = Introduced to California

\* Listed as invasive by California Invasive Plant Council

The dominant native species on SEFI is the annual *Lasthenia maritima* (maritime goldfields), an ornithocoprophilous species with range generally limited to offshore rocks and islands from California's central coast to southwestern British Columbia (Vasey 1985). Forming dense springtime stands on SEFI, *L. maritima* is utilized by birds as both nesting material and protective cover for fledglings (Vasey 1985; Ainley & Boekelheide 1990; USFWS 2009). Other prominent native species include the ruderal annual *Claytonia perfoliata* and the stout perennial *Spergularia macrotheca*. In combination with *L. maritima*, *S. macrotheca* constitutes a fairly distinct vegetation assemblage on the northwestern marine terrace highlighted by dense mats of low-growing *S. macrotheca* interspersed with *L. maritima* and non-native species.

Several non-native species dominate SEFI's landscape and of particular concern is the littoral, estuarine species *Tetragonia tetragonioides* (New Zealand spinach). Listed as invasive by the California Invasive Plant Council, *T. tetragonioides* is abundant on the southern and southeastern marine terrace and south-facing hillsides on SEFI and has been targeted for eradication by United States Fish and Wildlife Service (USFWS) (Cal-IPC 2006; Gray 1997). Presumed to have been introduced to SEFI as a garden vegetable, the

mat-forming *T. tetragonioides* reduces species richness through outcompeting native plant species and hinders seabird burrowing and nesting efforts (USFWS 2013). While generally having an annual growth habit, *T. tetragonioides* is capable of overwintering and functioning as a perennial under certain conditions, as is thought to occur on SEFI (Baldwin et al. 2012; Prakash 1967). The dispersal unit of *T. tetragonioides* is a reniform fruit consisting of up to nine potentially viable propagules, each capable of producing individual plants from the same fruit (Prakash 1967; Gray 1997; author observation) (Figure 2). The fruit itself is considered a hydrochore and can retain viability for more than a month while submerged in salt water (Taylor 1994; Gray 1997), making *T. tetragonioides* well adapted to the saline coastal environment and constant sea spray on SEFI.



**Figure 2:** *Tetragonia tetragonioides* fruit exhibiting multiple plant production from single unit.

Since at least the 19<sup>th</sup> century, SEFI has been subject to heavy anthropogenic disturbances including seal hunting, egg collection, occupation of the island by the United States Coast Guard, as well as the introduction of *Felis catus* (domestic cats), *Oryctolagus cuniculus* (European rabbits), and *Mus musculus* (Eurasian house mice), of which the former two have been successfully eradicated (USFWS 2013). Added to the

Farallon National Wildlife Refuge in 1969, SEFI has since been managed by USFWS and Point Blue Conservation Science, a non-profit conservation science organization, as de facto wilderness and wildlife habitat (USFWS 2013). SEFI is home to the largest seabird breeding colony in the contiguous United State, as well as the endemic *Farallonophilus cavernicolus* (Farallon camel cricket) (USFWS 2013).

### ***Seed bank sampling***

Seed bank characterization is accomplished through removing soil sample cores from the target ecosystem for *ex situ* examination. The volume of the soil sample core taken is dependent upon numerous factors, including the species present in the seed bank, size of the seeds present, vegetation community type, as well as number of samples taken (Gross 1990; Bakker et al. 1996). Sample core size should be large compared to the size of the seeds present and should include the litter layer, which is capable of harboring numerous seeds (Simpson et al. 1989). The literature shows 5 cm to be an acceptable depth for soil sample cores (Coffin & Lauenroth 1989; Simpson et al. 1989; Gross 1990; Bakker et al. 1996; Gonzalez & Ghermandi 2012; Abella et al. 2013).

Characterizations of seed banks attempt to capture the species richness, seed density, temporal variation, and viability of the target seed bank. Seed extraction methods, that

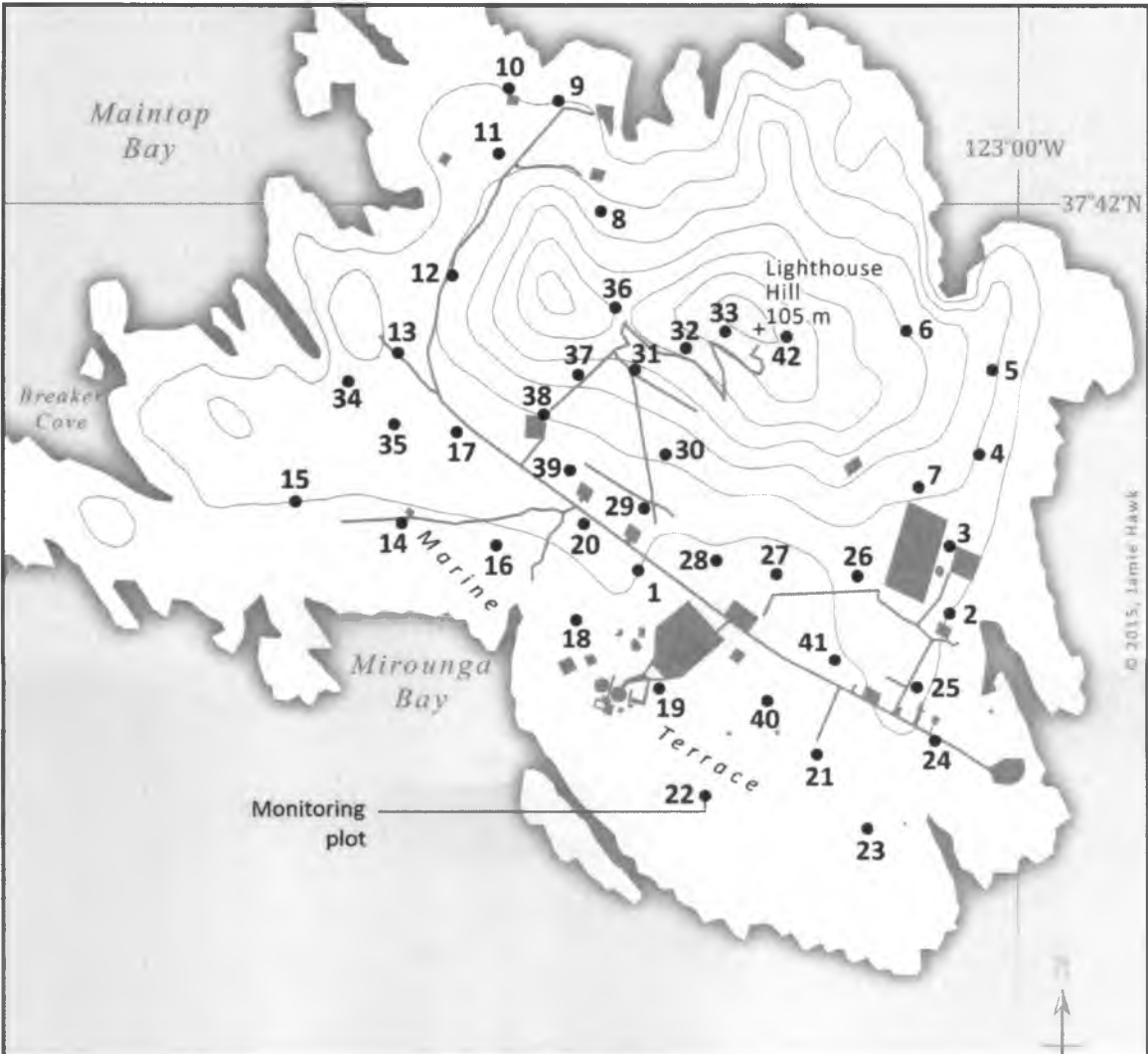
require separation of seeds from the soil and litter prior to identification, are known to detect high levels of species presence and allow species detection without simulating often complex or unknown germination cues (Gross 1990; Bakker et al. 1996; Abella et al. 2013). Seedling emergence methods capture species richness, seed density, temporal variation, and viability through stimulating germination and emergence of seeds in a controlled setting, and identifying seedling species upon emergence (Gross 1990; Malo et al. 1995; Luzuriaga et al. 2005; Robertson & Hickman 2012; Abella et al. 2013).

Seedling emergence methods have been shown to be an appropriate indicator of the total, non-dormant, viable seeds stored in the soil (Cardina & Sparrow 1996). It is less time and labor intensive than seed extraction methods, and avoids non-detection bias due to seed size, shape, or color associated with seed extraction methods (Gonzalez & Ghermandi 2012; Abella et al. 2013). Although seedling emergence methods are likely to miss the presence of large-seeded species, it is necessary to take specific site characteristics into account when evaluating efficiency and effectiveness of the method chosen (Gonzalez & Ghermandi 2012).

We sampled the seed bank in fall 2013, spring 2014, fall 2014, and spring 2015. Fall sampling occurred after senescence of aboveground vegetation and before precipitation events could trigger seed germination, while spring sampling occurred during peak growing season prior to seed dispersal. Timing of sampling also had to work around



seasons of high wildlife activity on the island. During each sampling season, we took two soil core samples 6 m from plot center at a random azimuth from 42 permanent monitoring plot markers throughout SEFI (Figure 3). The sample was a cylinder of 5 cm depth and 10 cm diameter (representing 392.7 cm<sup>3</sup>) and incorporated everything in the soil profile including litter. We immediately placed the samples in sealed plastic bags for



**Figure 3:** Map of SEFI showing locations of 42 existing permanent monitoring plots throughout the island. Anthropogenic structures are in gray. Map credit: Jamie Hawk (2015).

transport and subsequent analysis. Access to certain parts of the island are periodically restricted due to nesting and/or burrowing seabirds as well as roosting pinnipeds. For this reason, we were unable to complete sampling of all plots during each sampling season. We sampled the seed banks in 15 plots in fall 2013, 41 in spring 2014, 40 in fall 2014, and 39 in spring 2015 (Appendix – Table A1).

We initially utilized the seed extraction method but abandoned it following higher detection of both species richness and density using germination methods. We moistened the soil samples and placed them in cold stratification in a dark refrigerator of  $\sim 4^{\circ}\text{C}$  until radicles were observed (approximately 3 weeks), at which point we immediately transferred them to a greenhouse facility with natural light on the San Francisco State University campus. We then spread the soil samples thinly ( $<0.5\text{ cm}$ ) in flats of  $30\text{ cm} \times 30\text{ cm}$  prepared with  $5\text{ cm}$  of a mixture of sterile sand and vermiculite and kept them

consistently moist (Gross 1990; Malo et al. 1995; Luzuriaga et al. 2005; Robertson & Hickman 2012; Abella et al. 2013) (Figure 4). Control flats of sterile sand and vermiculite were placed



**Figure 4:** Seed bank germination assays in SFSU greenhouse.

randomly among the experimental flats to monitor for any seedlings that may have arisen from the sand or from the greenhouse environment. We identified emergent seedlings to the lowest taxonomic ranking as early as possible, counted, and removed them from the flats (Gross 1990; Malo et al. 1995; Luzuriaga et al. 2005; Robertson & Hickman 2012; Abella et al. 2013). We repotted difficult to identify specimens and grew them until identification was possible (Gross 1990; Malo et al. 1995; Robertson & Hickman 2012). To bring buried seeds closer to the surface, we stirred the soil 60 days after initiation of the experiment and after a period of one week during which no seedlings emerged (Robertson & Hickman 2012; Malo et al. 1995). A majority of seed germination occurred in the initial few weeks, although seeds continued to germinate for multiple weeks. After a period of two weeks during which no seedlings emerged following stirring, we terminated the use of the samples. No attempt was made to recover ungerminated seeds from the remnant soil samples. Duration of the experiment extended from August 2014 until July 2015.

### ***Aboveground vegetation sampling***

We surveyed the aboveground vegetation in fall 2013, spring 2014, fall 2014, and spring 2015 utilizing point-intercept methods (Knapp 1984). We surveyed along two random 10 m transects within the same 42 permanent monitoring plots mentioned above, collecting intercept data (species, substrate type) at intervals of 0.5 m. We aimed to capture the

maximum vegetative development in spring surveys and post-senescence vegetative cover in fall surveys. The area within these 10 m circular monitoring plots were excluded from biannual herbicide applications conducted by the USFWS, while a majority of the area where seed bank sampling occurred was subject to these herbicide applications. Because of this and the resulting differences in vegetation composition inside and outside the exclusion plots, we use these vegetation data to make general comparisons with the seed bank data and to provide a general idea of the vegetation communities and their fluctuations, as their use in more in-depth statistical analysis is not appropriate. Due to the access limitations discussed above, we sampled vegetation in 40 plots in fall 2013, 42 in spring 2014, 40 in fall 2014, and 40 in spring 2015 (Appendix – Table A1).

### *Statistical analysis*

Due to the non-parametric nature of the data and the uneven sample sizes, Kruskal Wallis K tests (rank analysis,  $p \leq 0.05$ ) were used to detect significant differences in seed bank density, richness, and temporal variation. Kruskal Wallis K tests were also used to assess differences in richness, coverage values, and temporal variation in the aboveground vegetation. Bray Curtis dissimilarity indices, ecological measures which calculate similarity between communities based on richness, composition, and abundance, were used to assess similarities between seed bank samples each within sample season. Kruskal Wallis and Bray Curtis analyses were conducted within the R statistical

environment (version 3.0.0, <http://www.R-project.org>). Jaccard similarity coefficients, ecological measures which compare similarity and diversity of communities based on species incidence, were used to assess similarities between clumped seed bank sample seasons. Jaccard similarity coefficient calculations were conducted in Microsoft Excel.

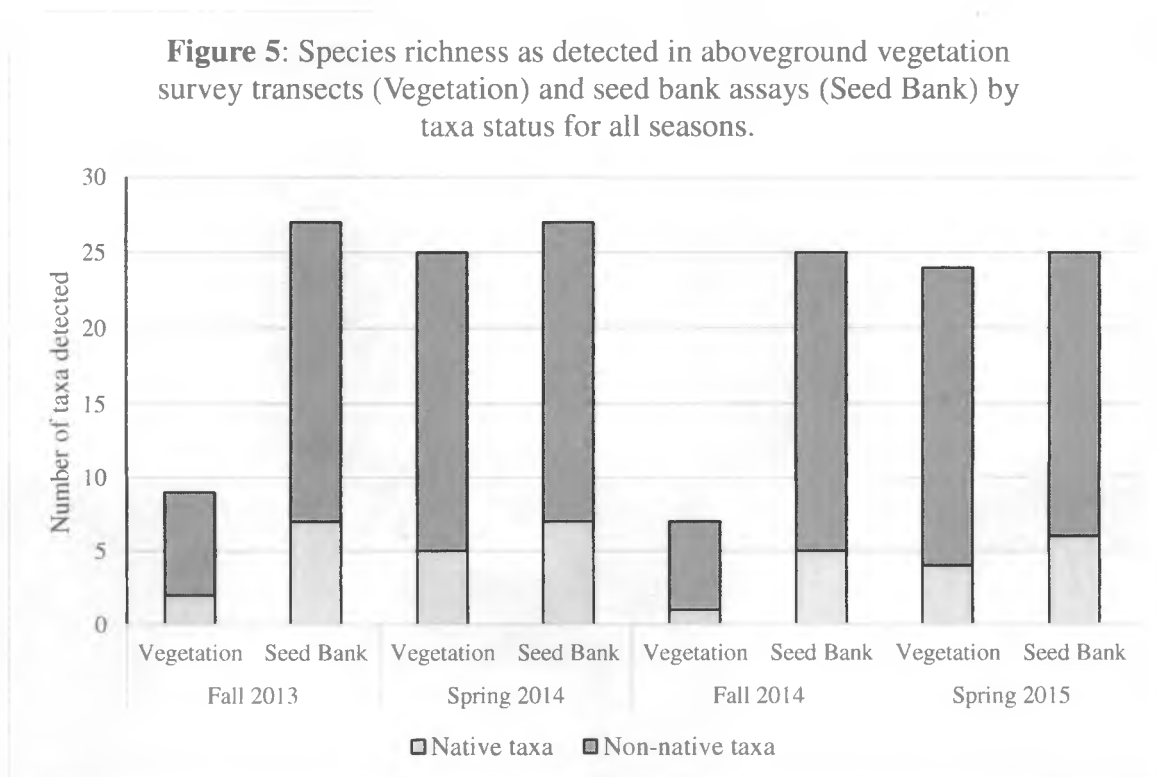
## **Results**

### ***Seed bank assay***

In total, 32 taxa (28 taxa identified to species and four to genera) were detected in the seed bank assays compared to 46 found through vegetation transect surveys and incidental observations (see Table 1). Eight taxa belonged to the Poaceae, five to the Asteraceae, four to Caryophyllaceae, and the remaining 15 came from 14 other families (see Table 1). Taxa native to coastal California habitats were represented by at least eight taxa (25%) in the seed banks. Given the locally limited distribution or lack of reproductive ability of the remaining four native taxa, seed bank assays detected the full range of native taxa we expected to. The remainder were non-native, six of which are considered invasive by the California Invasive Plant Council (Cal-IPC 2006) (see Table 1). Twenty-six of the taxa detected in the seed banks were annuals and three were perennials. Seed bank assays detected three taxa which had not been recorded on SEFI in either aboveground vegetation surveys or through incidental observation, including

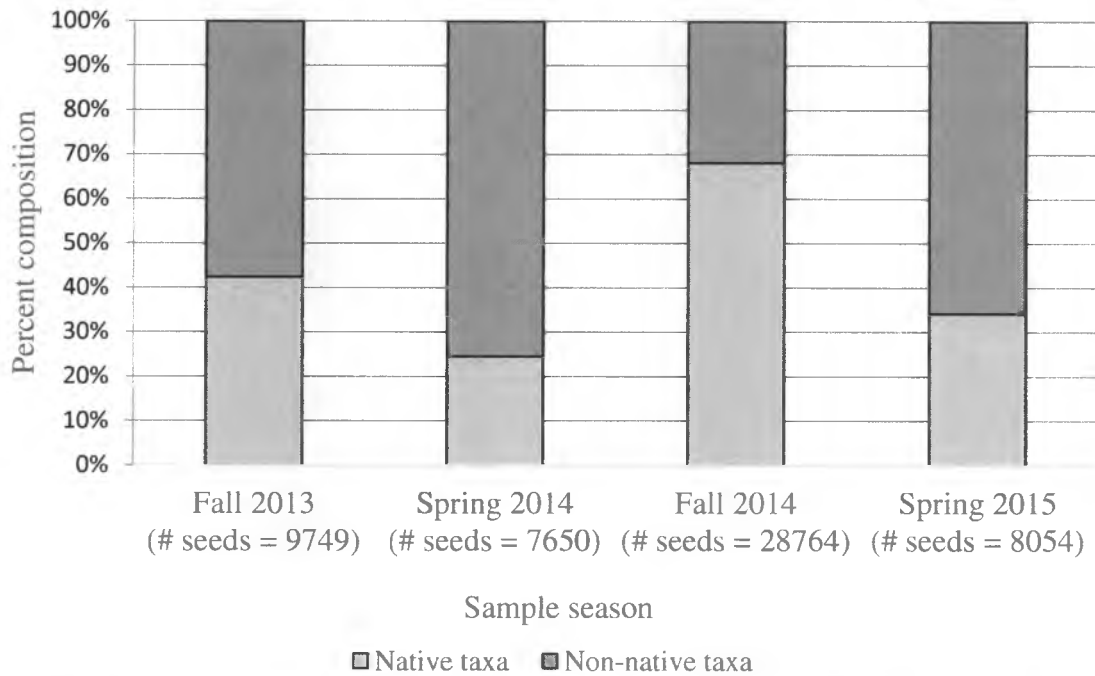
*Mollugo verticillata*, a *Lupinus* sp., and a *Rubus* sp., with the latter two dying prior to specific identification.

In the seed bank assays, more non-native taxa were detected than native taxa in each sample season (Figure 5 & Appendix – Table B1). Similarly, increased species richness detected in the seed banks was more strongly correlated with increased non-native species than with native species for each sample season.



Seeds of native taxa accounted for 42.36% of total seed density in fall 2013, 24.51% in spring 2014, 68.09% in fall 2014, and 34.13% in spring 2015 (Figure 6). The dominant native taxon in the seed bank assays was *Lasthenia maritima* in fall 2013, fall 2014, and spring 2015, and *Spergularia macrotheca* in spring 2014 (Table 2). Seeds of native taxa were present in 93.33% of samples in fall 2013, 92.68% in spring 2014, 97.5% in fall 2014, and 100% in spring 2015. The most widespread native taxa in the seed bank assays were both *S. macrotheca* and *L. maritima* in fall 2013 (both present in 86.67% of samples), *S. macrotheca* in spring 2014 (73.17% of samples), and *L. maritima* in fall 2014 and spring 2015 (95% and 92.05% of samples respectively).

**Figure 6:** Percent composition of seeds detected in SEFI seed bank assays by taxa status per sample season.



Seeds of non-native taxa accounted for 57.64% of total seed density in fall 2013, 75.49% in spring 2014, 31.91% in fall 2014, and 65.87% in spring 2015 (see Figure 6). The dominant non-native taxon in the seed bank assays was *Urtica urens* in fall 2013 and fall 2014, and *Lepidium didymum* in spring 2014 and spring 2015 (see Table 2). Seeds of non-native taxa were present in 93.33% of samples in fall 2013, 97.56% in spring 2014, 97.5% in fall 2014, and 97.44% in spring 2015. The most widespread non-native taxon in the seed bank assays was *L. didymum* in all four sample seasons (present in 73.33% of



**Table 2:** Seed bank density by taxa per sample season (No.), percent composition by taxa per sample season (%) and percent of plots species was detected in (Dist.). \* indicates native species.

Species	Fall 2013 (n=15)			Spring 2014 (n=41)			Fall 2014 (n=40)			Spring 2015 (n=39)		
	No.	%	Dist.	No.	%	Dist.	No.	%	Dist.	No.	%	Dist.
<i>Amsinckia spectabilis</i> *	10	0.10	26.67	10	0.13	12.20	103	0.36	27.50	12	0.15	12.82
<i>Avena barbata</i>	3	0.03	13.33	-	-	-	2	0.01	5.00	1	0.01	2.56
<i>Bromus carinatus</i> *	13	0.13	26.67	1	0.01	2.44	-	-	-	-	-	-
<i>Bromus diandrus</i>	73	0.76	20.00	2	0.03	4.88	10	0.03	10.00	1	0.01	2.56
<i>Calandrinia menziesii</i> *	1	0.01	6.67	1	0.01	2.44	-	-	-	-	-	-
<i>Chenopodium murale</i>	14	0.15	26.67	377	4.93	36.59	353	1.23	32.50	402	4.99	23.08
<i>Claytonia perfoliata</i> *	1438	14.90	80.00	63	0.82	36.59	313	1.09	52.50	297	3.69	64.10
<i>Cotula australis</i>	122	1.26	26.67	79	1.03	12.20	152	0.53	30.00	34	0.42	33.33
<i>Ehrharta erecta</i>	1	0.01	6.67	-	-	-	-	-	-	-	-	-
<i>Erodium</i> spp.	27	0.28	40.00	12	0.16	14.63	224	0.78	32.50	21	0.26	25.64
<i>Festuca bromoides</i>	-	-	-	-	-	-	165	0.57	2.50	2	0.02	2.56
<i>Hordeum murinum</i> subsp. <i>leporinum</i>	207	2.14	46.67	1	0.01	2.44	9	0.03	15.00	4	0.05	5.13
<i>Juncus bufonius</i> *	44	0.46	26.67	479	6.26	17.07	550	1.91	15.00	5	0.06	7.69
<i>Lasthenia maritima</i> *	1463	15.16	86.67	346	4.52	68.29	14280	49.65	95.00	1259	15.63	82.05
<i>Lepidium didymum</i>	953	9.87	73.33	2291	29.95	68.29	1047	3.64	65.00	1786	22.18	76.92
<i>Lupinus</i> sp. *	-	-	-	-	-	-	-	-	-	1	0.01	2.56
<i>Lysimachia arvensis</i>	94	0.97	46.67	45	0.59	26.83	119	0.41	30.00	23	0.29	17.95
<i>Malva</i> spp.	3	0.03	13.33	1	0.01	2.44	8	0.03	10.00	3	0.04	5.13
<i>Mollugo verticillata</i>	-	-	-	1	0.01	2.44	-	-	-	-	-	-

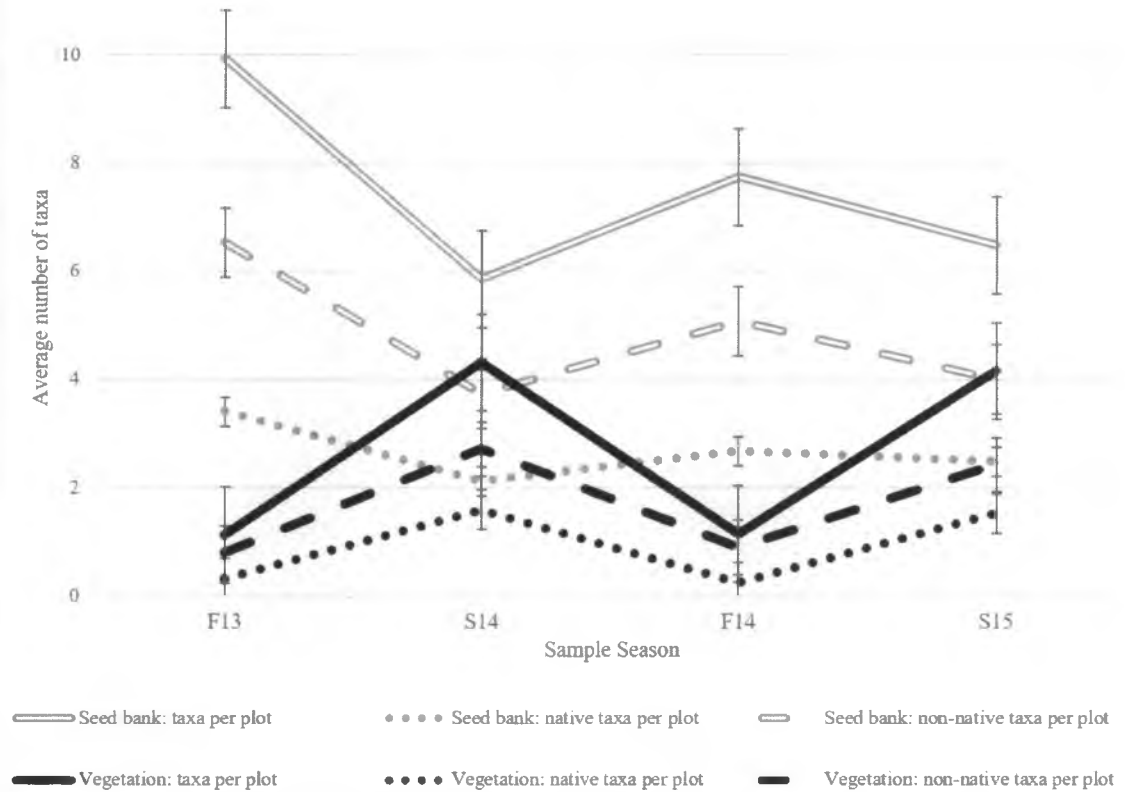
Table 2 continued

Species	Fall 2013			Spring 2014			Fall 2014			Spring 2015		
	No.	%	Dist.	No.	%	Dist.	No.	%	Dist.	No.	%	Dist.
<i>Plantago coronopus</i>	861	8.92	40.00	300	3.92	14.63	1416	4.92	22.50	462	5.74	12.82
<i>Poa annua</i>	2	0.02	6.67	1	0.01	2.44	133	0.46	7.50	5	0.06	2.56
<i>Polycarpon tetraphyllum</i>	94	0.97	13.33	16	0.21	7.32	23	0.08	7.50	-	-	-
<i>Polypogon monspeliensis</i>	135	1.40	20.00	199	2.60	9.76	577	2.01	25.00	142	1.76	28.21
<i>Rubus</i> sp.	-	-	-	1	0.01	2.44	-	-	-	-	-	-
<i>Senecio vulgaris</i>	1	0.01	6.67	5	0.07	4.88	-	-	-	1	0.01	2.56
<i>Sonchus asper</i> subsp. <i>asper</i>	-	-	-	-	-	-	1	0.00	2.50	-	-	-
<i>Sonchus oleraceus</i>	6	0.06	20.00	6	0.08	7.32	37	0.13	17.50	3	0.04	5.13
<i>Spergularia macrotheca</i> *	1161	12.03	86.67	975	12.75	73.17	4340	15.09	77.50	1175	14.59	79.49
<i>Spergularia media</i> var. <i>media</i>	300	3.11	40.00	531	6.94	24.39	2170	7.54	60.00	1280	15.89	30.77
<i>Stellaria media</i>	661	6.85	66.67	704	9.20	56.10	408	1.42	50.00	126	1.56	51.28
<i>Tetragonia tetragonioides</i>	205	2.12	60.00	38	0.50	24.39	94	0.33	30.00	338	4.20	30.77
<i>Urtica urens</i>	1857	19.24	66.67	1165	15.23	48.78	2230	7.75	52.50	671	8.33	41.03
Total	9749	100	-	7650	100	-	28 764	100	-	8054	100	-
Total Native	4130	42.36		1875	24.51		19586	68.09		2749	34.13	
Total Non-native	5619	57.64		5775	75.49		9178	31.91		5305	65.87	

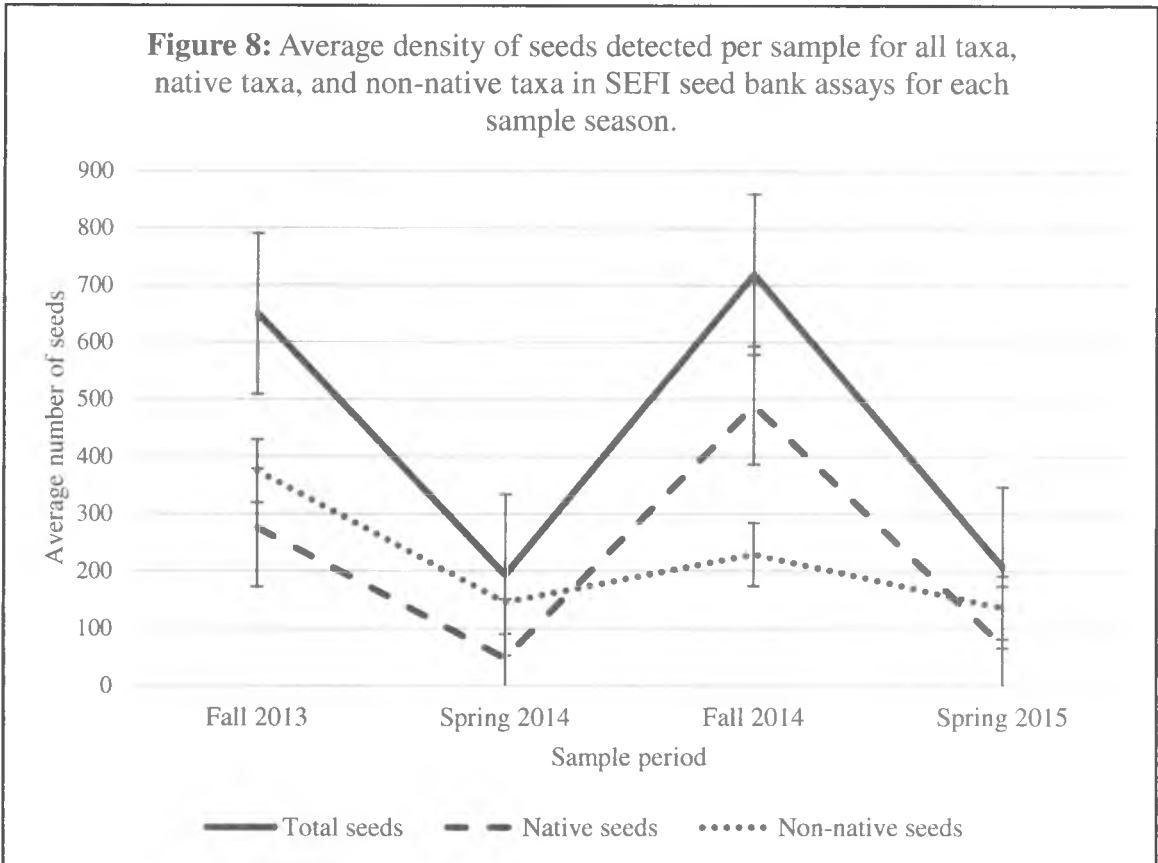
Seed bank assays detected more taxa per sample in fall sample seasons than in spring sample seasons (Figure 7), although the only significant variation was between the fall 2013 and the spring 2014 sample seasons (Appendix – Table B2). Total seed density per sample also varied between fall and spring sample seasons, with significantly more seeds per sample detected in fall sample seasons than in spring sample seasons (Figure 8 & Appendix – Table B3). The same significance was detected when native seed density per sample was assessed, but not when non-native seed density per sample was assessed (see Figure 8 & Appendix – Tables B4 & A5). High Jaccard similarity coefficients reflected high levels of homogeneity in species presence/absence in the belowground community between sample seasons (Table 3).

Seed bank assays did not detect any noteworthy patterns in spatial distribution of seed density, species richness, or composition in any sample season and instead reflect a largely homogenous belowground community across SEFI. Average Bray Curtis similarity indices of  $0.77 \pm 0.17$  within fall 2013,  $0.87 \pm 0.16$  within spring 2014,  $0.81 \pm 0.21$  within fall 2014, and  $0.83 \pm 0.17$  within spring 2015 (Appendix– Figure C1) reflect this homogeneity in overall belowground community composition.

**Figure 7:** Average number of taxa detected per sample in SEFI seed bank assays and aboveground vegetation survey transects throughout sample period



**Figure 8:** Average density of seeds detected per sample for all taxa, native taxa, and non-native taxa in SEFI seed bank assays for each sample season.



**Table 3:** Jaccard similarity indices for between season comparisons based on species presence/absence as detected in seed bank assays. Value of 1 indicates uniform communities, 0 indicates highly dissimilar communities.

<b>Sample years</b>	<b>Jaccard indices</b>
Fall 2013 - Spring 2014	0.86
Fall 2013 - Fall 2014	0.79
Fall 2013 - Spring 2015	0.79
Spring 2014 - Fall 2014	0.73
Spring 2014 - Spring 2015	0.73
Fall 2014 - Spring 2015	0.85

### *Aboveground vegetation survey*

Thirty-one taxa (29 identified to species, two to family) were detected in the aboveground vegetation survey transects compared to 46 total (see Table 1). Seven taxa belonged to the family Poaceae, six to Asteraceae, four to Caryophyllaceae, four to Malvaceae, and the remaining 10 came from 9 other families (see Table 1). Taxa native to coastal California habitats were represented by at least five taxa (15.15%) in the aboveground vegetation community (see Table 1). The remainder were non-native, six of which are considered invasive by the California Invasive Plant Council (Cal-IPC 2006) (see Table 1). Twenty-four of the taxa detected in the aboveground vegetation were annuals, five were perennials, and the life history of two unknown graminoid taxa were unknown.

Native taxa accounted for 29.47% of the total aboveground vegetative cover in fall 2013, 40.80% in spring 2014, 16.49% in fall 2014, and 42.39% in spring 2015 (Table 4). The

dominant native taxon was *Spergularia macrotheca* in fall 2013 and in fall 2014, and *Lasthenia maritima* in spring 2014 and spring 2015. Native taxa were detected in 32.5% of surveyed plots in fall 2013, 80.95% in spring 2014, 25% in fall 2014, and 92.5% in spring 2015. The most widespread native taxon was *S. macrotheca* in fall 2013 and fall 2014 (30% and 25% of surveyed plots respectively), and *L. maritima* in spring 2014 and spring 2015 (76.19% and 90% respectively).

**Table 4:** Aboveground vegetative cover from transect by taxa per survey season.  
\* indicates native species.

Species	Fall 2013	Spring 2014	Fall 2014	Spring 2015
	(n=42)	(n=42)	(n=40)	(n=40)
	%	%	%	%
<i>Amsinckia spectabilis</i> *	-	0.09	-	0.39
<i>Bromus carinatus</i> *	0.35	0.28	-	-
<i>Bromus diandrus</i>	-	5.00	-	5.97
<i>Chenopodium murale</i>	3.86	1.02	4.12	0.31
<i>Claytonia perfoliata</i> *	-	2.41	-	2.20
<i>Cotula australis</i>	-	-	-	0.16
<i>Cotula coronopifolia</i>	-	-	-	0.08
<i>Erharta erecta</i>	0.35	-	-	0.00
<i>Erodium cicutarium</i>	-	1.67	-	0.08
<i>Erodium moschatum</i>	-	1.67	-	0.47
<i>Festuca bromoides</i>	-	0.19	-	0.08
<i>Hordeum murinum</i> subsp. <i>leporinum</i>	-	2.22	0.26	8.40
<i>Lasthenia maritima</i> *	-	25.07	-	29.75
<i>Lepidium didymum</i>	-	4.16	-	0.55
<i>Malva arborea</i>	-	0.09	-	0.08
<i>Malva neglecta</i>	0.70	-	0.26	-
<i>Malva parviflora</i>	-	0.09	-	1.10
<i>Malva pseudolavatera</i>	-	0.28	-	0.47
<i>Plantago coronopus</i>	14.04	6.66	17.01	4.40
<i>Poaceae</i> sp.	-	0.28	-	-
<i>Poaceae</i> sp. 2	-	0.37	-	-
<i>Polycarpon tetraphyllum</i>	-	-	-	0.31
<i>Rumex crispus</i>	0.70	0.28	-	-
<i>Senecio vulgaris</i>	-	0.19	-	-
<i>Sonchus asper</i> subsp. <i>asper</i>	-	0.09	0.26	0.16
<i>Sonchus oleraceus</i>	0.35	-	-	0.08
<i>Spergularia macrotheca</i> *	29.12	12.95	16.49	10.05
<i>Spergularia media</i> var. <i>media</i>	-	0.74	-	1.10
<i>Stellaria media</i>	-	0.46	-	0.55
<i>Tetragonia tetragonioides</i>	50.53	29.69	61.60	32.89
<i>Urtica urens</i>	-	4.07	-	0.39
Total	100	100	100	100
Total Native	29.47	40.80	16.49	42.39
Total Non-native	70.53	59.20	83.51	57.61



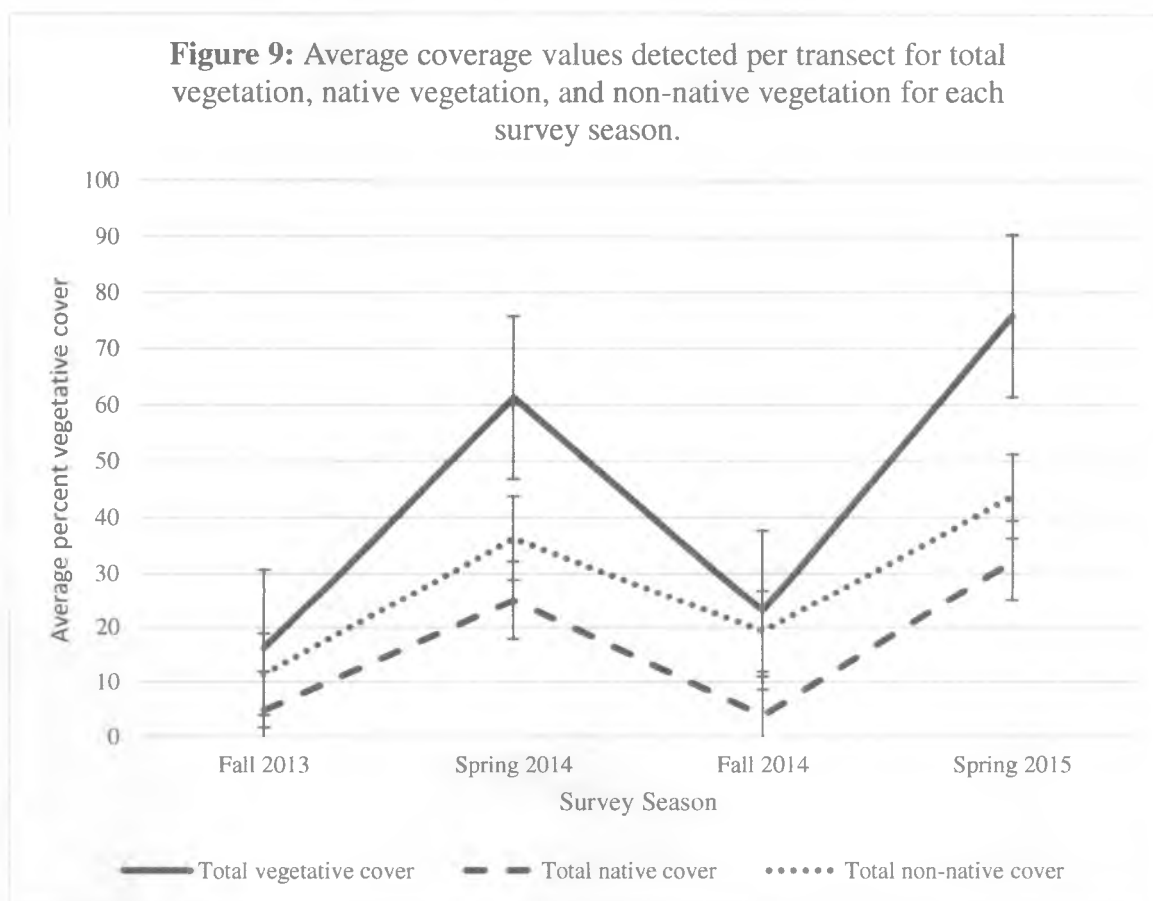
Non-native taxa accounted for 70.53% of the total aboveground vegetative cover in fall 2013, 59.20% in spring 2014, 83.51% in fall 2014, and 57.61% in spring 2015. The dominant non-native taxon was *Tetragonia tetragonioides* in all four survey seasons.

Non-native taxa were detected in 60% of surveyed plots in fall 2013, 85.71% in spring 2014, 70% in fall 2014, and 95% in spring 2015. The most widespread non-native taxon was *T. tetragonioides* in fall 2013, fall 2014, and spring 2015 (37.5%, 50%, and 57.5% of surveyed plots respectively) and *Lepidium didymum* in spring 2014 (40.48%).

In the aboveground vegetation surveys, species richness per sample was significantly higher for non-native taxa than for native taxa in all survey seasons except spring 2014 (see Figure 7 & Appendix – Table B6). Similarly, in the aboveground vegetation surveys, increased species richness was more strongly correlated with increased non-native species than with native species for each survey season.

The aboveground vegetation surveys detected significantly more taxa per sample in spring sample seasons than in fall survey seasons, reversing the pattern observed in the seed bank assays (see Figure 7 & Appendix – Table B7). Average vegetative cover per sample varied between spring and fall survey seasons, with significantly higher total coverage values being recorded in spring survey seasons than in fall survey seasons

(Figure 9 & Appendix – Table B8). The same pattern was reflected in total vegetative cover of both native and non-native taxa for each survey season (see Figure 9). Significantly higher total native coverage values were detected in spring survey seasons as compared to fall survey seasons when native cover is assessed (Appendix – Table B9). Although the same pattern and significance was detected when non-native cover is assessed, the difference between spring 2014 and fall 2014 values were not significant



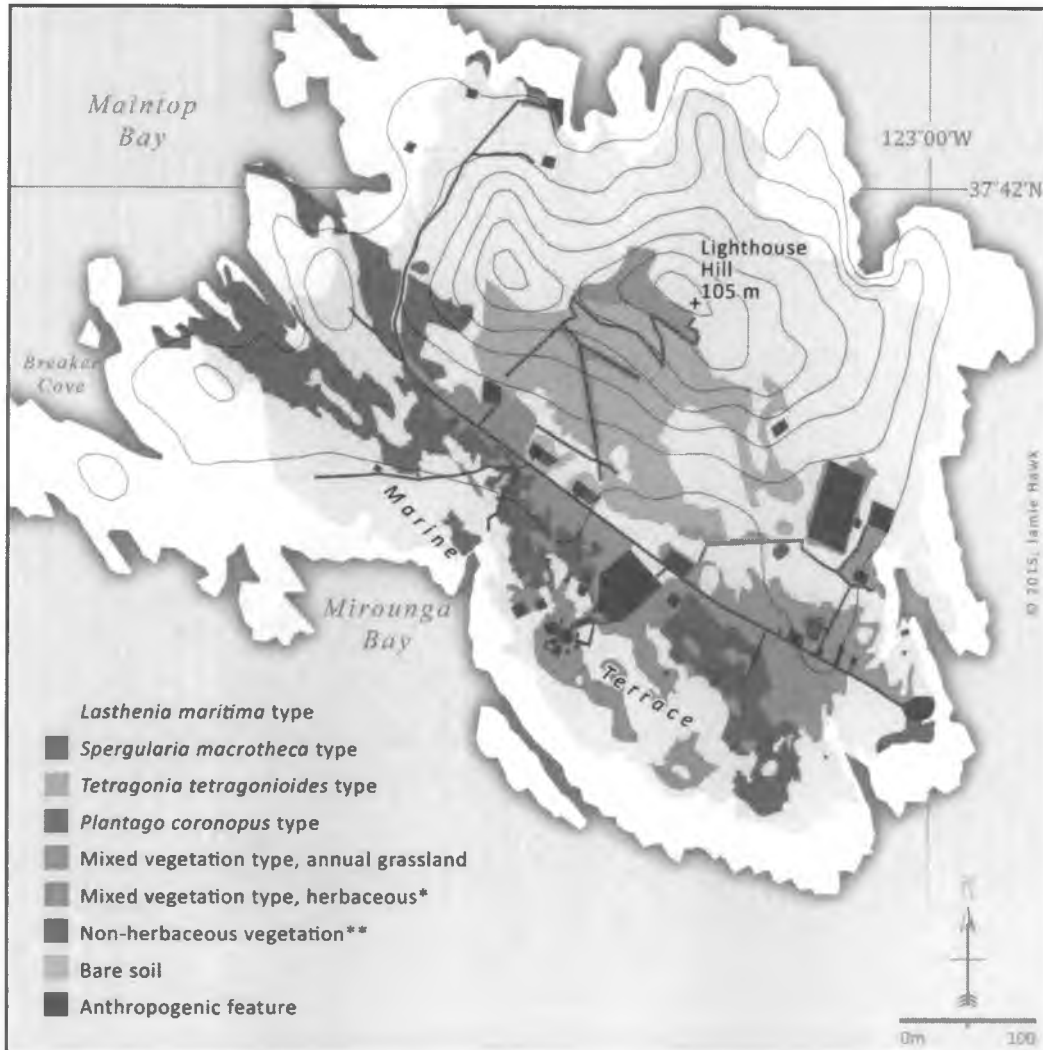
(Appendix – Table B10).

Previous analysis of the spatial distribution of aboveground vegetation identified and mapped five major vegetation types on SEFI based on combined coverage values for spring 2013 and spring 2014; a native *Spergularia macrotheca* type, a native *Lasthenia maritima* type, a non-native mixed herbaceous type, a non-native *Plantago coronopus* type, and a non-native *Tetragonia tetragonioides* type (Hawk 2015). The native *L. maritima* type was the most extensive of the types mapped and covers more than half the mapped area of the island (Figure 10). Analysis of fall survey season vegetative cover values has yet to be completed and would shed light on year round vegetative cover patterns on SEFI.

## **Discussion**

The results presented here show that the seed banks on SEFI are dominated by non-native species in richness, density, and distribution, but seeds of native species are present and widespread, highlighting the potential for utilization of seed banks in restoration of native species assemblages on the island. Higher non-native species richness was detected across all four sampling seasons in the seed bank. Seeds of non-native species dominated the seed bank in density in the fall 2013, spring 2014, and spring 2015 sample seasons, although seeds of native species were dominant in the fall 2014 sample season. Seeds of native and non-native species share similar distribution across the island, with both native and non-native species being detected in more than 92% of samples across all four sample seasons. The seed banks vary seasonally with higher values detected in fall

sample seasons for number of species per sample and total seed density, highlighting the annual character of the vegetation communities. No significant yearly variation was detected in the seed banks.



**Figure 10:** Map of SEFI showing spatial distribution of aboveground vegetation types (Hawk 2015). Map credit: Jamie Hawk (2015).

Similar patterns emerged in the aboveground vegetation, with non-native species returning higher values for species richness and vegetative cover and showing a system dominated by non-natives. Unlike the seed bank, non-native species in the aboveground vegetation show a more consistently widespread distribution across the island than do native species in all four survey seasons. Aboveground vegetation exhibited seasonal

variation as well, returning higher values in the spring sample seasons for both number of species per sample and average vegetative cover. No significant yearly variation was detected in the aboveground vegetation.

### *Aboveground vegetation versus seed banks*

Previous studies have often shown a general lack of correlation between the aboveground vegetation in a given system and its seed bank (Thompson & Grime 1979; Coffin & Lauenroth 1989; Warr et al. 1994; Cline et al. 2008). Our data do not reflect this on SEFI. The seed bank assays and aboveground vegetation surveys described here both detected similar species richness values throughout the four sample and survey seasons, and altogether detected 21 similar taxa (see Table 1). Seed bank assays consistently detected higher native species richness per sample season than the aboveground vegetation surveys, and in one sample season (spring 2015) they detected higher non-native species richness than the aboveground vegetation surveys (see Figure 5). No taxa dominant in the seed bank were absent from the aboveground vegetation and no taxa dominant in the aboveground vegetation were absent from the seed bank.

A total of ten taxa were not detected in either seed bank assays or in aboveground vegetation surveys (see Table 2). These taxa – eight of which are non-native – are known

to exist solely through incidental observations by the author and in most cases are known from single specimens or isolated populations on SEFI and their absence is not surprising. Two (*Crassula connata* and *Erigeron glaucus*) are native to coastal California and have locally limited distributions on SEFI, the latter being largely restricted to rocky outcrops on the western and northern end of the island. The non-native *Sisymbrium orientale* has eluded detection by both seed bank assay and aboveground vegetation survey, although historic observations exist and incidental observations do not reflect a strongly limited distribution on SEFI. *Oxalis pes-caprae* is known from two small, isolated populations on SEFI and while this taxa is not thought to reproduce from seed in California, it can become problematic once established and warrants concern and perhaps management actions.

Three taxa were detected in the seed bank assays which have not been recorded historically on SEFI and were not detected in the aboveground vegetation surveys – an unknown *Lupinus* sp., *Mollugo verticillata*, and an unknown *Rubus* species. All three are represented by single specimens in the seed bank assays. The detection of the former two are no cause for concern as the *Lupinus* genus lacks non-native species in California and *M. verticillata* is non-problematic in areas where it is naturalized. The *Rubus* sp. specimen detected in the seed bank assay died prior to specific identification, although personal communication with a SEFI volunteer supports the presence and immediate

removal of the invasive *Rubus armeniacus* on the island (Bryan White, personal communication, March 26, 2014). Listed as invasive by Cal-IPC and capable of becoming problematic when established, the appearance of this taxon in both the aboveground vegetation and the seed banks on SEFI it warrants concern and potential management action.

As noted before, the aboveground vegetation on SEFI has been classified into five distinct vegetation communities including two native assemblages and three non-native assemblages (Hawk 2015) (see Figure 10). The results of the seed bank assay presented here do not reflect these communities in the belowground community and instead reveal a seed bank that is largely homogenous across the island with both native and non-native species present in large percentages of samples. The aboveground vegetation – again, dominated by annual species – may then be seen as the annual expression of these seed banks based on a variety of probable factors including levels and types of disturbance, environmental factors, edaphic factors, specific germination cues, previous season's seed rain, as well as any dormant seed from the previous >1 year's seed input. Given the variability of these factors, the composition of the aboveground vegetation can be seen as highly fluid and able to fluctuate between growing seasons and between years.



The assessment of true overall site diversity as well as future makeup of vegetation communities are difficult to reveal with measurement of aboveground vegetation alone and these measures are best ascertained in concert with characterization of a site's seed banks (Warr et al. 1994, Cline et al. 2008). While the seed bank assay described here reveals few surprises, through detecting certain taxa overlooked by aboveground vegetation surveys, detecting a higher native species richness per sample season than aboveground vegetation surveys, highlighting three previously unrecorded taxa on SEFI, and revealing a largely homogenous seed bank across the island, it successfully expands the knowledge base surrounding the composition and future makeup of the island's aboveground vegetation communities. In addition to furthering our understanding of this unique insular ecosystem, this information will prove useful in future and ongoing management of the island's native vegetation.

### ***Historic conditions and maintenance of diversity***

A particular site's seed bank is representative of conditions that have historically prevailed in that site and seed bank assays provide a sort of snapshot of past vegetation makeup (Baker 1989, Gross 1990). As noted earlier, species composition on SEFI is dominated by annual species. Annual plants of Mediterranean climates tend to exhibit a characteristic growth pattern which can be divided into five stages: 1) fall precipitation inducing germination of seed produced at the end of previous growing season, 2) seedling

establishment, 3) slow vegetative growth through fall and winter, 4) increased vegetative growth followed by flowering and seed production in spring and summer and subsequent seed rain, senescence, and death, and 5) summer carry-over of seed (Bartolome 1976).

Seed bank assays from fall sample seasons taken prior to fall germination then reflect in part the aboveground conditions prevalent in the previous growing season. These offer a glimpse of past aboveground vegetation community makeup as indicated by input and storage of viable seeds in the soil. Samples taken in spring following seed germination represent the previous season's and potentially prior year's seed input that failed to germinate, and highlight the level at which environmental cues and stimulation of germination were met or not met following fall precipitation events.

Seed banks have been shown to play a crucial role in maintaining ecological and genetic diversity in aboveground vegetation communities (Baker 1989; Gross 1990). On SEFI, aboveground vegetation surveys consistently detect higher values for non-native species richness than native species richness across survey seasons, indicating a system impacted by the introduction of non-native species. Seed bank assays display the same pattern, detecting higher values for non-native species richness across all sample seasons than native species richness. However, for all four seasons, seed bank assays detect higher native species richness than do aboveground vegetation surveys by at least two taxa per season. So while certain native taxa are not expressing themselves in the aboveground

vegetation or are doing so in low enough quantities so as to escape detection in the transects, they are present in the seed banks and retain the true ecological and genetic diversity of the island's vegetation communities.

Along the same vein, seed banks are important components of an ecosystem's resilience and ability to respond to disturbance (Coffin & Lauenroth 1989; Merou et al. 2013). Disturbance in the case of SEFI is represented by introduction of non-native taxa and subsequent reduction in cover and distribution of native taxa. As shown above, while certain native taxa may currently not be expressing themselves in the aboveground vegetation, either at all or to the extent necessary for detection, they remain present and viable in the island's seed banks. These seed banks then act as a type of ecological insurance, ensuring that native taxa remain present in SEFI's ecosystem as viable seed in the soil, capable of emerging and reentering the aboveground vegetation community following the fulfillment of appropriate germination conditions or the removal or cessation of disturbance.

### ***Temporal variation***

As noted earlier, Mediterranean systems dominated by annual plants tend to exhibit a characteristic growth pattern of plants entering the aboveground vegetation community in

late fall/early winter following precipitation events, dropping seed in later summer, and dying back in fall (Bartolome 1976). This is represented on SEFI in the significantly different values for aboveground species richness per sample by season, with aboveground vegetation exhibiting higher species richness and coverage values in spring survey seasons than in fall survey seasons. As would be expected, this pattern is reversed in SEFI seed banks, with significantly higher species richness per plot and seed density values being detected in fall sample seasons – when taxa express themselves largely in the seed banks – than in spring sample seasons. This boom-bust cycle is representative of and characteristic of the aboveground annual vegetation community on the island.

While non-native seed density follows this trend, the variation between seasons is not as consistently significant. This appears to be in large part due to two species, *Lepidium didymum* and *Tetragonia tetragonioides*, and their general deviation from this trend. *Lepidium didymum*, an abundant non-native species in the seed bank, is not recognized as a late season annual species (Baldwin et al. 2012), but reverses this pattern with higher seed densities in spring sample seasons and lower seed densities in fall seasons (see Table 2). This could be due to site-specific germination of summer seed rain prior to the occurrence of fall sampling. While supported by the presence of *L. didymum* in spring season vegetation surveys only, the data presented here are unable to ascertain the specific cause of this fluctuation. *Tetragonia tetragonioides*, generally treated as an

annual but capable of functioning as a perennial, exhibits no apparent pattern in seasonal density fluctuation (see Table 2). Whether this is indicative of specialized dormancy, fluctuation in seed rain, or the ability of this taxon to germinate throughout the year given proper conditions is again unable to be determined given the data presented here.

### ***Invasion processes, restoration potentials, and management concerns***

In invaded communities, dominant native species are often absent from the seed banks (van der Valk & Pederson 1989; Robertson & Hickman 2012). Our data do not reflect this, as native species are present in >92% of samples in which viable seeds were detected across all sample seasons. Regeneration of degraded vegetation communities following disturbance or introduction of invasive species is thought to lie in the potential contribution of buried native seed populations (Bakker et al. 1996), which sheds a hopeful light on the restoration of the invaded vegetation communities on SEFI. Native species are present both in both the aboveground vegetation community and in the seed banks, indicating that propagule sources are healthy, seed input is robust, and obstacles to dispersal are limited on the island. Restoration of native plant communities on this unique insular system is then not an issue of reintroducing source material of native species, but more one of removing the obstacles provided by the offending invaders, namely *Tetragonia tetragonioides*.

The seasonal variation in germinable *Lasthenia maritima* seed density on SEFI reflects the fall boom – spring bust pattern discussed above, with seed densities significantly higher in fall than in spring. As discussed earlier, *Tetragonia tetragonioides* displays no such pattern in the seed bank, instead maintaining a steady, albeit less dense, presence throughout the year. Current management actions on SEFI aim to eradicate *T. tetragonioides* with targeted foliar applications of systemic herbicide in both spring and fall (USFWS 2009; Jonathan Shore, personal communication, January 19, 2016). The spring herbicide applications occur when germinable *L. maritima* seed bank densities are at their lowest and standing *L. maritima* are flowering and producing seed in the aboveground community. Benefits of spring herbicide applications are the removal of *T. tetragonioides* from the aboveground vegetation in spring, subsequent reduction in its seed rain potential the following summer, and a reduced seed bank the following fall. This simultaneously releases *L. maritima* from aboveground resource competition with *T. tetragonioides* during spring and summer flowering and seed production, enabling a more robust *L. maritima* seed rain and subsequently stronger seed bank.

Fall herbicide applications occur at a time when germinable *Lasthenia maritima* seed banks are at their most dense and the seeds are stored in the soil until environmental cues can induce germination and seedling establishment. The benefit of the fall herbicide application is the prevention of *Tetragonia tetragonioides* from entering the aboveground

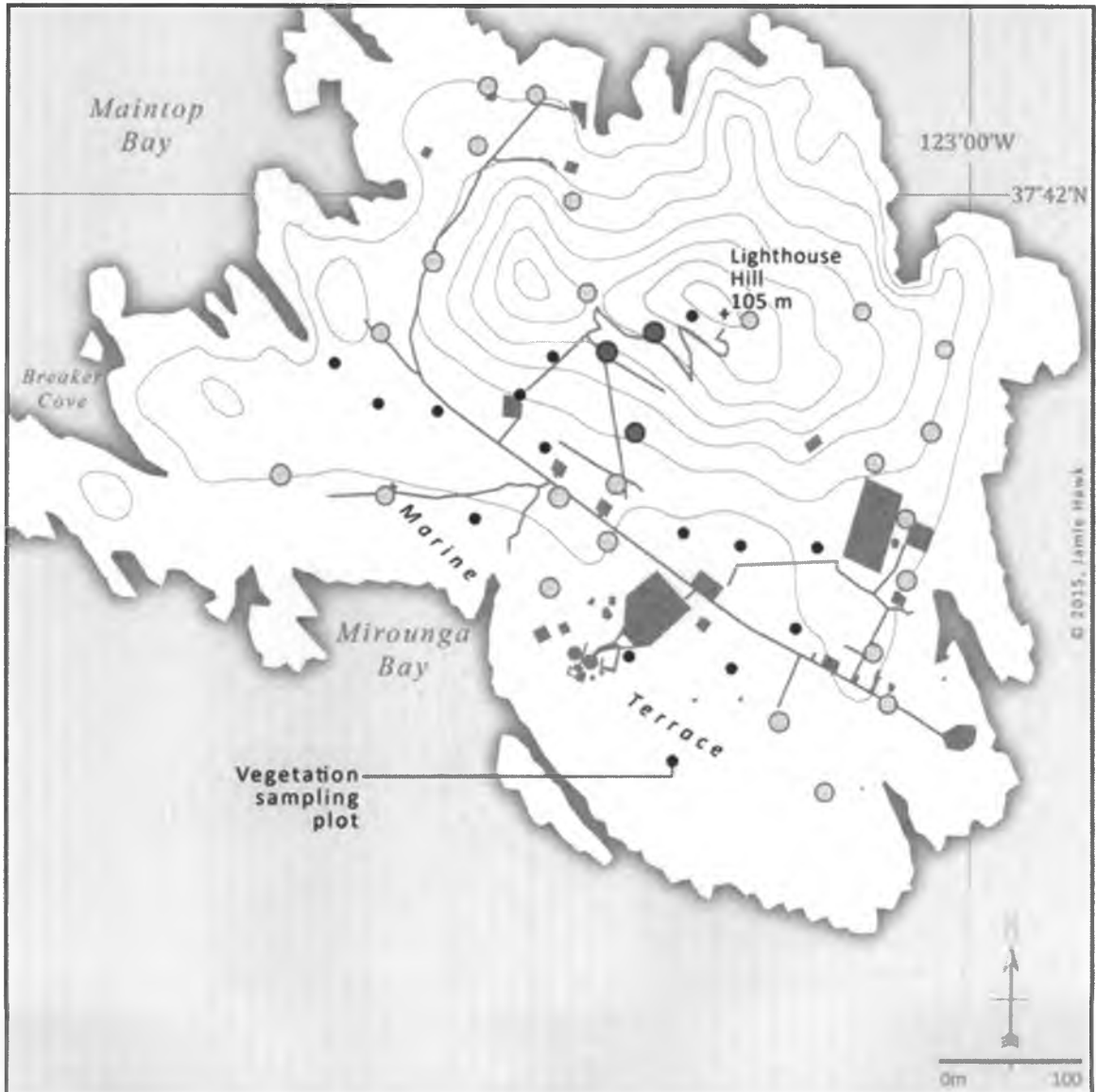
vegetation the following winter and allowing the dense fall *L. maritima* seed bank to fully express itself the following winter and spring without resource competition with *T. tetragonioides*. This in turn has a domino effect of benefits, allowing for healthier aboveground spring *L. maritima* cover, subsequent heavy summer seed rain, and a dense seed bank the following fall. Fall removal of *T. tetragonioides* from the aboveground community again serves to disrupt this taxa's seed rain and can lead to continuing reductions in its seed bank.

In short, *Lasthenia maritima* seed bank densities in fall are in part a function of aboveground *L. maritima* from previous spring's seed inputs, which in turn may be a result of the control of aboveground *Tetragonia tetragonioides* in previous fall seasons and the competitive release of *L. maritima*. The seed bank impacts of restoration actions are thus delayed and will not be realized until an entire growing season has passed. While delayed, the impacts in the seed bank appear to be positive and the continued implementation of both fall and spring herbicide application hold potential for the restoration of native vegetation on SEFI.

As noted earlier, native species are widespread in the seed bank and present in a majority of the sample plots that holds potential benefits for restoration of native vegetation on the

island. Non-native species are also present in a majority (>93%) of the plots sampled here across survey seasons, although *Tetragonia tetragonioides* does not share this widespread distribution being present in only 60% of sampled plots in fall 2013, 24% in spring 2014, 30% in fall 2014, and 31% in spring 2016. Plots in which *T. tetragonioides* was detected are generally concentrated in the more disturbed areas of the island, while plots in the less traversed de facto wilderness areas tend to be free of this taxa (Figure 11). Effective





**Figure 11:** Map of SEFI showing locations of plots in which no viable *Tetragonia tetragonioides* seed were detected (green circles) and plots in which viable seed of *T. tetragonioides* (red circles) were detected in all four sample seasons. Map credit: Jamie Hawk (2015).

control of *T. tetragonioides* on SEFI should then focus on limiting the spread of its propagules into uninvaded areas, and removing propagule sources in invaded areas.

Although generally thought to be a hydrochore. It has been proposed that *T.*

*tetragonioides* propagules can be dispersed on SEFI following fruit predation and propagule movement by birds (USFWS 2009). Stomach content studies of Eurasian house mice on the island do not support the notion that they serve as dispersal agents of *T. tetragonioides* (Jones & Golightly 2006), although rodents are known dispersal agents and seed predators in other ecosystems and Eurasian house mice may very well be influencing distribution as well as seasonal fluctuations in density (Louda 1989). As prevention of dispersal by birds is not feasible, priority should be given to prevention of anthropogenic movement of propagules as well as early detection and rapid response to newly established individuals to prevent the establishment of *T. tetragonioides* seed banks in uninvaded areas on the island.

## CONCLUSION

The seed bank assay presented here in combination with the results of aboveground vegetation surveys on SEFI provide numerous insights into the previously understudied seed banks and vegetation systems of this disturbed insular ecosystem. The results show a system largely dominated above- and belowground by non-native annual taxa in both density and richness, albeit with a solid presence of native taxa throughout the study period and throughout the island as sampled. The seed banks and aboveground vegetation exhibit a clear seasonal pattern characteristic of Mediterranean systems dominated by annual taxa. Seed banks are homogenous across the island and no significant spatial

pattern in seed bank distribution arises in the assay provided here, although patterns in distribution of certain taxa (namely *Tetragonia tetragonioides*) hold implications for proper management of the island's vegetation communities. Widespread presence of native species in the seed banks, in particular the dominant native species *Lasthenia maritima*, but also *Spergularia macrotheca*, holds potential for restoration of the native vegetation community on SEFI with continued and focused effort.

## **FUTURE RESEARCH**

The results of the seed bank assays presented here represent a baseline assessment of SEFI seed banks. Predicting trajectories based on two years of sampling is difficult if not impossible. Analysis of future fall and spring seed bank samples would greatly benefit our understanding of the temporal variation in SEFI seed banks as well as the impacts ongoing management actions are having on them. Furthermore, given the proposed eradication of Eurasian house mice on SEFI (USFWS 2013), the data presented here can be used with future assessments to gain a better understanding of the impacts invasive rodent eradication has on seed banks of insular ecosystems. This information will prove useful in evaluating the outcomes of this proposed action and can be used to more effectively guide similar actions in the future, both on SEFI and other temperate islands around the world.

Due to the heavy use of the northeastern section of SEFI by wildlife sensitive to anthropogenic presence, the monitoring plots – from which both seed bank assays and vegetation surveys originate – are concentrated heavily on the southwestern section of the island (Figure 3). Relative to the northeastern section, the southwestern section has been subject to more frequent and intense anthropogenic disturbance and, presumably due to this, appear to be more impacted by non-native plant species. Future studies of SEFI seed banks and aboveground vegetation would benefit greatly from heavier sampling in the less disturbed sections of the island.

As noted above, the aboveground vegetation survey results originate from within 10 m circular monitoring plots which are excluded from biannual herbicide applications, while seed bank samples were taken from areas outside of these plots. Due to the dramatic variation in aboveground vegetative cover inside and outside of these plots, statistical comparison between the seed bank data and aboveground vegetative cover data presented here may be problematic. Future analysis and an increased understanding of relationships between the seed banks and aboveground vegetation would benefit greatly from aboveground vegetation surveys in areas of the island subject to similar management actions as those areas from which seed bank samples were taken.

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## Appendix A

<b>Table A-1:</b> Checklist of plots sampled in seed bank assays and aboveground vegetation surveys per season.								
Plot #	Fall 2013		Spring 2014		Fall 2014		Spring 2015	
	Seed Bank	Vegetation	Seed Bank	Vegetation	Seed Bank	Vegetation	Seed Bank	Vegetation
1		•	•	•	•	•	•	•
2		•	•	•	•	•	•	•
3		•	•	•	•	•	•	•
4		•	•	•	•	•	•	•
5			•	•	•	•	•	•
6				•	•			•
7		•	•	•	•	•	•	•
8		•	•	•	•	•	•	•
9		•	•	•	•	•	•	•
10	•	•	•	•		•	•	•
11		•	•	•	•	•	•	•
12		•	•	•	•	•	•	•
13	•	•	•	•	•	•	•	•
14		•	•	•	•	•		
15		•	•	•	•			
16		•	•	•	•	•	•	•
17	•	•	•	•	•	•	•	•
18		•	•	•	•	•	•	•
19	•	•	•	•	•	•	•	•
20	•	•	•	•	•	•	•	•
21	•	•	•	•	•	•	•	•
22	•	•	•	•	•	•	•	•
23		•	•	•	•	•	•	•
24		•	•	•	•	•	•	•
25	•	•	•	•	•	•	•	•
26	•	•	•	•	•	•	•	•
27		•	•	•	•	•	•	•
28	•	•	•	•	•	•	•	•
29		•	•	•	•	•	•	•
30	•	•	•	•	•	•	•	•
31	•	•	•	•	•	•	•	•
32	•	•	•	•	•	•	•	•
33		•	•	•	•	•	•	•
34	•	•	•	•		•	•	•
35		•	•	•	•	•	•	•
36		•	•	•	•	•	•	•
37		•	•	•	•	•	•	•
38	•	•	•	•	•	•	•	•
39		•	•	•	•	•	•	•
40		•	•	•	•	•	•	•
41		•	•	•	•	•	•	•
42		•	•	•	•	•	•	•

## Appendix B

**Table B-1: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of native vs non-native species richness in SEFI seed banks per sample season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	P	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 native vs non-native species richness	7.067	0.008	1	F13 Native sp.-F13 Non-native sp.	8.333	6.300	True
Spring 2014 native vs non-native species richness	9.3435	0.002	1	S14 Native sp.- S14 Non-native sp.	15.829	10.309	True
Fall 2014 native vs non-native species richness	15.809	7.006e-05	1	F14 Native sp.-F14 Non-native sp.	20.175	10.184	True
Spring 2015 native vs non-native species richness	11.193	0.001	1	S15 Native sp.- S15 Non-native sp.	16.744	10.058	True

**Table B-2: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of species richness per sample for each sample season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	p	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 species richness per sample	15.862	0.001	3	Fall 2013-Fall 2014 seed # per sample	23.671	31.244	False
				Fall 2013-Spring 2014 seed # per sample	43.404	31.14	True
				Fall 2013-Spring 2015 seed # per sample	36.477	31.353	True
				Fall 2014-Spring 2014 seed # per sample	19.733	22.934	False
				Fall 2014-Spring 2015 seed # per sample	12.806	23.223	False

				Spring 2014-Spring 2015 seed # per sample	6.927	23.083	False
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**Table B-3: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of total seed density per sample for each sample season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	$p$	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 total seed # per sample	37.608	3.421e-08	3	Fall 2013-Fall 2014 seed # per sample	5.546	31.244	False
				Fall 2013-Spring 2014 seed # per sample	48.331	31.14	True
				Fall 2013-Spring 2015 seed # per sample	42.964	31.353	True
				Fall 2014-Spring 2014 seed # per sample	42.785	22.934	True
				Fall 2014-Spring 2015 seed # per sample	37.418	23.222	True
				Spring 2014-Spring 2015 seed # per sample	5.367	23.083	False

**Table B-4: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of native seed density per sample for each sample season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	<i>p</i>	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 native seed # per sample	43.207	2.224e-09	3	Fall 2013-Fall 2014 seed # per sample	1.25	31.244	False
				Fall 2013-Spring 2014 seed # per sample	52.205	31.14	True
				Fall 2013-Spring 2015 seed # per sample	35.220	31.353	True
				Fall 2014-Spring 2014 seed # per sample	50.955	22.934	True
				Fall 2014-Spring 2015 seed # per sample	33.971	23.223	True
				Spring 2014-Spring 2015 seed # per sample	16.984	23.083	False

**Table B-5: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of non-native seed density per sample for each sample season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	<i>p</i>	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 non-native seed # per sample	14.404	0.0024	3	Fall 2013-Fall 2014 seed # per sample	26.217	31.244	False
				Fall 2013-Spring 2014 seed # per sample	39.518	31.14	True
				Fall 2013-Spring 2015 seed # per sample	40.836	31.353	True
				Fall 2014-Spring 2014 seed # per sample	13.301	22.934	False
				Fall 2014-Spring 2015 seed # per sample	14.619	23.223	False
				Spring 2014-Spring 2015 seed # per sample	1.318	23.083	False

**Table B-6: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of native vs non-native species richness in aboveground vegetation surveys per survey season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	<i>P</i>	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 native vs non-native species richness	7.854	0.005	1	Fall 2013 Native sp.- Fall 2013 Non-native sp.	13.167	10.433	True
Spring 2014 native vs non-native species richness	3.363	0.067	1	Spring 2014 Native sp.- Spring 2014 Non-native sp.	9.548	10.433	False
Fall 2014 native vs non-native species richness	17.48	2.904e-05	1	Fall 2014 Native sp.- Fall 2014 Non-native sp.	19.25	10.184	True
Spring 2015 native vs non-native species richness	4.406	0.036	1	Spring 2015 Native sp.- Spring 2015 Non-native sp.	10.475	10.184	True

**Table B-7: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of aboveground species richness for each survey season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	<i>p</i>	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 total species richness	79.831	1.591e-12	11	Fall 2013-Fall 2014 species per sample	0.138	27.673	False
				Fall 2013-Spring 2014 species per sample	65.727	27.342	True
				Fall 2013-Spring 2015 species per sample	70.625	27.673	True
				Fall 2014-Spring 2014 species per sample	65.589	27.342	True
				Fall 2014-Spring 2015 species per sample	70.488	27.673	True
				Spring 2014-Spring 2015 species per sample	4.898	27.342	False

**Table B-8: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of total aboveground vegetative cover values for each survey season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	$p$	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 total vegetative cover	104.057	2.162e-07	41	Fall 2013-Fall 2014 vegetative cover	10.766	27.679	False
				Fall 2013-Spring 2014 vegetative cover	62.571	27.339	True
				Fall 2013-Spring 2015 vegetative cover	83.141	27.679	True
				Fall 2014-Spring 2014 vegetative cover	51.805	27.679	True
				Fall 2014-Spring 2015 vegetative cover	72.375	28.014	True
				Spring 2014-Spring 2015 species per sample	20.57	27.679	False

**Table B-9: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of native aboveground vegetative cover values for each survey season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

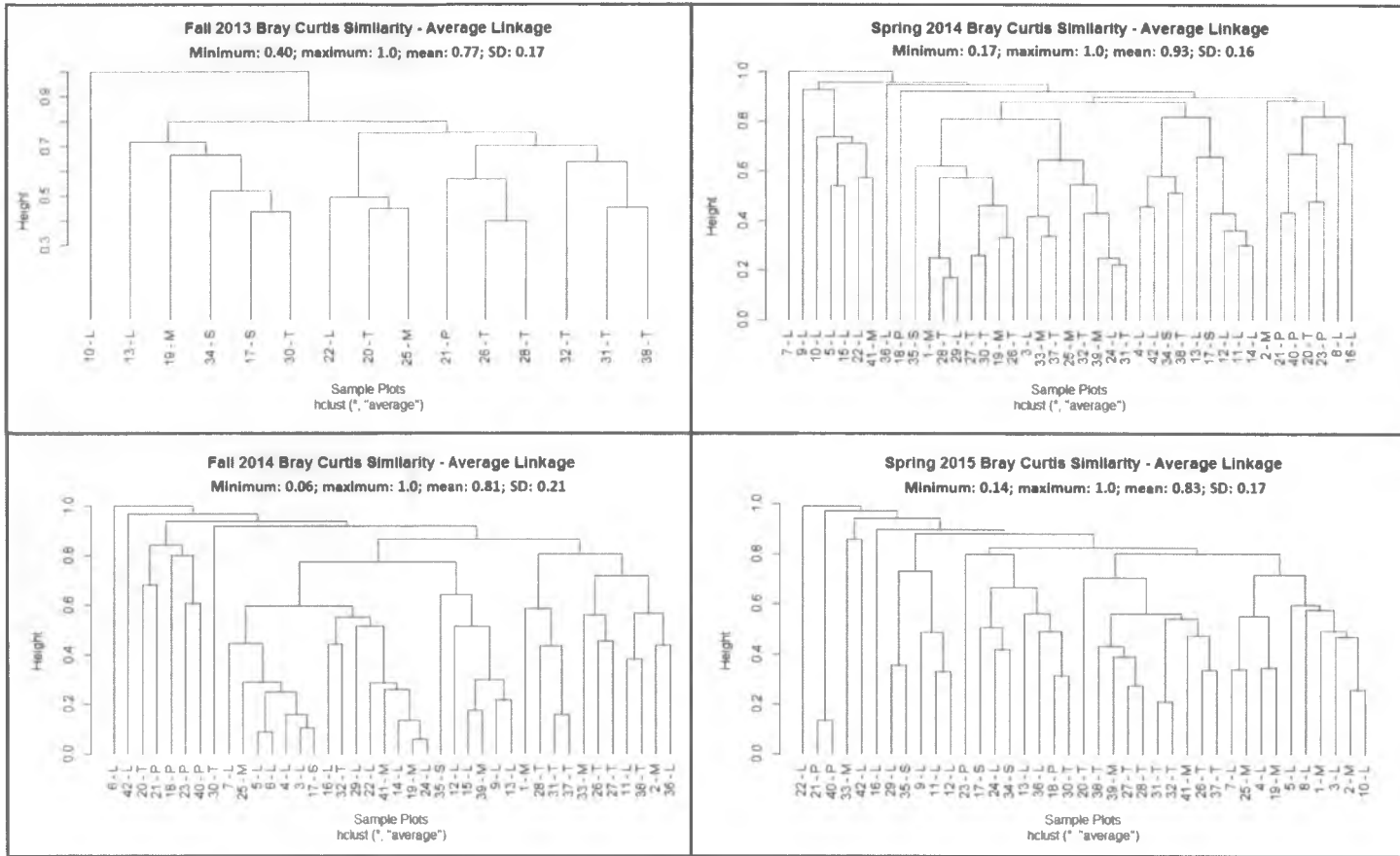
Test	Chi-square	$p$	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 native vegetative cover	71.079	2.155e-05	29	Fall 2013-Fall 2014 native cover	3.749	27.679	False
				Fall 2013-Spring 2014 native cover	48.989	27.339	True
				Fall 2013-Spring 2015 native cover	57.789	27.679	True
				Fall 2014-Spring 2014 native cover	52.737	27.679	True
				Fall 2014-Spring 2015 native cover	61.538	28.014	True

				Spring 2014-Spring 2015 native cover	8.801	27.679	False
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**Table B-10: Kruskal Wallis K test statistics ( $p \leq 0.05$ ) and post hoc results from comparison of non-native aboveground vegetative cover values for each survey season. Diff. column “True” value indicates critical difference has been exceeded and null hypothesis (that the two communities are statistically similar) is rejected.**

Test	Chi-square	$p$	df	Post hoc analysis			
				Comparison	Obs. diff.	Crit. diff.	Diff.
Fall 2013 – Spring 2014 – Fall 2014 – Spring 2015 non-native vegetative cover	59.649	0.0182	39	Fall 2013-Fall 2014 non-native cover	13.717	27.679	False
				Fall 2013-Spring 2014 non-native cover	37.857	27.339	True
				Fall 2013-Spring 2015 non-native cover	48.692	27.679	True
				Fall 2014-Spring 2014 non-native cover	24.141	27.679	False
				Fall 2014-Spring 2015 non-native cover	34.975	28.014	True
				Spring 2014-Spring 2015 non-native cover	10.835	27.679	False





Appendix C

**Figure C-1:** Hierarchical clustered dendrograms of Bray Curtis similarity indices for fall 2013, spring 2014, fall 2014, and spring 2015 seed bank assays. Plot numbers are marked with aboveground vegetation community abbreviations to highlight lack of consistent groupings between above- and belowground communities (L=*Lasthenia maritima* Type, S=*Spergularia macrotheca*, P=*Plantago coronopus* Type, T=*Tetragonia tetragonioides* Type, M=Mixed vegetation Type). Bray-Curtis value of 1 indicates uniform communities; 0 indicates highly dissimilar communities.

Table D1: Fall 2013 seed bank sample data.

Plot #	AMSP	AVBA	BRCA	BRDI	CAME	CHMU	CLPE	COAU	EHER	Erodium spp.	HOMU	JUBU	LAMA	LEDI	LYAR	Malva spp.	PLCO	POAN	POMO	POTE	SEVU	SOOL	SPMA	SPME	STME	TETE	URUR
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	0	0	0	0	0	1	258	0	0	0	0	0	16	329	0	0	0	0	0	100	0	0	254	63	10	0	5
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	0	0	0	0	0	0	3	0	0	0	0	0	18	42	1	1	1	0	41	0	0	1	68	0	55	1	69
20	0	0	0	0	0	2	202	0	0	0	9	1	423	68	27	0	185	0	0	34	0	1	4	41	63	0	0
21	1	0	0	21	0	1	170	0	0	0	1	8	9	0	4	2	590	0	0	0	0	4	0	0	206	0	130

Appendix D

Table D1 continued

Plot #	AMSP	AVBA	BRCA	BRDI	CAME	CHMU	CLPE	COAU	EHER	Erodium spp.	HOMU	JUBU	LAMA	LEDI	LYAR	Malva spp.	PLCO	POAN	POMO	POTE	SEVU	SOOL	SPMA	SPME	STME	TETE	URUR
22	0	2	1	0	0	0	34	0	0	0	81	0	256	11	0	0	72	0	53	0	0	0	3	0	0	6	0
23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	2	0	5	0	0	10	0	0	0	2	86	26	368	44	48	0	0	0	0	1	0	0	4	0	76	0	146
26	5	0	4	49	0	0	387	3	0	0	13	9	45	60	5	0	0	0	0	0	0	0	6	1	125	13	188
27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28	0	0	3	0	0	0	196	0	0	1	0	0	11	33	8	0	0	0	0	0	0	0	4	0	27	25	109
29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	0	0	0	0	1	0	157	37	0	5	0	0	0	165	1	0	12	2	0	0	0	0	159	0	14	85	78
31	0	0	0	0	0	0	3	6	0	9	1	0	16	8	0	0	1	0	0	0	0	0	2	2	1	13	135
32	0	1	0	0	3	0	14	76	1	9	3	0	162	0	0	0	0	0	0	0	1	0	201	0	84	37	694
33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	0	0	0	0	0	0	13	0	0	0	0	0	62	187	0	0	0	0	0	0	0	0	95	3	0	2	0
35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38	2	0	0	0	0	0	0	0	0	1	0	0	67	0	0	0	0	0	0	0	0	0	15	0	0	23	303
39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table D2: Spring 2014 seed bank sample data.

Plot #	AMSP	BRCA	BRDI	CAME	CHMU	CLPE	COAU	Erodium spp.	HOMU	JUBU	LAMA	LEDI	LYAR	Malva spp.	MOVE	PLCO	POAN	POMO	POTE	Rubus spp.	SEVU	SOOL	SPMA	SPME	STME	TETE	URUR
1	0	0	0	0	83	0	0	2	0	0	5	38	3	0	0	0	0	0	0	0	0	0	0	0	3	0	17
2	0	0	0	0	32	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	1	0	0	0	4
3	2	0	0	0	9	0	0	0	0	0	7	23	0	0	0	0	0	0	0	0	0	1	7	0	1	0	44
4	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	23	0	0	0	1
5	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0
9	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0	0	0
10	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	144	0	0	0
12	0	0	0	0	0	2	0	0	0	0	2	8	0	0	0	0	0	0	0	0	0	0	0	79	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	88	0	0	0	0	0	0	0	0	0	0	340	85	0	0	0
14	0	0	0	0	1	0	0	0	0	0	1	24	0	0	0	0	0	0	1	0	0	0	54	120	0	0	0
15	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	2	34	0	0	0	0	0	0	0	0	0	0	5	5	27	5	0
17	0	0	0	0	0	1	0	0	0	0	0	36	0	0	0	0	0	0	0	0	0	0	25	57	1	1	0
18	0	0	0	0	0	1	0	0	0	442	0	25	0	0	0	1	0	4	0	0	0	0	33	0	5	0	0
19	0	0	0	0	12	0	0	1	0	0	0	68	0	0	0	0	0	10	0	0	0	4	2	7	5	0	61
20	0	0	0	0	76	10	0	0	0	0	1	34	10	0	0	0	0	4	0	0	0	4	0	0	30	0	7
21	0	0	0	0	14	1	0	0	0	4	6	0	4	0	0	75	0	0	0	0	0	0	0	0	48	0	0

Table D2 continued

Plot #	AMSP	BRCA	BRDI	CAME	CHMU	CLPE	COAU	Erodium spp.	HOMU	JUBU	LAMA	LEDI	LYAR	Malva spp.	MOVE	PLCO	POAN	POMO	POTE	Rubus spp.	SEVU	SOOL	SPMA	SPME	STME	TETE	URUR
22	0	0	0	0	0	2	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
23	0	0	0	0	91	2	0	0	0	2	0	1	1	0	0	33	1	0	0	0	4	1	181	0	37	0	0
24	1	1	0	0	28	12	0	0	0	0	8	5	0	0	0	0	0	0	0	0	1	0	19	0	19	0	158
25	5	0	1	0	6	3	0	0	1	1	107	8	3	0	0	0	0	0	0	0	0	0	0	0	26	0	64
26	0	0	0	1	1	4	0	0	0	13	3	94	0	0	0	0	0	0	0	0	0	1	1	9	0	0	33
27	0	0	0	0	0	0	2	0	0	0	0	210	0	0	0	0	0	0	0	0	0	0	2	0	1	1	64
28	0	0	0	0	0	0	51	1	0	6	9	460	2	0	0	0	0	0	0	1	0	0	58	0	0	0	62
29	0	0	0	0	0	0	0	0	0	0	25	432	0	0	0	2	0	0	0	0	0	0	30	13	2	0	10
30	0	0	0	0	0	0	13	1	0	0	1	165	0	0	0	0	0	0	0	0	0	6	0	0	0	3	5
31	0	0	1	0	0	0	9	1	0	0	16	5	0	0	0	0	0	0	0	0	0	1	0	0	11	3	151
32	0	0	0	0	0	1	4	0	0	0	35	1	0	0	0	0	0	0	0	0	0	0	30	0	2	11	290
33	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	30
34	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	61	0	0	0	0
35	0	0	0	0	0	6	0	0	0	0	4	141	0	0	0	0	0	0	193	0	0	0	23	0	4	6	0
36	0	0	0	0	0	8	0	0	0	0	4	0	1	0	0	0	0	0	0	0	0	9	0	420	0	0	0
37	1	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	6	0	0	0	5	37
38	0	0	0	0	2	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	19	0	0	0	1	12
39	1	0	0	0	18	0	0	6	0	0	16	5	2	1	0	0	0	0	1	0	0	1	0	0	29	2	114
40	0	0	0	0	0	7	0	0	0	11	11	1	14	0	0	154	0	2	0	0	0	0	0	0	14	0	0
41	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1
42	0	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	22	0	0	3	0	0

Table D3: Fall 2014 seed bank sample data.

Plot #	AMSP	AVBA	BRDI	CHMU	CLPE	COAU	Erodium spp.	FEBR	HOMU	JUBU	LAMA	LEDI	LYAR	Malva spp.	PLCO	POAN	POMO	POTE	SOAS	SOOL	SPMA	SPME	STME	TETE	URUR
1	1	0	0	26	0	0	1	0	0	0	12	88	6	0	0	0	0	1	1	2	5	1	56	0	119
2	8	0	0	101	0	0	17	0	1	0	155	0	3	4	11	0	0	0	23	11	11	0	16	0	51
3	0	0	0	5	0	2	0	0	0	0	1044	6	0	0	0	0	0	0	0	0	201	27	0	0	1
4	0	0	0	0	0	0	0	0	0	0	851	8	0	0	0	0	0	0	0	0	13	1	0	0	0
5	0	0	0	0	0	5	0	0	0	0	1615	0	0	0	0	0	1	0	0	0	10	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	2	0	0	0	0	0	0	0	0	0	2724	6	0	0	0	0	0	0	0	0	4	0	13	0	211
8	0	0	0	0	1	0	0	0	0	0	1370	1	0	0	0	0	0	0	0	0	0	2	10	0	0
9	0	0	0	50	14	0	0	0	0	0	132	1	0	0	0	3	0	0	0	0	368	462	0	0	0
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	0	0	0	0	1	0	0	0	0	0	81	2	0	0	0	0	0	0	0	0	0	14	0	0	0
12	0	0	0	0	6	0	0	0	0	0	13	43	0	0	0	0	0	0	0	0	1687	418	4	0	0
13	0	0	0	0	3	0	0	0	0	0	197	76	0	0	0	0	0	0	0	0	647	429	0	0	0
14	0	0	0	1	0	0	0	0	0	0	415	0	0	0	0	0	0	0	0	0	1	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	381	42	0	0	0	0	1	0	0	0	348	334	0	0	0
16	1	0	0	0	27	0	0	0	0	0	237	1	1	0	0	0	206	0	0	0	106	8	2	16	1
17	0	0	0	0	11	0	0	0	0	1	998	6	0	0	0	0	30	0	0	0	53	14	0	2	0
18	0	0	0	0	85	1	1	0	0	486	106	5	50	0	101	0	1	1	0	0	19	0	22	0	0
19	0	0	0	1	0	0	0	0	0	0	334	0	1	0	0	0	0	0	0	0	0	1	0	0	1
20	47	0	0	109	38	0	26	0	0	1	2	4	6	1	18	0	21	0	0	7	1	2	17	0	28
21	0	0	0	2	21	0	70	0	1	0	8	0	9	2	71	0	0	0	2	1	1	0	115	0	1

Table D3 continued

Plot #	AMSP	AVBA	BRDI	CHMU	CLPE	COAU	Erodium	FEBR	HOMU	JUBU	LAMA	LEDI	LYAR	Malva	PLCO	POAN	POMO	POTE	SOAS	SOOL	SPMA	SPME	STME	TETE	URUR
22	0	0	0	0	1	0	0	0	0	0	599	13	0	0	0	0	1	0	0	0	3	9	0	1	0
23	0	0	1	0	8	0	0	0	2	51	1	2	0	0	311	0	0	0	0	0	5	2	2	0	0
24	0	0	0	6	5	0	1	0	0	0	327	0	0	1	0	0	0	0	0	0	0	0	0	0	2
25	4	1	0	45	0	0	1	0	2	0	963	13	3	0	0	0	0	0	0	1	2	0	29	0	367
26	0	0	1	0	2	0	0	0	0	0	36	4	0	0	0	0	0	0	0	0	0	0	0	0	28
27	8	0	0	0	1	16	0	0	0	0	29	18	0	0	0	0	0	0	0	0	4	4	1	17	58
28	0	0	7	0	0	5	1	0	0	0	10	0	0	0	0	0	0	0	0	1	20	2	9	18	161
29	6	0	0	0	0	3	0	0	1	0	379	414	6	0	0	1	0	45	0	1	9	44	32	0	133
30	0	0	0	0	17	67	4	0	0	0	3	44	0	0	0	0	0	0	0	0	12	0	0	11	0
31	15	0	0	0	1	13	0	0	0	0	4	10	0	0	0	0	0	0	0	0	0	2	0	19	360
32	3	1	0	0	0	28	4	0	0	0	243	1	0	0	0	0	0	0	0	0	110	11	17	1	256
33	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	3	4	0	0	22
34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	0	0	0	0	13	4	0	0	0	0	6	200	0	0	0	0	0	290	0	0	534	2	0	0	0
36	0	0	0	0	12	0	0	0	0	0	138	0	1	0	0	0	0	0	0	0	8	0	19	0	0
37	8	0	0	0	0	0	2	0	0	0	27	0	0	0	0	0	0	0	0	0	24	0	0	2	402
38	0	0	0	2	0	0	0	0	0	0	59	1	0	0	1	0	0	0	0	0	23	0	0	0	10
39	0	0	0	1	0	7	0	0	0	0	341	38	0	0	0	0	1	0	0	0	106	376	11	0	1
40	0	0	1	0	11	0	28	165	2	2	0	38	0	0	898	129	0	0	0	0	0	1	4	1	0
41	0	0	0	4	35	1	68	0	0	9	431	0	7	1	4	0	0	0	0	0	0	1	28	4	17
42	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	0	0

Table D4: Spring 2015 seed bank sample data.

Plot #	AMSP	AVBA	BRDI	CHMU	CLPE	COAU	Erodium spp.	FEBR	HOMU	JUBU	LAMA	LEDI	Lupinus spp.	LYAR	Malva spp.	PLCO	POAN	POTE	SEVU	SOOL	SPMA	SPME	STME	TETE	URUR
1	0	0	0	13	0	0	6	0	0	0	43	13	0	6	2	1	0	2	0	0	3	0	0	0	0
2	0	0	0	24	0	0	1	0	0	0	57	0	0	2	0	0	0	0	0	0	1	0	6	0	0
3	0	0	0	0	2	0	0	0	0	0	33	7	0	0	0	0	0	0	0	0	17	1	0	0	0
4	0	0	0	0	2	0	0	0	0	0	301	65	0	0	0	0	0	0	0	0	55	0	1	0	0
5	0	0	0	6	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	5	0	0	0	0	0
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	0	0	0	0	0	1	0	0	0	0	176	1	0	0	0	0	0	0	0	0	5	0	7	0	17
8	0	0	0	0	11	0	0	0	0	0	26	1	0	0	0	0	0	0	0	0	1	2	22	0	0
9	0	0	0	39	1	0	0	0	0	0	81	1	0	0	0	0	5	0	0	0	0	193	0	0	0
10	0	0	0	0	0	0	0	0	0	0	53	0	0	0	0	0	0	0	0	2	0	0	0	0	0
11	0	0	0	0	18	0	0	0	0	0	3	5	0	0	0	0	0	0	0	0	0	424	0	0	0
12	0	0	0	0	2	7	0	0	0	0	15	20	0	0	0	0	0	0	0	0	150	309	0	0	0
13	0	0	0	0	8	0	0	0	0	0	22	42	0	0	0	0	0	1	0	0	30	46	0	0	0
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	0	0	0	0	7	0	0	0	0	0	2	1	0	0	0	0	0	15	0	0	3	0	1	115	0
17	0	0	0	0	3	0	0	0	0	0	1	82	0	0	0	0	0	39	0	0	120	25	0	0	0
18	0	0	0	0	50	1	0	0	0	2	9	53	0	0	0	1	0	2	1	0	48	0	2	0	0
19	0	0	0	0	6	1	1	0	0	0	138	13	0	0	0	0	0	0	0	0	90	0	0	3	0
20	0	0	1	299	8	0	0	0	0	0	0	81	0	4	1	0	0	2	0	0	2	0	2	0	62
21	0	0	0	0	4	0	0	0	0	0	0	1	0	3	0	243	0	0	0	0	0	0	1	0	0



Table D4 continued

Plot #	AMSP	AVBA	BRDI	CHMU	CLPE	COAU	Erodium spp.	FEBR	HOMU	JUBU	LAMA	LEDI	Lupinus spp.	LYAR	Malva spp.	PLCO	POAN	POTE	SEVU	SOOL	SPMA	SPME	STME	TETE	URUR
22	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
23	0	0	0	0	11	0	0	0	0	0	1	5	0	0	0	17	0	0	0	0	8	0	2	0	0
24	0	0	0	11	32	0	0	0	0	0	3	8	0	1	0	0	0	0	0	145	1	0	0	0	
25	0	1	0	0	0	0	0	0	3	0	97	2	0	0	0	0	0	0	0	0	0	31	0	27	
26	0	0	0	0	0	1	0	0	0	0	23	38	0	0	0	0	0	0	0	0	0	18	27	109	
27	3	0	0	0	5	3	0	0	0	0	2	64	0	0	0	0	0	0	0	3	1	1	9	62	
28	0	0	0	1	1	2	1	0	0	0	20	70	0	0	0	0	0	2	0	12	0	6	49	53	
29	0	0	0	0	1	1	0	0	0	0	6	392	0	0	0	0	0	1	0	11	276	1	0	5	
30	0	0	0	0	57	8	2	0	0	0	0	88	0	0	0	0	0	0	0	17	1	3	14	0	
31	1	0	0	0	0	2	0	0	0	0	2	18	0	0	0	0	0	0	0	10	1	0	47	44	
32	0	0	0	0	0	1	1	0	0	0	8	2	0	0	0	0	0	1	0	12	0	0	53	30	
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	6	
34	0	0	0	0	0	0	0	0	0	0	15	1	0	0	0	0	0	0	0	294	0	0	0	0	
35	1	0	0	0	22	0	0	0	0	0	0	410	0	0	0	0	0	69	0	58	0	1	4	0	
36	0	0	0	0	35	0	0	0	0	0	4	0	0	0	0	0	0	0	0	41	0	10	0	1	
37	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	11	103	
38	0	0	0	0	0	0	0	0	0	0	1	102	0	0	0	0	0	0	0	19	0	0	5	18	
39	0	0	0	8	1	5	1	0	0	0	92	72	1	0	0	0	0	0	3	0	0	0	1	38	
40	0	0	0	1	4	0	1	0	0	2	1	0	0	4	0	200	0	8	0	0	0	0	8	0	
41	2	0	0	0	5	0	5	2	0	0	3	7	0	3	0	0	0	0	0	0	0	0	2	0	
42	0	0	0	0	0	1	0	0	0	0	5	0	0	0	0	0	0	0	0	1	0	0	0	0	