



Diverse native island flora shows rapid initial passive recovery after exotic herbivore removal on Santa Rosa Island, California

Diane M. Thomson · A. Kathryn McEachern · Emily L. Schultz · Kenneth Niessen · Dieter Wilken · Katherine Chess · Lauren F. Cole · Ruth Y. Oliver · Jennifer D. Phillips · Acadia Tucker

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Abstract Removing exotic vertebrates from islands is an increasingly common and potentially effective strategy for protecting biodiversity. Yet, surprisingly few studies evaluate large-scale effects of island removals on native plants. We surveyed 431 hectares of habitat in 7 canyons on Santa Rosa Island just after exotic herbivore control began (1994–1996), and again after two herbivore species had been eradicated and ~90% of herbivores removed (2010–2012). We searched for 68 endemic and/or rare native plant taxa, mapping and recording abundances for the 39 found. Initially most of these 39 species were absent from most canyons (79.9% species-canyon combinations). Nearly 35% of absences changed to presences by 2010–2012, while only 5.5% of presences

changed to absences. Thirty-six of these 39 species increased in total area, and 38 increased in total abundance. Graminoids increased more and shrubs less than other life histories, for both apparent colonizations and abundances. Beta diversity and species turnover between canyons was high at both surveys. Although a diversity of the 39 located taxa showed substantial gains, nearly half remained uncommon in 2010–2012. These results reinforce the devastating effects of exotic vertebrate herbivores on island native plants, particularly long-lived, slow-growing species. They also demonstrate significant potential benefits of exotic herbivore removal even without other active restoration, not only for vegetative cover but for a number of rare taxa. Our surveys were more spatially extensive than most post-removal studies; high spatial turnover in these data suggests that larger-scale monitoring may be critical to capture full effects of exotic animal removal.

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D. M. Thomson (✉) · E. L. Schultz · L. F. Cole · R. Y. Oliver · J. D. Phillips · A. Tucker
W.M. Keck Science Department, The Claremont Colleges,
925 N. Mills Avenue, Claremont, CA 91711, USA
e-mail: dthomson@kecksci.claremont.edu

A. K. McEachern · K. Niessen · K. Chess
U.S. Geological Survey, Western Ecological Research
Station, Channel Islands Field Station, 1901 Spinnaker Dr,
Ventura, CA 93001, USA

D. Wilken
Santa Barbara Botanic Garden, 1212 Mission Canyon Rd,
Santa Barbara, CA 93105, USA

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Introduction

Oceanic islands support high levels of endemism and a disproportionate share of global biodiversity relative to their area (Myers et al. 2000; Kier et al. 2009; Caujape-Casells et al. 2010). Islands are also especially vulnerable to the negative effects of exotic

species introductions (Courchamp et al. 2003; Reaser et al. 2007). The majority of anthropogenically-driven extinctions documented to date have occurred on islands, with exotic species the most common cause (McCreless et al. 2016; Whittaker et al. 2017). Islands are also more tractable targets for exotic control than mainland habitats (Simberloff et al. 2019). As a result, island exotic removals may be a particularly high-impact and effective strategy for channeling conservation resources (Jones et al. 2016; McCreless et al. 2016).

A number of studies show substantial conservation benefits of exotic species removal, including on islands (Jones et al. 2016; Schweizer et al. 2016; Prior et al. 2018). Still, exotic control alone is not always sufficient to restore native species (Bullock et al. 2002). Some exotics generate legacy effects that continue to suppress natives even after their removal (Skurski et al. 2019). Efforts to remove exotics have also raised concerns about potential negative indirect effects (Zavaleta et al. 2001; Zavaleta 2004). Exotic animals may exert top-down control on other non-native species; for example, removal of an introduced herbivore could lead to increases in exotic plants (Klinger et al. 2002; Chapuis et al. 2004).

Given these issues, long-term research evaluating the effects of island exotic removals is surprisingly uncommon (Jones et al. 2016; Schweizer et al. 2016). Many studies monitor for only a few years after removal, and factors such as rainfall can generate wide temporal background variation in vegetation and responses to management (Donlan et al. 2002, 2003; Erskine Ogden and Rejmánek 2005). The majority of previous work focuses on recovering vertebrate species such as seabirds (Smith et al. 2006; Jones et al. 2016). This scarcity of information to evaluate outcomes is unfortunate, given that exotic removal can be both expensive and controversial (Howald et al. 2007; Blackburn et al. 2019).

Native island plants are particularly understudied in this context. An extensive recent review identified fewer post-eradication studies for plants than animals, and also found that plants were less likely to recover passively from exotic removal (Prior et al. 2018). Most post-removal studies for plants focus on broad community responses such as cover and species richness (Beltran et al. 2014; Hughes et al. 2014; Bastille-Rousseau et al. 2017; Summers et al. 2019), or on a single species (Woolsey et al. 2019). As individual

species or functional groups likely respond to removals in distinct ways, predictions about which natives may require additional restoration and management are critical to conservation success (Hamann 1993; Klinger et al. 2002). Understanding how life history traits influence patterns of response would facilitate better planning, but would require large-scale, multi-species data.

Exotic vertebrate herbivores pose among the greatest threats to island endemic plants (Caujape-Casells et al. 2010). Multiple studies document species loss due to exotic herbivores (Donlan et al. 2003; Reaser et al. 2007). Many island endemics evolved in the absence of large, hooved animals and are poorly adapted to trampling, grazing and browsing (Courchamp et al. 2003). Exotic herbivores can dramatically reduce vegetative cover (Reaser et al. 2007). Seed scarcity and low dispersal may create additional barriers to post-removal recovery for native plants, compared with mobile species such as birds (Erskine Ogden and Rejmánek 2005; Bellingham et al. 2010). Data on patterns of spatial recovery are especially valuable for assessing the role of dispersal limitation in shaping post-removal responses.

The eight California Channel Islands (USA) are rich in plant diversity, supporting 281 endemic taxa (McEachern et al. 2016). Introductions of exotic vertebrate herbivores such as sheep, cattle, pigs, elk, and deer over the last 150 years led to dramatic changes in island vegetation and declines of some rare plants (Bowen & Van Vuren 1997; McEachern et al. 2009; Van Vuren & Coblenz 1987). By 1995, the United States National Park Service (NPS) and The Nature Conservancy had assumed management of the northern four Channel Islands and initiated an exotic herbivore control and eradication program. Program goals included promoting regeneration of native vegetation largely lost after herbivore introductions, as well as increasing abundances of rare and endemic plants to reduce extinction risk (Rick et al. 2014). In this study, we define initial “recovery” as substantial progress towards those management goals, consistent with other recent work on island exotic herbivore removals (Prior et al. 2018) and usage in rare and endangered species conservation (Scott et al. 2005).

We compared the occupancy, spatial extent, and abundance of 68 native taxa in 431 hectares of canyon habitat on Santa Rosa Island (SRI) between two surveys: the first as exotic removal began (1994–1996),

and the second a decade after pigs and cattle had been completely eradicated and total herbivore numbers reduced by approximately 90% (2010–2012). We used these data to ask: (1) What was the status of native and endemic plants at the initial survey, soon after herbivore removal began? (2) How had different components of the plant community changed in distribution and abundance by 2010–2012? (3) Which taxa remain rare? (4) Did life history affect responses to herbivore removal? (5) How did baseline community composition and changes between surveys vary spatially, as measured by beta diversity?

Methods

Study site

Santa Rosa Island (SRI) is the second largest (215 km²) of the northern California Channel Islands, located 47.3 km from the mainland. A ridge peaking at 482.5 m divides SRI from east to west. Streams drain north through uplifted marine terraces covered with alluvium and colluvium, or southward through steeper and more erosion-resistant terrain constrained by bedrock (Dibblee and Ehrenspeck 2002). The climate is coastal Mediterranean, with rainfall concentrated into cooler winter months followed by hot, dry summers (Summers et al. 2019). Summer fog provides a critical additional seasonal source of moisture for many plants (Woolsey et al. 2019). The flora includes 500 taxa, 80% of them native, with 44 Channel Islands endemics (Davidson et al. 2019).

SRI was used as a ranch from the mid-1800s to 2011, stocking sheep, pigs, cattle, deer, and elk (McEachern et al. 2016). Up to 70,000 sheep were present until the early 1900s, when ranching shifted to cattle. All sheep were gone by the early 1960s. At peak, cattle numbers ranged from 6000 to 8000 animals (National Park Service 2013). Exotic eradication began with total removal first of approximately 1400 pigs from 1990 to 1992, then cattle in 1998 (Lombardo and Faulkner 1999). Elk and deer were reduced gradually starting in 2007, resulting in full removal by 2011 (McEachern et al. 2016). Surveys from 2009 estimated approximately 500 elk and 500 deer remained (Griffin et al. 2009). The exact numbers of elk and deer present during the first two years of our resurvey in 2010–2011 are unknown, but would

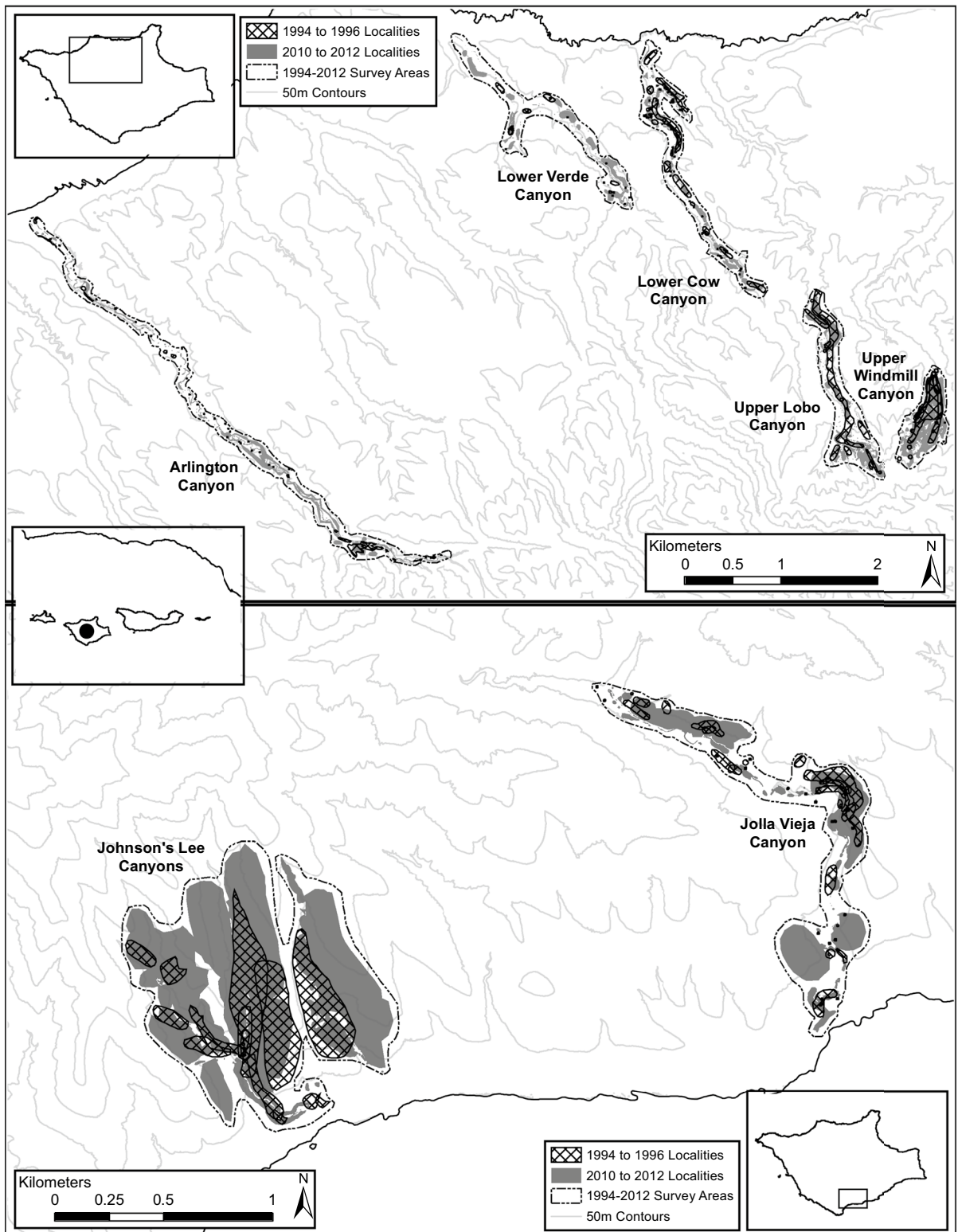
have represented at most about 10% of historic non-native herbivore abundances on SRI. All elk and most deer had been eradicated by December 2011; only 12 radio-collared deer remained until 2015, to help confirm eradication success.

Paleo-ecological studies, historical records, and comparisons with similar sites support that chaparral and sage scrub dominated SRI prior to exotic herbivore introductions, along with some grassland and woodland habitat (Rick et al. 2014). Under ranching, native vegetation largely converted to exotic annual grasslands and eroded bare ground (Clark et al. 1990, Summers et al. 2019). Estuarine sedimentation rates during the 1800s went up by more than 32 times relative to the previous 5000 years, demonstrating the severity of vegetation loss and erosion caused by exotic herbivores (Cole and Liu 1994). Native plants persisted as remnant stands on canyon walls and coastal bluffs inaccessible to vertebrate herbivores.

Field surveys

From 1994 to 1996, the U.S. Geological Survey (USGS) searched for 105 rare and endemic plant species thought to potentially occur on SRI and mapped any occurrences found. The goals were to determine whether populations documented in historic accounts and collections were present, and to estimate their distribution and abundances. These 105 species included 14 candidates for listing under the United States Endangered Species Act, as well as a suite of rare and endemic plants selected by botanists with local expertise. Potential habitat maps were developed for each taxon using herbarium labels, field notes, and knowledge of species habitat requirements. Seventy-one of the 105 species on this initial list had potential habitat in canyons and were subsequently confirmed to occur on SRI (67.6%; Supplementary Information, Table S1; hereafter referred to as target species or taxa). Other habitat types were also surveyed but are not included in this analysis, because time and funding constraints limited the area we could revisit in 2010–2012.

In 1994–1996, pairs of botanists walked both the bottoms and rims of the 14 canyons on SRI and mapped occurrences for any target species found. The survey took place between April and August when most of these plants flower or fruit (Fig. 1). Binoculars were used to scan for and observe occurrences not



◀**Fig. 1** Canyon habitat surveyed (enclosed by dashed lines) on Santa Rosa Island in 1994–1996 as exotic herbivore removal began and again in 2010–2012. Areas with target taxa present are hatched for 1994–1996 and filled for 2010–2012. The top panel and insert show five canyon complexes on the north side of the island, and the bottom panel and insert two canyon complexes on the south side

accessible on foot given steep terrain. Each species occurrence was drawn onto 1:24,000 scale USGS topographic quadrangle maps and abundances recorded. Abundances were estimated when individuals could not be counted accurately, almost always because numbers were too high. Occurrences generally were mapped as points when one or a few individuals were concentrated in an area less than approximately 5 m in radius; otherwise, polygons were drawn.

Between 2010 and 2012, we repeated the survey for seven canyons (Fig. 1). We could not resurvey all 14 canyons because of time constraints. Data collection took longer in the resurvey, primarily because: (1) regrowth of vegetation slowed foot travel (Supplementary Information, Fig. S1); (2) recording polygon boundaries took longer with GPS than paper maps; and (3) far more occurrences were encountered (see Discussion). Resurveyed canyons were selected to capture the range of south–north and east–west geographic variation in this habitat type (Fig. 1). We also prioritized canyons where a greater area was visited in 1994–1996.

Canyon bottoms and rims were walked using the same protocol as in 1994–1996, by a botanist and a research associate trained in identification of target flora. On approximately 50% of resurvey days, between one and three additional assistants helped record occurrences for a subset of the most common species. One of the botanists from the original survey accompanied the resurvey team on several days, to verify the same protocol was applied. A total of 430.86 hectares from the total canyon area searched and mapped in 1994–1996 was resurveyed in 2010–2012 (mean \pm one standard error per canyon: 61.55 ± 8.82 ha). Even using the same search protocol and effort as in the baseline survey, the total number of days required to complete data collection in these 7 canyons (431 ha) increased from 11 to 30. Both surveys concentrated predominately in May, June, and July, with some data collection in April (1 day 1994–1996, 2 days 2010–2012).

We mapped each target species occurrence with the same methods as in the initial survey, except that Trimble Juno SB GPS units with ArcPad v. 10.0 (ESRI, Redlands, CA) were used instead of paper maps. GPS units were pre-loaded with aerial photos, topographic maps, and occurrences from the 1994–1996 survey, to ensure coverage of the same areas. For almost all occurrences, numbers of plants were counted or estimated as in 1994–1996 (85.4% of records, $n=1914$). For some occurrences observed through binoculars or with large numbers of individuals, we estimated cover (3.4%) or density (4.1%). Patches within an occurrence sometimes were drawn as separate polygons and merged during data processing to facilitate more precise mapping. We followed guidelines from the California Natural Diversity Database to combine points and polygons for the same species within 400 m of each other into the same record, for both surveys (California Department of Fish and Wildlife 2018). This rule did not affect any of the response measures used in our analyses. Additional data on habitat and site characteristics also were recorded (Supplementary Information, Table S2).

Data processing and analysis

The 1994–1996 paper maps were digitized by hand into ArcInfo coverages then transferred into an ArcGIS 10.7.0 geodatabase (ESRI, Redlands, CA). Several target subspecies or hybrids were difficult to identify in the field, and so combined for analysis. *Dudleya greenei*, *D. candelabrum* and their hybrids were grouped into a single taxon (*D. greenei*), as were *Arctostaphylos confertiflora* and *A. tomentosa* (*A. confertiflora*). Consolidation resulted in 68 total canyon taxa, 25 of them endemic to the California Channel Islands. We broadly categorized the life history of each species as fern, graminoid (grasses and rushes), herbaceous, shrub, or tree; 95% of species were perennial (Supplementary Information, Table S1).

We first evaluated the effects of (1) endemic status and (2) life history on the probability that the 68 target taxa were detected in at least one survey, with Fisher's Exact Tests (FET). All subsequent analyses of changes between 1994–1996 and 2010–2012 included only species verified to occur in surveyed canyon habitat (i.e., present in at least one canyon in at least one survey, $n=39$ total). We quantified

changes between surveys for these 39 species with three measures: (1) apparent local colonization and extinction events in individual canyons; (2) differences in total area; and (3) differences in total abundance. We did not compare numbers of individual occurrences or polygons, because GPS mapping in 2010–2012 facilitated finer-scale definition of these features than paper maps in 1994–1996. Moreover, polygon and occurrence numbers correlated strongly with total area and abundance.

We categorized all potential combinations of species and canyons as absent in both surveys, present followed by absent (apparent local extinction), absent followed by present (apparent local colonization), or present in both surveys (7 canyons by 39 species observed to occur in canyon habitat = 273 potential species-canyon occurrences). Local colonization rates were compared among different life histories with FET. Not enough apparent local extinctions were observed to test for differences among life histories.

Total area and abundance for each of the 39 species analyzed were summed across all individual occurrences by canyon. For density records, we converted to total plant numbers by multiplying occurrence area and density. When abundances were estimated as a range we used the midpoints in combining occurrences. The few cover estimates recorded could not readily be converted to numbers, so were left out of the analysis. In both surveys, abundances were not estimated for some occurrences (1994–1996: 7.3%, $n=287$; 2010–2012: 7.1%, $n=1914$). Analyses of abundance only included species-canyon combinations where data were available for all occurrences in both surveys. In total, 30 of 273 cases were excluded because of insufficient data. More than a third (11) of these cases were for ferns or grasses, and another four for *Typha domingensis* (southern cattail) (Supplementary Information, Table S3).

Area and abundance data were converted to ranked categories ($N=7$ for each measure), making analyses more conservative and robust to differences in observers. An increase of one category represented a five-fold change in the upper bound, with the smallest category $\leq 100 \text{ m}^2$ for area and ≤ 10 individuals for abundance (Supplementary Information, Table S4). We used Kruskal–Wallis one-way ANOVA rank tests to compare changes in area and abundance categories

among life histories, followed by Dunn's post-hoc tests for significant differences. Means and standard errors of the mean were calculated by bootstrapping because of skew. Trees and ferns were not included in life history comparisons for area and abundance since few records were available (5 species-canyon combinations each).

We used the R package betapart (Baselga et al. 2018) to estimate and partition beta diversity among canyons at each survey (Baselga and Orme 2012). The Sørensen dissimilarity index was calculated, along with measures of nestedness and turnover. Finally, we identified those of the 39 species found in at least one survey that remained rare in 2010–2012, based on whether they occurred in fewer than two canyons or in a total area less than 500 m^2 .

Results

Species occurrences

The 1994–1996 survey recorded 21 of the 68 target taxa in at least one canyon (30.9%). All but one of those 21 taxa was relocated in 2010–2012, along with 18 newly observed species (Supplementary Information, Table S5). Twenty-nine taxa were missing in both surveys (42.6%; Supplementary Information, Table S6). About the same percentage of endemics (56.0%) were found as non-endemics (58.1%). Life history did not affect the probability of locating a species (FET, $P=0.28$).

For the 39 taxa found in at least one survey, only 55 of 273 potential species-canyon combinations (20.1%) were presences at the first survey. Transitions from absent to present at the resurvey (local apparent colonization rate) far exceeded changes from present to absent (local apparent extinction rate). Of 218 absences recorded during the initial survey, 34.9% (76) changed to present in the 2010–2012 resurvey. In contrast, only 3 initial presences (5.5%) changed to absences. Local apparent colonization differed significantly across life histories (FET, $P<0.001$). Graminoids had higher colonization rates ($P<0.001$, 3 species) and shrubs lower colonization rates ($P=0.001$, 23 species) than ferns, herbaceous plants, or trees (Table 1).

Table 1 Frequency of presences at the initial and resurvey and apparent rates of colonization between surveys, by life history

Group	Species	Initial present (%)	Resurvey present (%)	Colonization (%)
Ferns	2	0	35.7	35.7
Graminoids	3	23.8	85.7	81.2
Herbaceous	17	19.3	47.9	38.5
Shrubs	15	25.7	41	20.5
Trees	2	0	35.7	35.7

Only the 39 species located in at least one survey are included. Presences were scored by both species and canyon, so each species had 7 potential occurrences. Apparent colonization rate is the percent of species-canyon combinations absent in the initial survey that were present in the resurvey

Area and abundance

Total area per canyon for species-canyon combinations found in the initial survey predominately fell into categories one ($\leq 100 \text{ m}^2$, 29.1%) or two (101 m^2 to 500 m^2 , 23.6%). By 2010–2012, only 7.8% of species-canyon occurrences were in area category one and 16.4% in category two. Abundance showed similar patterns, with 35.9% and 23.1% of initial species-canyon occurrences in categories one (1–10 individuals) and two (11–50 individuals), compared to only 17.4% and 16.3% at the resurvey. All but three of the 39 located species recorded higher total area across all canyons in the resurvey, and all but one greater abundance.

For species-canyon combinations present at both surveys, area increased by a mean of 1.27 ± 0.20 categories ($n=52$) and abundance by 1.11 ± 0.18 categories ($n=36$). Including all species-canyon combinations found in either survey, area increased by 2.37 ± 0.15 ($n=131$) and abundance by 2.18 ± 0.17 ($n=101$) categories. Life history strongly affected changes in abundance ($X^2=21.9$, $df=2$, $P<0.0001$; Fig. 2) but only weakly related to changes in area ($X^2=5.2$, $df=2$, $P=0.07$; Fig. 3). Graminoids increased in abundance by more than twice as many categories as herbaceous species ($Z=3.53$, $P<0.0001$) and shrubs ($Z=4.58$, $P<0.0001$). Herbaceous species increased in abundance marginally more than did shrubs ($Z=1.95$, $P=0.05$).

The grass *Stipa diegoense* showed greater net change in both area and abundance than any other species (Table 2). Another graminoid,

Juncus phaeocephalus, ranked third in total abundance change even though data were missing for one canyon. The endemics *Dudleya greenii* (herbaceous succulent), *Calystegia macrostegia* subsp. *macrostegia* (herbaceous vine), *Diplacus parviflorus* (shrub) and *Acmispon dendroideus* var. *dendroideus* (shrub) were among the top eight species in both net area and abundance change (Table 2). Abundance changes were difficult to quantify for several clonal species that ranked highest in area change, because their numbers could not be estimated in some occurrences (*Typha domingensis*, *Elymus condensatus*; see Methods, Data Processing and Analysis).

Many of the most widespread species from 1994 to 1996 in terms of total area remained so in the 2010–2012 survey (Supplementary Information, Table S5). *Arctostaphylos confertiflora* (endemic shrub), *Malacothrix saxatilis* var. *implicata* (endemic herb), *Peritoma arborea* (shrub), and *Salvia brandegei* (shrub) all ranked in the top four taxa for the initial survey and the top 7 for the resurvey. Still, not all these species were present across most canyons; *P. arborea* and *A. confertiflora* occurred in only two canyons each, but in large patches.

Species richness and beta diversity

Canyons ranged from 4 to 15 species in initial richness, and added between 5 and 20 new species by the resurvey (Table 3). These differences did not obviously correspond to the area surveyed within each canyon (Table 3). The Sørensen dissimilarity index dropped slightly from the initial (0.74) to the resurvey (0.63) but remained relatively high. Dissimilarity predominately resulted from species turnover between canyons (initial: 0.61, resurvey: 0.51) rather than nestedness (initial: 0.14, resurvey: 0.12). In 1994–1996, canyon species similarity roughly matched geographic proximity (Fig. 4a). This association mostly disappeared by 2010–2012 (Fig. 4b).

Many species remained rare in the resurvey. Of the 39 species observed in at least one survey, 11 (28.2%) were not found or were present in only a single canyon in 2010–2012 (Supplementary Information, Table S5). Fifteen (38.5%) were recorded on a total of 5000 m^2 or less, and 10 (25.6%) on less than 500 m^2 . The least common species included four endemics: *Ceanothus megacarpus* subsp. *insularis* (shrub),

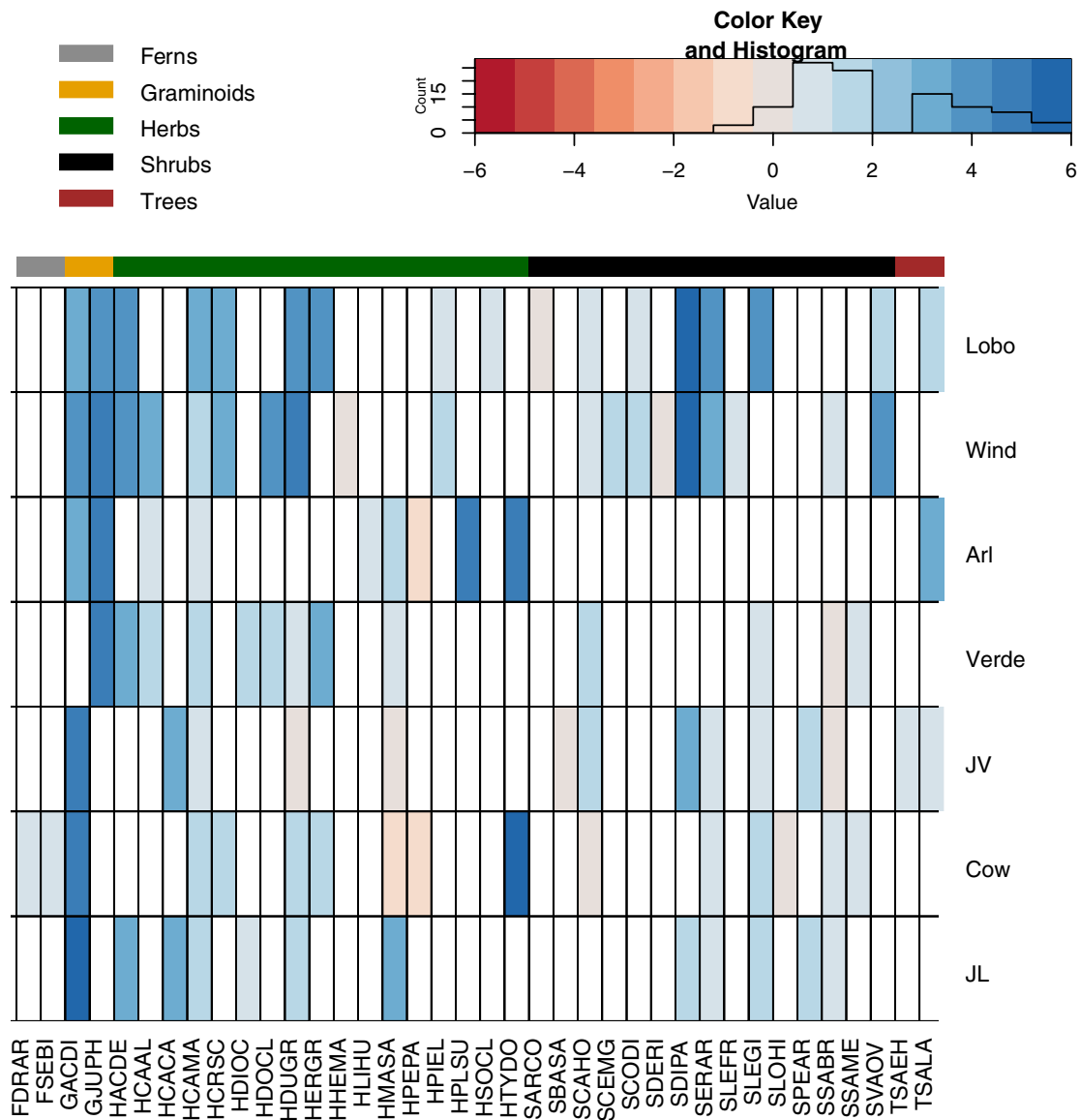


Fig. 2 Change in abundance category between the initial (1994–1996) and second (2010–2012) survey, by species (horizontal axis) and canyon (vertical axis). Species are organized by life history, from left to right. Life history is also designated by letter at the beginning of each species code (F=fern, G=graminoid, H=herbaceous, S=shrub, T=tree). Full species names for each code can be found in Supplementary Infor-

mation, Table S1. From top to bottom, the canyons are Arlington (Arl), Lobo, Windmill (Wind), Johnson's Lee (JL), Verde, Jolla Vieja (JV) and Cow. White boxes indicate either that the species was not found in that canyon or that abundance data were not available for some occurrences at one or both surveys (see Supplementary Information, Table S5 for a summary of missing records)

Dendromecon harfordii (shrub), *Plantago subnuda* (perennial herb) and *Solanum clokeyi* (perennial herb). In addition, 11 of the 29 species not found during either survey were endemic (Supplementary Information, Table S6).

A post-hoc analysis was used to check whether differences in sampling days and numbers of researchers might have affected comparisons between 1994–1996 and 2010–2012. We randomly simulated a resurvey with the same number of days (11) as the initial one and limited to records collected by the two primary

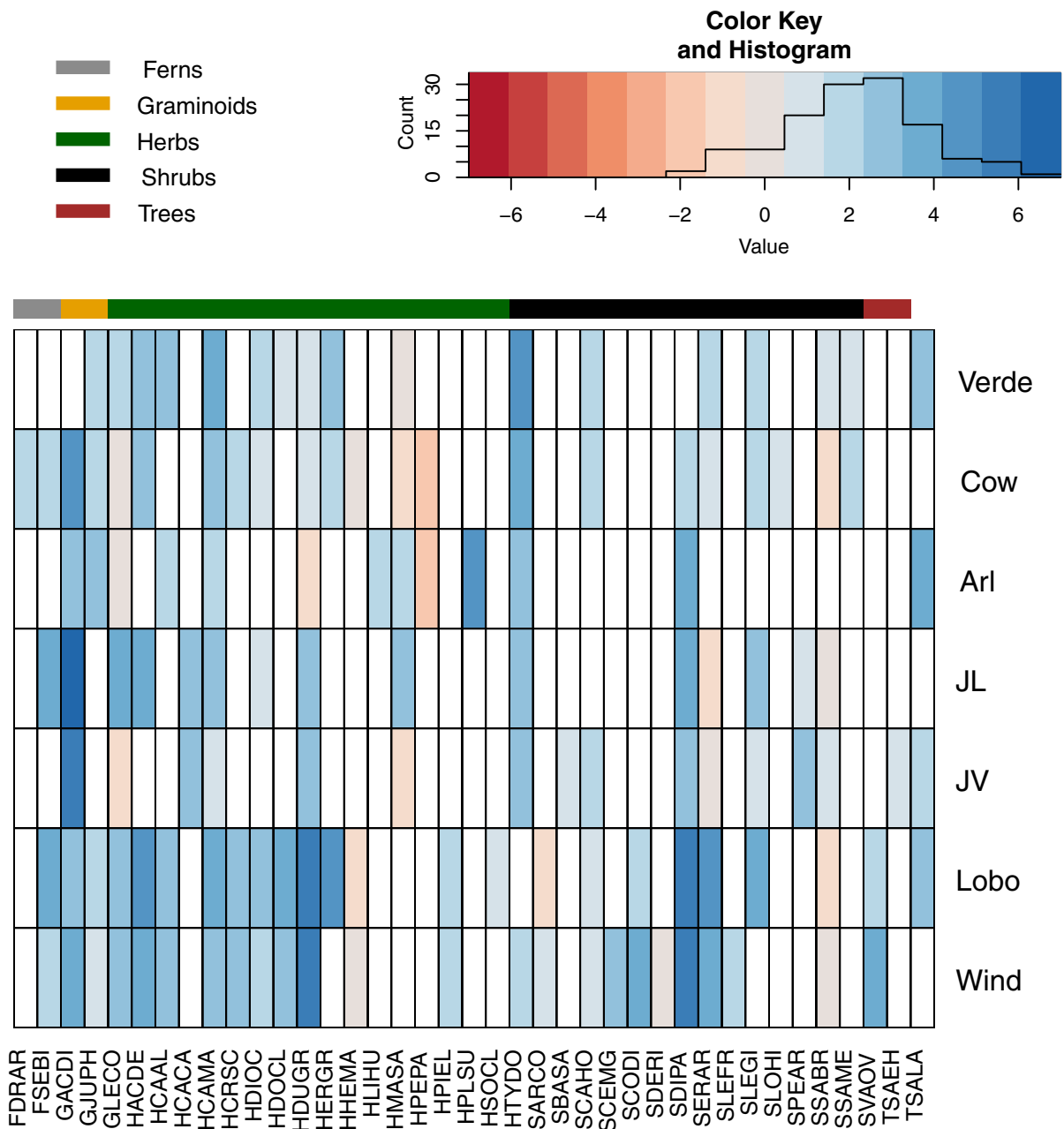


Fig. 3 Change in area category between the initial (1994–1996) and second (2010–2012) survey, by species (horizontal axis) and canyon (vertical axis). Species are organized by life history, from left to right. Life history is also designated by letter at the beginning of each species code (F=fern, G=graminoid, H=herbaceous, S=shrub, T=tree). Full species names

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researchers (65.7% of total). In 10,000 replicate subsamples using these conservative assumptions, none yielded as few species or species-canyon occurrences

as the initial survey (21 species, 54 occurrences; mean \pm SD for simulation: 34.3 ± 2.5 species, 78.9 ± 8.1 occurrences).

Table 2 The 14 species that increased in area most, measured by the sum of categorical abundance measures across all canyons where the species was observed. Changes in categorical abundance are also shown for all records

Code	Species	Life history	Endemic	Canyons initial	Canyons resurvey	Change area	Change abundance	Missing counts
ACDI	<i>Stipa diegoense</i>	Graminoid	No	0	6	28	26	0
DIPA	<i>Diplacus parviflorus</i>	Shrub	Yes	2	6	25	23	2
TYDO	<i>Typha domingensis</i>	Herbaceous	No	2	6	20	37	5
CAMA	<i>Calystegia macrostegia</i> ssp. <i>macrostegia</i>	Herbaceous	Yes	4	7	20	13	0
ACDE	<i>Acmispon dendroideus</i> var. <i>dendroideus</i>	Herbaceous	Yes	1	5	19	17	1
DUGR	<i>Dudleya greenii</i>	Herbaceous	Yes	5	7	19	14	1
LEGI	<i>Leptosyne gigantea</i>	Shrub	No	4	5	12	10	0
SALA	<i>Salix lasiolepis</i>	Tree	No	0	5	12	8	1
SEBI	<i>Selaginella bigelovii</i>	Fern	No	0	4	12	1	3
ERAR	<i>Eriogonum arborescens</i>	Shrub	Yes	4	6	11	11	1
CAAL	<i>Calochortus albus</i>	Herbaceous	No	0	4	11	10	1
LECO	<i>Leymus condensatus</i>	Graminoid	No	4	7	11	9	9
JUPH	<i>Juncus phaeocephalus</i>	Graminoid	No	1	5	10	24	1
ERGR	<i>Eriogonum grande</i> var. <i>rubescens</i>	Herbaceous	Yes	2	3	10	9	0

Missing counts indicate the total number of canyons where some occurrences were missing abundance data, summed over both surveys

Discussion

Our results illustrate that island plant communities can show rapid initial positive responses within the first 15 years after exotic herbivore removal, even without additional active restoration. Landsat data similarly show a 68.3% decline in bare ground and corresponding increase in shrubland on SRI between 1989 and 2015 (Summers et al. 2019). On Santa Cruz Island, bare ground was 30% lower and woody cover 23% higher nearly 30 years after sheep removal (Beltran et al. 2014). Native vegetative cover has steadily

increased on an Australian island over ten years since sheep removal (van Dongen et al. 2019). Yet community cover measures do not fully capture how herbivore removal affects a diversity of island plant species. We found substantial gains across many taxa, including rare or endemic species of high conservation concern. Effects were apparent within 15 years after control efforts began, even though final eradication of deer and elk was not yet complete (McEachern et al. 2016). Benefits were consistent across response measures, including number of canyons occupied, area, abundance, and species richness.

This high degree of passive initial recovery is encouraging and demonstrates the substantial potential payoffs of exotic herbivore eradication. Still, the baseline level of disturbance was extremely high when removals began. More than 80% of target canyon species were not detected in the initial survey, and occurrences mostly consisted of small patches with fewer than 10 individuals. Records from the initial survey regularly noted that native plants were restricted to areas inaccessible to grazers, such as steep canyon walls, ledges, and cliff faces. Soil erosion and gullying remain widespread 25 years after exotic eradication began (Davidson et al. 2019). More than 60% of occurrence records in the resurvey

Table 3 Species richness of target taxa in each canyon for both the initial and resurveys

Canyon	Area (ha)	Initial richness	Resurvey richness	Change
Wind	32.59	5	24	19
Jolla Vieja	42.4	10	16	6
Lobo	56.25	4	24	20
Verde	57.45	9	17	8
Cow	59.65	15	20	5
Arlington	80.12	6	12	6
Johnson's Lee	102.4	6	15	9

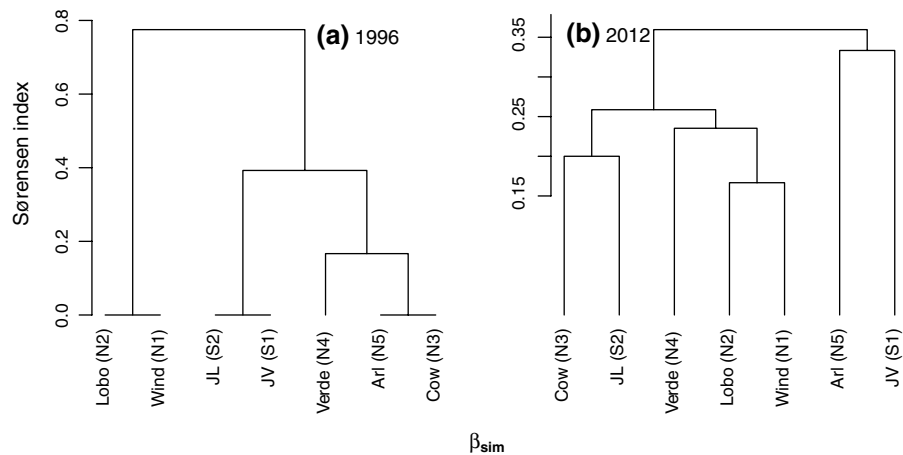


Fig. 4 Dendrograms for canyon similarity, using presence-absence data for both (a) the initial survey (1994–1996) and (b) resurvey (2010–2012). Plots were generated based on species turnover (β_{sim}) using the R package betapart, with the Sørensen index. Letter labels indicate which side of the island each canyon is located on (N=north, S=south). Numbers

indicate the east to west order of canyons on their respective sides (1–5 for the north side, 1–2 for the south side). North side canyons include Windmill (Wind), Lobo, Cow, Verde and Arlington (Arl). South side canyons include Johnson’s Lee (JL) and Jolla Vieja (JV)

identified nearby erosion as a potential threat. Steep slopes in particular have recovered woody cover more slowly (Summers et al. 2019). Introduced goats on Mediterranean islands similarly initiate a process of soil erosion and loss that continues even after their removal (Gizicki et al. 2018). Promisingly, two riparian specialists, *Juncus phaeocephalus* (graminoid) and *Typha domingensis* (herbaceous), were among the most rapidly expanding species. Growth in riparian vegetation should slow water velocities and increase sediment deposition, promoting long-term recovery of ecosystem dynamics (Supplementary Information, Fig. S1).

A majority of the 39 taxa detected in at least one survey remained rare in 2010–2012, with one missing and a number found only in small patches at low abundances (Supplementary Information, Table S5). Given the large survey area (431 hectares), this suggests that many of these species remain at high risk. Moreover, 29 of the original 68 canyon target taxa were missing from both surveys. If these species were included as zeros, the estimates of mean area and abundance change would be considerably lower, although still clearly positive. Some of the 29 missing taxa were small herbaceous species that may have been hard to detect during drier spring and summer months (Supplementary Information, Table S6). Still,

about a third were shrubs and trees. Five of 7 target fern species were not found; these taxa typically occur in moist seeps and canyon bottoms heavily impacted by pig and elk rooting and wallowing (McEachern, *per. obs.*). Several missing taxa were federally listed as endangered (*Boechea hoffmannii*, *Berberis pinnata* ssp. *insularis*) or threatened (*Crocotanthemum greenii*) species. The two missing trees were previously documented on SRI from only a single historic occurrence each (*Populus trichocarpa* and *Quercus engelmannii*).

Graminoids experienced by far the strongest gains but represented a small number of native species (N=3). SRI likely was dominated by shrub communities before ranching, and shrubs responded significantly less than herbaceous plants and grasses (Table 1, Table 2). These differences match the prediction that long-lived, slower-growing species with more limited recruitment will need longer to recover after herbivore control (Hamann 1993). For example, Van Vuren (2014) found shrub recovery on Santa Cruz Island dominated by less woody, palatable species such as *Eriogonum arborescens* and *Acmispon dendriodeus*, taxa that also rebounded quickly on SRI.

Our 2010–2012 resurvey took place only a little over a decade after cattle removal, and before elk and deer were fully eradicated. Evidence of herbivore

activity such as browsing, trampling, or tracks still was noted in nearly 20% of resurvey occurrences (Supplementary Information, Table S7). Persistence of older disturbances likely explains many of these observations, but continued presence of some elk and deer through 2011 also may have played a role. Regardless, it is possible that the early positive responses we observed might not be sustained now that all herbivores have been removed. For example, some authors have raised concerns that complete removal of island herbivores could benefit exotic plants, leading to suppression of native species (Zavaleta et al. 2001). Klinger et al. (2002) found that initial gains in herbaceous plant diversity after herbivore removal on Santa Cruz Island disappeared as exotic grasses rebounded. The dramatic increases we observed in native graminoids reinforce that exotic grasses could similarly experience strong release from herbivores. Encroachment by exotic plants was noted as a potential threat in 17% of resurvey records (Supplementary Information, Table S7). Spread of non-native plants may prove an even greater impact in non-canyon habitats not included in our analysis, such as grasslands. Still, anecdotal observations since 2012 support that native perennials have continued to re-establish in canyons and other habitats on SRI (McEachern and Thomson, *pers. obs.*). Evaluation with ongoing vegetation monitoring is critical to determine the longer-term effects of herbivore removal.

Another important qualification on our findings is the difficulty of ensuring comparable effort between the two surveys. The 2010–2012 survey involved both more days and more data collectors. This difference resulted from the need to map a much larger number of occurrences, not additional search effort (see Methods). Reassuringly, post-hoc simulations support that these findings are robust to effects of sampling days or researcher numbers. Moreover, higher cover (Summers et al. 2019) reduced visibility compared to the initial survey (Supplementary Fig. S1). Total cover recorded on five long-term monitoring transects in canyon riparian areas on SRI increased by $38.9 \pm 18.8\%$ between the initial and resurvey periods, primarily because of growth in herbaceous cover ($56.5 \pm 22.8\%$). Use of GPS also facilitated more precise mapping, reducing occurrence areas relative to drawing of broad distributions on paper in 1994–1996. These issues seem likely if anything to

have biased towards lower detectability and reduced area estimates in the resurvey.

We observed a surprisingly large number of changes from absent to present within canyons, even for shrubs and trees (Table 1). Many of these apparent colonizations likely resulted from local regeneration of populations present in the initial survey but below detection threshold, rather than dispersal into unoccupied habitat. Many plants were browsed and trampled down to the soil surface in the initial survey, making identification difficult (McEachern, *per. obs.*). Research from other islands supports that some individual trees and shrubs can survive up to 100 years under intense herbivore disturbance, sustaining populations for a period of time without recruitment (Allen et al. 1994). Some longer-lived species that may have likewise persisted on SRI now are successfully establishing seedlings, but others show little evidence of recruitment. Absence of a seed bank or dispersers might slow return of shrubs (Erskine Ogden and Rejmánek 2005). Poor seedling survival due to unfavorable abiotic conditions and competition from exotic species could also limit recovery (Bellingham et al. 2010; Yelenik and Levine 2010; Woolsey et al. 2019; Yelenik 2019).

Substantial spatial heterogeneity in species composition among canyons led to high beta diversity. Dissimilarity resulted primarily from species turnover rather than nestedness, as is common in most communities (Soininen et al. 2018). Turnover between canyons might reflect habitat heterogeneity, dispersal processes or disturbance history. Disturbance can increase beta diversity even when the environment becomes more homogeneous, because of spatial patchiness in effects or neutral sampling processes that strengthen if most species in the community are rare (Socolar et al. 2016). While geographic proximity roughly paralleled floristic similarity in the initial survey, any pattern had mostly disappeared by the resurvey (Fig. 4). Given that many of the new ‘presences’ probably represent recoveries of existing populations, dispersal limitation seems a less likely explanation for spatial correlation among canyons. Instead, this may indicate variability in disturbance history coupled with abiotic conditions and micro-climate. For example, Lobo and Windmill canyons may show greater similarity because both were predominately sampled in upper reaches that extend to higher elevation

(Fig. 1, Fig. 4). Whatever the cause, smaller-scale sampling typical of most studies would not have effectively detected large-scale changes in species richness or the strength of responses across taxa (Socolar et al. 2016). Similarly, Erskine Ogden and Rejmánek (2005) found that a small-scale pilot study did not predict landscape-scale responses to exotic fennel control on Santa Cruz Island.

Conclusion

Our findings document substantial potential benefits of removing exotic herbivores from an oceanic island, not just for dominant plant species or community cover but also a diversity of rare taxa. They also support that vertebrate herbivore control can yield important and rapid gains even where total eradication is not possible or resources for active restoration are unavailable. The observed increases in area and abundance may help buffer some taxa against high extinction risk characteristic of very small populations. At the same time, these results reinforce the devastating effects of introduced herbivores on island plants. Even with dramatic early responses by many native species, the majority of target taxa remain rare. Further habitat management may be needed to achieve their recovery. Given that island species are vulnerable to multiple threats (Harter et al. 2015), prioritizing achievable goals like exotic species removal may be an effective approach to reducing near-term loss of endemic diversity.

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Oliver: Data Curation, Investigation. A. Tucker: Data Curation, Investigation.

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Declaration

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Table S1. Species on the canyon search list and their characteristics Code= species code used in figures; Endemic= whether endemic to California Channel Islands Merged= taxonomic group merged with for analysis; Life cycle- perennial or annual; Life history= fern, graminoid, herbaceous, shrub or tree; Subtype= any additional life form information; Riparian= riparian habitat specialist.

Taxonomic names according to Jepson Flora Project (eds.) 2020, Jepson eFlora, <https://ucjeps.berkeley.edu/eflora/>, accessed on August 03, 2020.

Species	Subspecies/variety	Code	Endemic	Merged	Life cycle	Life history	Subtype	Riparian
<i>Acmispon dendroideus</i>	var. <i>dendroideus</i>	ACDE	yes		perennial	herb		
<i>Adiantum capellis-veneris</i>		ADCA			perennial	fern		
<i>Arctostaphylos confertiflora</i>		ARCO	yes	with ARTO	perennial	shrub		
<i>Arctostaphylos tomentosa</i>		ARTO	yes		perennial	shrub		
<i>Athyrium felix-femina</i>		ATFE			perennial	fern		
<i>Baccharis salicifolia</i>		BASA			perennial	shrub		yes
<i>Berberis pinnata</i>	ssp. <i>insularis</i>	BEPI	yes		perennial	shrub		
<i>Boechera hoffmannii</i>		BOHO	yes		perennial	herb		
<i>Boschniakia strobilacea</i>		BOST			perennial	herb	parasitic	
<i>Calochortus albus</i>		CAAL			perennial	herb	geophyte	
<i>Calochortus catalinae</i>		CACA			perennial	herb	geophyte	
<i>Calystegia macrostegia</i>	ssp. <i>macrostegia</i>	CAMA	yes		perennial	herb	vine	
<i>Castilleja hololeuca</i>		CAHO	yes		perennial	shrub		
<i>Ceanothus arboreus</i>	var. <i>glaber</i>	CEAG	yes		perennial	shrub		
<i>Ceanothus megacarpus</i>	ssp. <i>insularis</i>	CEMG	yes		perennial	shrub		
<i>Cercocarpus betuloides</i>	var. <i>blanchae</i>	CEBL			perennial	shrub		
<i>Chorizanthe wheeleri</i>		CHWH	yes		annual	herb		
<i>Comarostaphylis diversifolia</i>	ssp. <i>planifolia</i>	CODI			perennial	shrub		
<i>Crocانthemum greenei</i>		CRGR	yes		perennial	herb		
<i>Crocانthemum scoparium</i>		CRSC			perennial	herb		
<i>Dendromecon harfordii</i>		DERI	yes		perennial	shrub		
<i>Dichondra occidentalis</i>		DIOC			perennial	herb		
<i>Diplacus parviflorus</i>		DIPA	yes		perennial	shrub		
<i>Dodecatheon clevelandii</i>	ssp. <i>insulare</i>	DOCL			perennial	herb		
<i>Dryopteris arguta</i>		DRAR			perennial	fern		
<i>Dudleya candelabrum</i>		DUCN	yes	with DUGR	perennial	herb	succulent	

Species	Subspecies/variety	Code	Endemic	Merged	Life cycle	Life history	Subtype	Riparian
<i>Dudleya greenei</i>		DUGR	yes		perennial	herb	succulent	
<i>Dudleya greenei</i> X <i>candelabrum</i>		DGXC	yes	with DUGR	perennial	herb	succulent	
<i>Erigeron sanctarum</i>		ERSA			perennial	herb		
<i>Eriogonum arborescens</i>		ERAR	yes		perennial	shrub		
<i>Eriogonum cinereum</i>		ERCN			perennial	shrub		
<i>Eriogonum grande</i>	var. <i>rubescens</i>	ERGR	yes		perennial	herb		
<i>Eschscholzia ramosa</i>		ESRA	yes		perennial	herb		
<i>Galium angustifolium</i>	ssp. <i>foliosum</i>	GAAN	yes		perennial	herb		
<i>Galium californicum</i>	ssp. <i>miguelense</i>	GAMI	yes		perennial	herb		
<i>Galium nuttalii</i>	ssp. <i>insulare</i>	GANU	yes		perennial	herb		
<i>Hazardia detonsa</i>		HADE	yes		perennial	shrub		
<i>Heuchera maxima</i>		HEMA	yes		perennial	herb		
<i>Jepsonia malvifolia</i>		JEMA	yes		perennial	herb		
<i>Juncus phaeocephalus</i>		JUPH			perennial	graminoid	rush	yes
<i>Lepechinia fragrans</i>		LEFR			perennial	shrub		
<i>Leptosyne gigantea</i>		LEGI			perennial	shrub		
<i>Leymus condensatus</i>		LECO			perennial	graminoid		
<i>Lilium humboldtii</i>	ssp. <i>ocellatum</i>	LIHU			perennial	herb	geophyte	
<i>Lonicera hispidula</i>		LOHI			perennial	shrub		
<i>Malacothrix saxatilis</i>	var. <i>implicata</i>	MASA	yes		perennial	herb		
<i>Minuartia douglasii</i>		MIDG			annual	herb		
<i>Pellaea mucronata</i>		PEMU			perennial	fern		
<i>Peritoma arborea</i>		PEAR			perennial	shrub		
<i>Petunia parviflora</i>		PEPA			annual	herb		
<i>Piperia elongata</i>		PIEL			perennial	herb		
<i>Plantago subnuda</i>		PLSU	yes		perennial	herb		yes
<i>Polystichum munitum</i>		POMU			perennial	fern		
<i>Populus trichocarpa</i>		POTR			perennial	tree		yes
<i>Quercus englemannii</i>		QUEN			perennial	tree		
<i>Rhamnus pirifolia</i>		RHPI			perennial	shrub		
<i>Rosa californica</i>		ROCA			perennial	shrub		

Species	Subspecies/variety	Code	Endemic	Merged	Life cycle	Life history	Subtype	Riparian
<i>Rubus ursinus</i>		RUUS			perennial	shrub		
<i>Salix exigua</i>	var. <i>hindsiana</i>	SAEH			perennial	tree		yes
<i>Salix lasiolepis</i>		SALA			perennial	tree		yes
<i>Salvia brandegeei</i>		SABR			perennial	shrub		
<i>Sambucus mexicana</i>		SAME			perennial	shrub		
<i>Selaginella bigelovii</i>		SEBI			perennial	fern		
<i>Senecio aphanactis</i>		SEAP			annual	herb		
<i>Solanum clokeyi</i>		SOCL	yes		perennial	herb		
<i>Stipa diegoense</i>		ACDI			perennial	graminoid		
<i>Stylomecon heterophylla</i>		STHE			annual	herb		
<i>Thysanocarpus laciniatus</i>		THLA			annual	herb		
<i>Typha domingensis</i>		TYDO			perennial	herb		yes
<i>Vaccinium ovatum</i>		VAOV			perennial	shrub		
<i>Woodwardia fimbriata</i>		WOFI			perennial	fern		

Table S2. Data on site and community characteristics collected for rare plant occurrences at each survey. Entries annotated with * indicate measures estimated by surveyors in 1994-1996, and recorded by GPS units in 2010-2010.

Description of measure	Survey
Category of substrate: Soil, Rock, Mud, Litter	Both
Description of substrate	Both
Estimated minimum slope, in numeric degrees	Both
Estimated maximum slope, in numeric degrees	Both
Estimated minimum elevation	Initial*
Estimated maximum elevation	Initial*
Information on the general habitat	Both
Where known, a description of the microhabitat	Both
Comments on plant condition, e.g. phenology, apparent health, size, fecundity, dormancy	Both
Comments about threats to the plants at this site	Both
Percent plants not flowering/fruitleing	2010-2012
Percent plants flowering	2010-2012
Percent plants fruitleing	2010-2012
List of dominant plants in area	2010-2012
List of plants neighboring target species	2010-2012
Plant community classification, Channel Islands National Park system	2010-2012
List of dominant plants in area	2010-2012
List of plants neighboring target species	2010-2012
Aspect	2010-2012
Site quality, scored as fair, good or excellent	2010-2012
Notes on disturbance (erosion, herbivore use, exotic plants)	2010-2012
Notes on the condition of the physical environment	2010-2012

Table S3. Canyon/species occurrences where at least some abundance estimates were missing; these records were excluded from all analyses of abundance. Code= species code used in figures; Life history= F (fern), G (graminoid), H (herbaceous), S (shrub), T (tree); Canyon; Presence= present in canyon for initial survey, resurvey or both; Affected surveys= data missing for initial survey, resurvey or both.

Species	Subspecies/variety	Code	Life history	Canyon	Presence	Affected surveys
<i>Selaginella bigelovii</i>		SEBI	F	JL	Resurvey	Resurvey
<i>Selaginella bigelovii</i>		SEBI	F	Lobo	Resurvey	Resurvey
<i>Selaginella bigelovii</i>		SEBI	F	Wind	Resurvey	Resurvey
<i>Juncus phaeocephalus</i>		JUPH	G	Cow	Both	Initial
<i>Leymus condensatus</i>		LECO	G	Arl	Both	Both
<i>Leymus condensatus</i>		LECO	G	JV	Both	Both
<i>Leymus condensatus</i>		LECO	G	Cow	Both	Resurvey
<i>Leymus condensatus</i>		LECO	G	Verde	Both	Initial
<i>Leymus condensatus</i>		LECO	G	JL	Resurvey	Resurvey
<i>Leymus condensatus</i>		LECO	G	Lobo	Resurvey	Resurvey
<i>Leymus condensatus</i>		LECO	G	Wind	Resurvey	Resurvey
<i>Acmispon dendroideus</i>	var. <i>dendroideus</i>	ACDE	H	Cow	Both	Initial
<i>Calystegia macrostegia</i>	ssp. <i>macrostegia</i>	CAAL	H	Lobo	Resurvey	Resurvey
<i>Dodecatheon clevelandii</i>		DOCL	H	Lobo	Resurvey	Resurvey
<i>Dodecatheon clevelandii</i>	ssp. <i>insulare</i>	DIOC	H	Cow	Resurvey	Resurvey
<i>Dodecatheon clevelandii</i>	ssp. <i>insulare</i>	DIOC	H	Lobo	Resurvey	Resurvey
<i>Dodecatheon clevelandii</i>	ssp. <i>insulare</i>	DIOC	H	Wind	Resurvey	Resurvey
<i>Dudleya greenei</i>		DUGR	H	Arl	Both	Initial
<i>Heuchera maxima</i>		HEMA	H	Lobo	Both	Resurvey
<i>Heuchera maxima</i>		HEMA	H	Cow	Both	Initial
<i>Typha domingensis</i>		TYDO	H	JV	Both	Both
<i>Typha domingensis</i>		TYDO	H	JL	Both	Initial
<i>Typha domingensis</i>		TYDO	H	Wind	Resurvey	Resurvey
<i>Typha domingensis</i>		TYDO	H	Verde	Resurvey	Resurvey
<i>Arctostaphylos confertiflora</i>		ARCO	S	Wind	Both	Resurvey
<i>Diplacus parviflorus</i>		DIPA	S	Arl	Both	Initial

Species	Subspecies/variety	Code	Life history	Canyon	Presence	Affected surveys
<i>Diplacus parviflorus</i>		DIPA	S	Cow	Both	Initial
<i>Eriogonum arborescens</i>		ERAR	S	Verde	Both	Resurvey
<i>Salvia brandegeei</i>		SABR	S	Lobo	Both	Resurvey
<i>Salix lasiolepis</i>		SALA	T	Verde	Resurvey	Resurvey

Table S4. Categories defined for analyses of change in area occupied and abundance for target species. Units are in m² for area and numbers of individuals for abundance.

Measure	Lower bound	Upper bound	Category
Area	0	100	1
Area	101	500	2
Area	501	2500	3
Area	2501	12500	4
Area	12501	62500	5
Area	62501	312500	6
Area	312501	NA	7
Abundance	1	10	1
Abundance	11	50	2
Abundance	51	250	3
Abundance	251	1250	4
Abundance	1251	6250	5
Abundance	6251	31250	6
Abundance	31251	NA	7

Table S5. Summary of survey results for all 39 target canyon species found in at least one survey. Code= species code used in figures; Life history= F(fern), G (graminoid), H (herbaceous), S (shrub) or T (tree); Endemic= whether endemic to California Channel Islands; Canyons initial= number canyons present in initial survey; Canyons resurvey= number canyons present in resurvey; Area initial= total area in m² for initial survey; Area resurvey= total area in m² for resurvey; Number initial= total number individuals in initial survey; Number resurvey= total number individuals in resurvey; Miss initial= proportion of canyons with missing abundance data in initial survey; Miss resurvey= proportion of canyons with missing abundance data in resurvey.

Species	Subspecies/ variety	Code	Life history	Endemic	Canyons initial	Canyons resurvey	Area initial	Area resurvey	Number initial	Number resurvey	Miss initial	Miss resurvey
<i>Acmispon dendroideus</i>	var. <i>dendroideus</i>	ACDE	H	Yes	1	5	78	43124	NA	1258	1	0
<i>Arctostaphylos confertiflora</i>		ARCO	S	Yes	2	2	61917	103872	110	6274	0	0.5
<i>Baccharis salicifolia</i>		BASA	S		1	1	78	156	1	2	0	0
<i>Calochortus albus</i>		CAAL	H		0	4	0	5088	0	621	NA	0.25
<i>Calochortus catalinae</i>		CACA	H		0	2	0	3236	0	293	NA	0
<i>Calystegia macrostegia</i>	ssp. <i>macrostegia</i>	CAMA	H	Yes	4	7	938	36680	37	510	0	0
<i>Castilleja hololeuca</i>		CAHO	S	Yes	2	5	625	13684	123	337	0	0
<i>Ceanothus megacarpus</i>	ssp. <i>insularis</i>	CEMG	S	Yes	0	1	0	736	0	11	NA	0
<i>Comarostaphylis diversifolia</i>	ssp. <i>planifolia</i>	CODI	S		2	2	156	21467	19	413	0	0
<i>Crocanthemum scoparium</i>		CRSC	H		0	3	0	2131	0	403	NA	0
<i>Dendromecon harfordii</i>		DERI	S	Yes	1	1	78	160	5	5	0	0
<i>Dichondra occidentalis</i>		DIOC	H		0	5	0	1758	0	34	NA	0.6
<i>Diplacus parviflorus</i>		DIPA	S	Yes	2	6	234	312308	40	41721	1	0
<i>Dodecatheon clevelandii</i>	ssp. <i>insulare</i>	DOCL	H		0	3	0	10848	0	7520	NA	0.33
<i>Dryopteris arguta</i>		DRAR	F		0	1	0	156	0	2	NA	0
<i>Dudleya greenei</i>		DUGR	H	Yes	5	7	22904	254399	1604	16087	0.20	0
<i>Eriogonum arborescens</i>		ERAR	S	Yes	4	6	16965	48341	201	1807	0	0.17
<i>Eriogonum grande</i>	var. <i>rubescens</i>	ERGR	H	Yes	2	3	1094	61194	121	4523	0	0
<i>Heuchera maxima</i>		HEMA	H	Yes	3	3	34114	13695	500	966	0.33	0.33
<i>Juncus phaeocephalus</i>		JUPH	G		1	5	156	3857	NA	22222	1	0
<i>Lepechinia fragrans</i>		LEFR	S		0	1	0	391	0	5	NA	0
<i>Leptosyne gigantea</i>		LEGI	S		4	5	1994	48103	83	1257	0	0
<i>Leymus condensatus</i>		LECO	G		4	7	27794	45401	16	3634	0.75	0.86
<i>Lilium humboldtii</i>	ssp. <i>ocellatum</i>	LIHU	H		0	1	0	156	0	5	NA	0

Species	Subspecies/ variety	Code	Life history	Endemic	Canyons initial	Canyons resurvey	Area initial	Area resurvey	Number initial	Number resurvey	Miss initial	Miss resurvey
<i>Lonicera hispidula</i>		LOHI	S		1	1	78	184	1	4	0	0
<i>Malacothrix saxatilis</i>	var. <i>implicata</i>	MASA	H	Yes	4	4	38711	141914	767	6753	0	0
<i>Peritoma arborea</i>		PEAR	S		2	2	111770	645639	267	2049	0	0
<i>Petunia parviflora</i>		PEPA	H		2	0	547	0	15	0	0	NA
<i>Piperia elongata</i>		PIEL	H		0	2	0	429	0	47	NA	0
<i>Plantago subnuda</i>		PLSU	H	Yes	0	1	0	28089	0	3150	NA	0
<i>Salix exigua</i>	var. <i>hindsiana</i>	SAEH	T		0	1	0	31	0	2	NA	0
<i>Salix lasiolepis</i>		SALA	T		0	4	0	5008	0	102	NA	0.25
<i>Salvia brandegeei</i>		SABR	S		6	6	561227	421973	5300	22187	0	0.17
<i>Sambucus mexicana</i>		SAME	S		0	2	0	313	0	6	NA	0
<i>Selaginella bigelovii</i>		SEBI	F		0	4	0	16619	0	8	NA	0.75
<i>Solanum clokeyi</i>		SOCL	H	Yes	0	1	0	78	0	1	NA	0
<i>Stipa diegoense</i>		ACDI	G		0	6	0	461763	0	32687	NA	0
<i>Typha domingensis</i>		TYDO	H		2	6	156	30382	NA	604033	1	0.50
<i>Vaccinium ovatum</i>		VAOV	S		0	2	0	11193	0	305	NA	0

Table S6. The 29 of 68 target canyon species not found in either initial or resurvey. Code= species code used in figures; Life history= F (fern), G (graminoid), H (herbaceous), S (shrub), T (tree); Endemic= whether endemic to Santa Rosa Island. Some of these species are known on SRI from only one locality (QUEN) or historic collection (BEPI). One species is not uncommon outside of the sampling area (MIDG). Many others were likely missing because of rarity/range restriction (CEBL, CHWH, ERCN, ERSA, RHPI, ROCA, WOFI). Some are both rare and may have been difficult to detect because of small size or earlier phenology (PEMU, POMU, SEAP, STHE, THLA).

Species	Subspecies/variety	Code	Life history	Endemic
<i>Adiantum capellis-veneris</i>		ADCA	F	
<i>Athyrium felix-femina</i>		ATFE	F	
<i>Pellaea mucronata</i>		PEMU	F	
<i>Polystichum munitum</i>		POMU	F	
<i>Woodwardia fimbriata</i>		WOFI	F	
<i>Boechea hoffmannii</i>		BOHO	H	Yes
<i>Boschniakia strobilacea</i>		BOST	H	
<i>Chorizanthe wheeleri</i>		CHWH	H	Yes
<i>Crocانthemum greenei</i>		CRGR	H	Yes
<i>Erigeron sanctarum</i>		ERSA	H	
<i>Eschscholzia ramosa</i>		ESRA	H	Yes
<i>Galium angustifolium</i>	ssp. <i>foliosum</i>	GAAN	H	Yes
<i>Galium californicum</i>	ssp. <i>miguelense</i>	GAMI	H	Yes
<i>Galium nuttallii</i>	ssp. <i>insulare</i>	GANU	H	Yes
<i>Jepsonia malvifolia</i>		JEMA	H	Yes
<i>Minuartia douglasii</i>		MIDG	H	
<i>Senecio aphanactis</i>		SEAP	H	
<i>Stylomecon heterophylla</i>		STHE	H	
<i>Thysanocarpus laciniatus</i>		THLA	H	
<i>Berberis pinnata</i>	ssp. <i>insularis</i>	BEPI	S	Yes
<i>Ceanothus arboreus</i>	var. <i>glaber</i>	CEAG	S	Yes
<i>Cercocarpus betuloides</i>	var. <i>blanchae</i>	CEBL	S	
<i>Eriogonum cinereum</i>		ERCN	S	

Species	Subspecies/variety	Code	Life history	Endemic
<i>Hazardia detonsa</i>		HADE	S	Yes
<i>Rhamnus pirifolia</i>		RHPI	S	
<i>Rosa californica</i>		ROCA	S	
<i>Rubus ursinus</i>		RUUS	S	
<i>Populus trichocarpa</i>		POTR	T	
<i>Quercus englemannii</i>		QUEN	T	

Table S7. Observations of habitat conditions for occurrences in 2010-2012. Each record was scored by whether soil erosion or exotic plants in the area represented potential threats, as well as on whether notes documented signs of herbivore browsing, other evidence of herbivore activity such as tracks or feces, and the presence of old herbivore trails (y=yes, n=no).

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Wind	ACDE	y	n	y	y	n
Wind	ACDE	y	n	y	n	n
Wind	ACDE	y	n	n	n	n
Wind	ACDI	y	n	n	y	y
Wind	ACDI	y	n	n	n	n
Wind	ARCO	y	n	n	n	n
Wind	ARCO	y	n	n	n	n
Wind	ARCO	y	n	n	n	y
Wind	CAAL	n	n	n	y	n
Wind	CAAL	y	n	n	n	n
Wind	CAAL	y	n	n	n	n
Wind	CAAL	y	n	n	n	n
Wind	CAHO	y	y	n	n	n
Wind	CAHO	y	n	y	y	n
Wind	CAMA	y	n	n	n	n
Wind	CEAG	y	n	n	n	n
Wind	CEMG	n	n	n	n	n
Wind	CEMG	n	n	n	n	n
Wind	CODI	y	n	n	n	n
Wind	CODI	y	n	n	n	n
Wind	CRGR	n	y	n	n	n
Wind	CRSC	n	y	n	n	n
Wind	DERI	y	n	n	n	n
Wind	DIOC	y	n	n	n	n
Wind	DIPA	n	n	n	n	y
Wind	DOCL	n	y	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Wind	DUGR	n	n	y	y	n
Wind	DUGR	y	n	n	n	n
Wind	DUGR	y	n	n	n	n
Wind	ERAR	y	n	n	n	n
Wind	ERAR	y	n	n	n	n
Wind	ERAR	y	n	n	n	n
Wind	ERAR	y	n	n	n	n
Wind	HEMA	y	n	n	n	n
Wind	HEMA	y	n	n	n	n
Wind	JUPH	n	n	n	n	n
Wind	JUPH	y	n	y	y	n
Wind	LECO	y	n	n	n	n
Wind	LEFR	n	y	n	n	n
Wind	LEFR	y	n	n	n	n
Wind	PIEL	n	n	y	n	n
Wind	PIEL	y	n	n	n	n
Wind	RUUR	y	n	n	n	n
Wind	RUUR	y	n	n	n	n
Wind	RUUR	y	n	n	n	n
Wind	SABR	n	n	n	n	n
Wind	SABR	y	n	n	n	n
Wind	SABR	y	n	n	n	n
Wind	SEBI	y	n	n	n	n
Wind	TYDO	n	n	n	n	n
Wind	VAOV	n	n	n	n	n
Wind	VAOV	y	n	n	n	n
Wind	VAOV	y	n	n	n	n
Verde	ACDE	n	n	n	n	n
Verde	ACDE	y	n	n	n	n
Verde	ACDE	y	n	n	n	n
Verde	CAAL	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Verde	CAHO	n	n	n	n	n
Verde	CAHO	y	n	n	n	n
Verde	CAHO	y	n	n	n	n
Verde	CAMA	n	n	n	y	n
Verde	CAMA	n	n	n	n	n
Verde	CAMA	y	n	y	n	n
Verde	DIOC	n	n	n	n	n
Verde	DOCL	y	n	n	y	n
Verde	DUGR	n	n	n	y	n
Verde	DUGR	n	n	n	n	n
Verde	DUGR	y	n	n	n	n
Verde	DUGR	y	n	n	n	n
Verde	DUGR	y	n	n	n	n
Verde	DUGR	y	n	n	n	n
Verde	DUGR	y	n	n	n	n
Verde	DUGR	y	n	n	n	y
Verde	ERAR	n	n	n	n	n
Verde	ERAR	y	n	n	y	n
Verde	ERAR	y	n	n	n	n
Verde	ERAR	y	n	n	n	n
Verde	ERGR	y	n	n	n	n
Verde	JUPH	n	n	n	y	n
Verde	JUPH	n	n	n	y	n
Verde	JUPH	n	n	n	y	n
Verde	JUPH	n	n	n	y	n
Verde	LECO	n	n	n	y	n
Verde	LECO	n	n	y	n	n
Verde	LECO	n	n	y	n	n
Verde	LEGI	y	n	n	y	n
Verde	LEGI	y	n	n	n	n
Verde	LEGI	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Verde	LEGI	y	n	n	n	n
Verde	MASA	n	n	n	n	n
Verde	MASA	n	n	n	n	n
Verde	MASA	n	n	n	n	n
Verde	MASA	y	n	n	n	n
Verde	MASA	y	n	n	n	n
Verde	RJUR	n	n	n	n	n
Verde	SABR	y	n	n	n	n
Verde	SABR	y	n	n	n	n
Verde	SALA	n	n	y	y	n
Verde	SALA	y	n	n	n	n
Verde	SAME	n	n	n	n	n
Verde	TYDO	n	n	n	y	n
Lobo	ACDE	y	n	n	n	n
Lobo	ACDI	y	n	n	n	n
Lobo	ARCO	y	n	n	n	n
Lobo	ARCO	y	n	n	n	n
Lobo	ARCO	y	n	n	n	n
Lobo	CAAL	y	n	n	n	n
Lobo	CAHO	y	n	n	n	n
Lobo	CAMA	y	y	n	n	n
Lobo	CAMA	y	n	n	n	n
Lobo	CEAG	y	n	n	n	n
Lobo	CEAG	y	n	n	n	n
Lobo	CODI	y	n	n	n	n
Lobo	CRGR	y	n	n	n	n
Lobo	CRSC	y	y	n	n	n
Lobo	DIOC	y	y	n	n	n
Lobo	DIOC	y	n	n	n	n
Lobo	DIPA	y	n	n	y	n
Lobo	DOCL	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Lobo	DUGR	y	n	n	n	n
Lobo	ERAR	y	n	n	n	n
Lobo	ERGR	y	n	n	n	n
Lobo	HEMA	n	y	n	n	n
Lobo	HEMA	n	n	n	n	n
Lobo	HEMA	n	n	n	n	n
Lobo	HEMA	y	n	n	n	n
Lobo	JUPH	n	y	n	n	n
Lobo	LECO	y	n	n	n	n
Lobo	LEGI	n	y	n	n	n
Lobo	PIEL	y	n	n	n	n
Lobo	RUUR	y	n	n	n	n
Lobo	SABR	y	n	n	n	n
Lobo	SALA	n	y	n	n	n
Lobo	SEBI	y	y	n	n	n
Lobo	SOCL	y	n	n	n	n
Lobo	VAOV	n	n	n	n	n
JV	ACDI	y	n	n	n	n
JV	ACDI	y	n	n	n	n
JV	ACDI	y	n	n	n	n
JV	BASA	n	n	n	n	n
JV	BASA	y	n	n	n	n
JV	CACA	n	y	n	n	n
JV	CACA	n	n	n	y	n
JV	CACA	y	y	n	n	n
JV	CAHO	n	n	n	y	n
JV	CAMA	y	n	n	n	n
JV	CAMA	y	n	n	n	n
JV	DIPA	n	n	n	y	n
JV	DUGR	y	n	y	n	n
JV	ERAR	y	n	n	y	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
JV	ISAR	y	n	n	n	n
JV	LECO	n	n	y	y	n
JV	LECO	n	n	n	n	n
JV	LECO	n	n	n	n	n
JV	LEGI	y	n	n	n	n
JV	LEGI	y	n	n	n	n
JV	LEGI	y	n	n	n	n
JV	MASA	y	n	n	n	n
JV	MASA	y	n	n	n	n
JV	MASA	y	n	n	n	n
JV	MASA	y	n	n	n	n
JV	SABR	y	n	n	n	n
JV	SABR	y	n	n	n	n
JV	SAEX	y	n	n	n	n
JV	SALA	n	n	n	n	n
JV	SALA	y	n	n	n	n
JV	TYDO	n	n	n	n	n
Jlee	ACDE	y	n	n	n	n
Jlee	ACDE	y	n	n	n	n
Jlee	ACDE	y	n	n	n	n
Jlee	ACDI	n	y	n	y	n
Jlee	ACDI	n	y	n	n	n
Jlee	ACDI	n	y	n	n	n
Jlee	ACDI	n	y	n	n	n
Jlee	CACA	n	y	n	n	n
Jlee	CACA	n	y	n	n	n
Jlee	CACA	y	y	n	n	n
Jlee	CACA	y	n	n	n	n
Jlee	CAMA	y	y	n	n	n
Jlee	CAMA	y	n	n	n	n
Jlee	CAMA	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Jlee	DIOC	y	n	n	n	n
Jlee	DIPA	y	n	n	n	n
Jlee	DIPA	y	n	n	n	n
Jlee	DUGR	n	y	n	n	n
Jlee	DUGR	y	n	n	n	n
Jlee	ERAR	y	n	n	n	n
Jlee	ERAR	y	n	n	n	n
Jlee	ERAR	y	n	n	n	n
Jlee	ISAR	n	y	n	n	n
Jlee	ISAR	y	y	n	n	n
Jlee	ISAR	y	n	n	n	n
Jlee	ISAR	y	n	n	n	n
Jlee	ISAR	y	n	n	n	n
Jlee	ISAR	y	n	n	n	y
Jlee	ISAR	y	n	n	n	y
Jlee	LECO	n	y	n	n	n
Jlee	LECO	y	n	n	y	n
Jlee	LECO	y	n	y	n	n
Jlee	LECO	y	n	n	n	n
Jlee	LECO	y	n	n	n	n
Jlee	LEGI	n	n	n	n	n
Jlee	LEGI	y	n	n	n	n
Jlee	LEGI	y	n	n	n	n
Jlee	LEGI	y	n	n	n	n
Jlee	MASA	n	n	n	n	n
Jlee	MASA	y	n	n	n	n
Jlee	MASA	y	n	n	n	n
Jlee	MASA	y	n	n	n	n
Jlee	SABR	y	y	n	n	n
Jlee	SABR	y	y	n	n	n
Jlee	SABR	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Jlee	SEBI	y	y	n	y	n
Jlee	SEBI	y	y	n	n	n
Jlee	SEBI	y	n	n	n	y
Jlee	SEBI	y	n	n	n	y
Jlee	TYDO	n	y	n	n	n
Jlee	TYDO	n	y	n	n	n
Cow	ACDE	n	y	n	n	n
Cow	ACDE	y	y	n	n	n
Cow	ACDI	n	y	n	n	n
Cow	ACDI	n	n	n	n	n
Cow	ACDI	y	n	n	n	n
Cow	CAHO	n	n	n	n	n
Cow	CAHO	n	n	n	n	n
Cow	CAHO	y	n	n	n	n
Cow	CAHO	y	n	n	n	n
Cow	CAMA	y	y	n	n	n
Cow	CRSC	y	n	n	n	n
Cow	DIOC	n	y	n	n	n
Cow	DIOC	y	n	n	n	n
Cow	DIPA	n	y	n	n	n
Cow	DIPA	n	n	n	n	n
Cow	DIPA	y	n	n	n	n
Cow	DIPA	y	n	n	n	n
Cow	DRAR	y	n	n	n	n
Cow	DUGR	y	y	n	n	n
Cow	DUGR	y	n	n	n	n
Cow	ERAR	y	n	n	n	n
Cow	ERAR	y	n	n	n	n
Cow	ERAR	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Cow	ERAR	y	n	n	n	n
Cow	ERGR	n	y	n	n	n
Cow	ERGR	y	y	n	n	n
Cow	ERGR	y	n	n	n	n
Cow	HEMA	n	y	n	n	n
Cow	HEMA	n	n	n	n	n
Cow	JUPH	n	y	n	y	n
Cow	JUPH	n	y	n	n	n
Cow	JUPH	n	n	n	n	n
Cow	JUPH	y	n	n	n	n
Cow	LECO	n	y	n	n	n
Cow	LECO	n	y	n	n	n
Cow	LECO	n	y	n	n	n
Cow	LECO	y	n	n	n	n
Cow	LECO	y	n	n	n	n
Cow	LEGI	y	n	n	n	n
Cow	LEGI	y	n	n	n	n
Cow	LEGI	y	n	n	n	n
Cow	LOHI	n	n	n	y	n
Cow	RUUR	n	n	n	n	n
Cow	RUUR	n	n	n	n	n
Cow	RUUR	n	n	n	n	y
Cow	RUUR	y	n	n	n	n
Cow	RUUR	y	n	n	n	n
Cow	SABR	n	n	n	y	n
Cow	SABR	y	y	n	n	n
Cow	SABR	y	n	n	n	n
Cow	SAME	n	y	n	n	n
Cow	SAME	n	n	n	n	n
Cow	SAME	n	n	n	n	n
Cow	SEBI	y	n	n	n	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Cow	TYDO	n	n	n	y	n
Cow	TYDO	n	n	n	n	n
Cow	TYDO	n	n	n	n	n
Arlington	ACDI	n	n	n	n	n
Arlington	ACDI	n	n	n	n	n
Arlington	CAAL	n	n	n	n	n
Arlington	CAMA	n	y	n	n	n
Arlington	CAMA	y	n	n	n	n
Arlington	DIPA	y	n	n	n	n
Arlington	DIPA	y	n	n	n	n
Arlington	DUGR	y	n	n	n	n
Arlington	DUGR	y	n	n	n	n
Arlington	JUPH	n	n	n	y	y
Arlington	JUPH	n	n	y	n	n
Arlington	JUPH	y	n	n	n	n
Arlington	LECO	y	n	n	y	n
Arlington	LECO	y	n	n	n	n
Arlington	LIHU	n	n	n	n	n
Arlington	MASA	y	n	y	y	n
Arlington	MASA	y	n	n	n	n
Arlington	PLSU	n	y	y	y	n
Arlington	PLSU	n	n	n	y	y
Arlington	PLSU	n	n	y	n	n
Arlington	RUUR	n	n	n	y	n
Arlington	SALA	n	n	y	n	n
Arlington	SALA	n	n	y	n	n
Arlington	SALA	y	n	n	n	n
Arlington	SALA	y	n	n	n	n
Arlington	TYDO	n	n	n	y	n
Arlington	TYDO	n	n	n	y	n
Arlington	TYDO	n	n	n	y	n

Canyon	Code	Erosion	Exotic plants	Browsing	Activity	Trails
Arlington	TYDO	n	n	y	n	n
Arlington	TYDO	n	n	n	n	n
Arlington	TYDO	n	n	n	n	n
Arlington	TYDO	n	n	n	n	n
Arlington	TYDO	n	n	n	n	n
Arlington	TYDO	n	n	n	n	y
Arlington	TYDO	n	n	n	n	y

(A. 1995)



(B. 2012)



Figure S1. Photographs documenting changes in vegetative cover in Arlington Canyon, between (A) 1995 and (B) 2012.