

# The response of herbaceous vegetation and endemic plant species to the removal of feral sheep from Santa Cruz Island, California

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**Abstract** From 1984 to 1998 we monitored the response of herbaceous vegetation and endemic plant species to the eradication of feral sheep from the western 90% of Santa Cruz Island, California. Total herbaceous cover increased and bare ground decreased after sheep were eradicated from the island. Alpha diversity of herbaceous vegetation reached a maximum in the two years prior to the end of eradication and the first two years after eradication, then declined. The number and relative frequency of native herbaceous species were inversely related to increased herbaceous cover and the relative frequency of alien species. The reduction in number of native species was due to alien species that already occurred in an area rather than with alien species invading the area. Thirty-three of the 43 endemic plant species on the island showed an increase in distribution and/or abundance following the eradication. New populations of two of the five rarest species on the island were discovered within seven years of the end of the eradication programme, and abundance of these two species increased. Of the other three species, the distribution and abundance of one remained unchanged while the two other species showed alarming declines. The declines of these two species were attributed to a proliferation of alien grasses and impacts from feral pigs. Because grasslands occupy almost 50% of the area of the island, the response of the herbaceous vegetation was relatively undesirable from a conservation perspective. But most of the endemic species showed positive responses, and other studies on Santa Cruz Island indicate that communities on the island that are dominated by shrubs and trees appear to be showing rapid rates of recovery from sheep impacts. A variety of outcomes can be expected to occur as a result of eradication of large numbers of grazing ungulates from islands, so eradication programmes should only be considered the first step in a long process of restoration rather than an end in themselves.

**Keywords** alien plants; eradication; feral animals; grasslands; islands; monitoring; restoration.

## INTRODUCTION

Invasions by alien species have been one of the most important forces altering biotic and abiotic processes on islands (Loope and Mueller-Dombois 1989). Predation by invasive alien animals has changed trophic structure and been a direct cause of extinction, while intense herbivory has drastically altered structure, species composition, and function of ecosystems, as well as been a major contributing factor in extinction (Savidge 1987; MacDonald *et al.* 1989). Alien plants have also modified species composition and ecosystem function (Mack and D'Antonio 1998), and although there are no documented cases of native species being driven to extinction as a direct result of interactions with alien plants, there is concern that this could eventually occur (Cronk and Fuller 1995).

Preserving or restoring native species and natural communities is one of the primary goals of virtually all invasive species control and eradication programmes. The goals are usually stated in terms of conserving or increasing diversity, although diversity is seldom explicitly defined. In situations where the decimation of an entire group of native organisms by an introduced predator is occurring (e.g. the effect of the brown treesnake *Boiga*

*irregularis* on the avifauna in Guam; Savidge 1987) the definition of diversity becomes obvious; reduction in gamma diversity is assured with extinction. However, in situations where extinction has not occurred but the relative abundance of native species is declining, diversity becomes a more complex issue. In this case eradication or control of an alien species will not affect gamma diversity, but both alpha and beta diversity can change. The desired outcome is that diversity will increase, but since most areas are invaded not just by one but by a suite of aliens (especially islands; Loope and Mueller-Dombois 1989), the question of what species are responsible for any changes in diversity becomes important.

Alien plants and animals have heavily invaded the California Channel Islands (Coblentz 1980; Van Vuren 1981; Junak *et al.* 1995). The greatest impacts have been by feral animals, primarily sheep (*Ovis aries*), goats (*Capra hircus*), and pigs (*Sus scrofa*) (Coblentz 1977, 1978, 1980; Van Vuren 1981, 1984). These impacts were especially severe on Santa Cruz Island (SCI), where sheep had been introduced in the early to mid 19<sup>th</sup> century (Van Vuren 1981). The sheep were mostly feral by the early 1870s, and more than 50,000 sheep were estimated to be on the island in the 1890s. Attempts were made in the 1900s to

control the sheep population by trapping and shooting, but the efforts were not successful (Van Vuren 1981). By the 1980s, there were an estimated 20,000 sheep on SCI (Van Vuren 1981). The density was more than double that of the maximum stocking rates of mainland sheep operations, and over one-third of the island was classified as being heavily impacted (Van Vuren 1981). This resulted in an increase in bare ground and subsequently higher erosion rates, decreased herbaceous vegetation, reduction and modification of shrub communities, and a decrease in abundance and diversity of birds (Brumbaugh 1980; Hobbs 1980; Hochberg *et al.* 1980; Minnich 1980; Van Vuren 1981).

Beginning in late 1981, The Nature Conservancy (TNC) undertook a programme to eradicate feral sheep from the western 90% of SCI that it managed. The goals of the programme were to preserve, protect, and enhance the natural systems, flora, and fauna of the island (Schuyler 1993). The eradication was completed successfully in 1988 after 36,000 sheep were shot off the western part of the island (Schuyler 1993). An estimated 1000 – 5000 sheep remained on the eastern 10% of the island (Klinger unpubl. data), so a control programme using a combination of fencing, drives, and shooting was implemented in 1989 to prevent incursions onto TNC land. An additional 4100 sheep were shot during the control programme, which continued into early 1997 (Klinger unpubl. data). During this time one band of three sheep was found 10 km from the boundary fence, but virtually all of the rest (>97%) were shot within 1 km of the fence. A small number of other groups were within 7 km of the fence, but were never resident for more than one month. The National Park Service acquired full ownership of the eastern 10% of the island in 1997, and in the next three years removed 9000 sheep from the eastern part of the island. There is cautious optimism that feral sheep no longer occur on SCI (K. Faulkner, Channel Islands National Park, pers. comm.).

In addition to the eradication and control programmes, monitoring programmes were established to evaluate the response of grassland vegetation and endemic species to the sheep eradication. A preliminary analysis (Klinger *et al.* 1994) indicated that there were changes in species com-

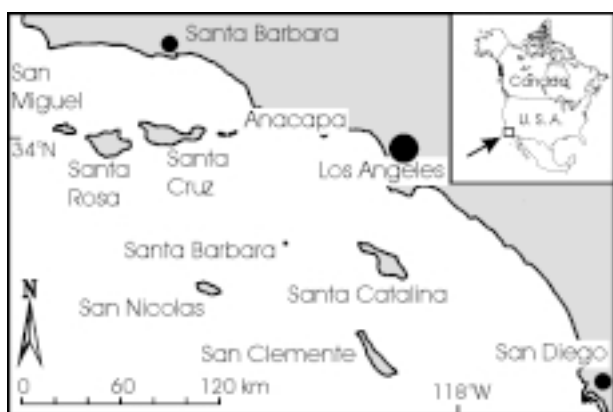
position in grasslands following eradication of the sheep, but these changes were neither systematic nor entirely predictable. In addition, removal of cattle and feral sheep was a likely trigger for the rapid expansion of fennel (*Foeniculum vulgare*), a highly-invasive herbaceous species from the Mediterranean (Brenton and Klinger 1994). In this paper we extend the prior analysis (Klinger *et al.* 1994) to examine in greater detail factors influencing changes in diversity and species composition in the grassland community, and also present data for the response of endemic species to the eradication.

## STUDY AREA

Santa Cruz Island is the largest of California's eight Channel Islands (Fig. 1). It lies approximately 40 km from the coast, and with a land area of over 250 km<sup>2</sup> it is considered the most topographically and ecologically diverse of the California islands (Junak *et al.* 1995). Like the rest of the California islands, evidence indicates that SCI has never been connected to the mainland (Vedder and Howell 1980). Consequently, it is considered a fringing rather than a continental island (Moody 2000).

Santa Cruz Island is divided along its long axis by a central valley flanked by two east-west tending mountain ranges. Six major vegetation communities occur on SCI, including grasslands, chaparral, woodland, coastal scrub, pine forest, and riparian (Philbrick and Haller 1977; Minnich 1980). A total of 650 plant taxa occur on the island, of which 26% (n=170) are alien (Junak *et al.* 1995). Despite their proximity to the mainland, the Channel Islands are known for having relatively high levels of endemism (Raven 1967). There are 43 species of island endemics on SCI, of which eight occur only on the island (Junak *et al.* 1995). Two taxa are considered to have gone extinct in the last 100 years (Junak *et al.* 1995), and although feral animals are considered to have played a role in these extinctions the degree to which they were involved is unknown.

Besides feral sheep, cattle and feral pigs have been resident on the island for >150 years. Except for a remnant herd that has been allowed to remain for historical rea-



**Fig. 1** Santa Cruz Island and the California Islands.

**Table 1** Annual rainfall recorded on Santa Cruz Island (Central Valley), 1984-1993.

Year	Rainfall (cm)
1984	25.4
1985	25.0
1986	49.5
1987	21.8
1988	24.3
1989	13.9
1990	10.0
1991	24.3
1992	32.9
1993	39.5

sons, the cattle were removed in 1988. Pigs occur across the island, and estimated numbers fluctuated from 800 to 4500 between 1991 and 1998 (Klinger unpubl. data).

The Mediterranean climate is modified by the surrounding maritime conditions. Winters are cool and wet, late summer, spring and fall are clear and warm, and early summer is foggy and cool. The 90-year average rainfall is 30.7 cm (L. Laughrin, U.C.S.B. Natural Reserve System, unpubl. data), with about 90% of the precipitation occurring from November–April. Rainfall can vary in different parts of the island, but these patterns tend to be constant from year to year. With the exception of 1986, a series of dry years occurred from 1984–1991 (Table 1).

Chumash Indians occupied SCI from approximately 7000 YBP to the early 1800s. Ranching and agriculture were the primary land use from the mid-1830s to 1977. TNC acquired an interest in the island in 1978 and full ownership of the western 90% in 1988. TNC managed the island as an ecological reserve through 1998, when it began to transfer most of the ecological management to Channel Islands National Park (CINP).

## METHODS

### Grassland Community

Data were collected from 21 plots in grassland habitat sampled in seven springs (March–May) between 1984 and 1993 (Table 2). Three to five 30 m transects were randomly selected along a 30 m baseline within each plot. Twenty 0.25 m<sup>2</sup> quadrats were spaced equidistantly along each transect, and the presence or absence of all herbaceous species was recorded within each quadrat (U.S. Forest Service 1983). Ocular estimates of the total percentage cover of live vegetation, litter (dead or dry organic material) and bare ground were made for each quadrat.

The estimated density of sheep were used to classify the plots as being in areas with high, moderate, or light impacts (Appendix 1). The density was estimated from the total number of sheep killed in an area (Schuyler 1993).

**Table 2 Sampling effort for monitoring the response of grassland vegetation to the removal of feral sheep on Santa Cruz Island, California. Sampling was not conducted in 1986, 1988, and 1990. There were twenty 0.25m<sup>2</sup> quadrats/transect.**

Year	Number of Plots	Number of Transects
1984	21	87
1985	21	87
1987	8	31
1989	10	42
1991	11	24
1992	18	54
1993	19	48

Vegetation species were initially grouped into seven different guilds: native annual grass, native annual forbs, native perennial grass, native perennial forbs, alien annual grass, alien annual forbs, and alien perennial forbs. Because alien perennial forbs and native annual grasses occurred infrequently, analyses were done for four guilds: alien grass, alien forbs (annual and perennial), native grass (annual and perennial), and native forbs.

Nested frequency data were analysed by summing the total number of occurrences across all four nests for each species for each year in each impact class. In 1987 only one plot was sampled in the medium-impact class and none in the low-impact class, so 1987 was omitted from the analysis. A disproportionately small number of low and medium-impact class plots were sampled in 1989 and 1991, so these classes were combined for analysis in all years. Differences in frequency of occurrence between guilds, impact, and years were first analysed with a log-linear test. Because the fully-saturated log-linear model was significant, Chi-square analyses were used to test differences in frequency of occurrence in different subsets of the full model. Because of the non-independence of multiple comparisons, a Bonferroni adjustment was used to guard against inflated type 1 error and determine significance of each of the comparisons (Sokal and Rohlf 1981).

The proportion of quadrats within each plot that a species occurred in was used as a measure of abundance for that species within the plot. Frequency values were summed for each species and standardised as a proportion of the total number of quadrats the species could have occurred in (Smith *et al.* 1987). Because a single number does not always adequately describe diversity patterns (Magurran 1988), we derived different indices of alpha diversity for each plot: species richness ( $N_0$ ), diversity ( $N_1$ , and  $N_2$ ; Hill 1973), and Molinari's index of evenness (Molinari 1989).  $N_1$  was calculated as  $\exp H'$  where  $H'$  is Shannon's diversity index and  $N_2$  as  $1/C$  where  $C$ =Simpson's index of concentration (Hill 1973). Because of a strong correlation between  $N_1$  and  $N_2$  ( $r = 0.98$ ) only  $N_0$  and  $N_2$  were used for analysis.

Diversity indices are known to be sensitive to sample size (Magurran 1988), and unequal sampling of the plots occurred during the study (Table 2). To test if the unequal sampling effort was leading to spurious diversity patterns, 30 runs were made for randomly-selected values of  $S$ ,  $N_2$ , and  $E$  for sample sizes ranging from 1–18 in the years 1984, 1985, 1992, and 1993. Regression analysis was then used to test if there was a correlation between the number of plots sampled and the indices of diversity. A separate analysis was done for each of the four years. There was no significant correlation between the diversity indices and the number of plots sampled for any of the years, suggesting that differences in diversity were not an artefact of sampling intensity.

Similarity in total species composition between years was analysed with the Morisita-Horn index (Magurran 1988). Cluster analysis (Gauch 1982) was used to construct

dendrograms to show relationships in species composition between years. Distances were based on chord Euclidean distance, and average linking was used as the linkage method (Sneath and Sokal 1973). Kendall's coefficient of concordance (Conover 1980) was used to test the rank abundance between years of the ten species with the greatest proportional occurrence values. Whittaker's index (Pielou 1975) was calculated for each plot and used to evaluate the turnover of species between years.

The relationship between the indices of alpha diversity and site characteristics was analysed with multiple regression procedures. Independent variables that were used in the analyses included: (1) the initial density of sheep in an area prior to the eradication, (2) the estimated density of sheep in the different years of vegetation sampling, (3) the number of years prior to and after eradication, (4) four different topographic measures (slope, aspect, elevation and cover of bare ground), and (5) two biotic variables (vegetation cover and percentage cover of organic litter). The relationship between the site characteristics, species richness, and relative frequency of the different guilds, was also analysed with multiple regression procedures. Least-squares regression was used to analyse the univariate relationship between alpha diversity and rainfall. Because least-squares and multiple regression analyses are sensitive to outliers, cases with Cook's distance  $>2.00$  were removed from the analyses. Residual plots were inspected for normality, equality of variance, independence, and linearity.

Canonical Correspondence Analysis (CCA) was used to analyse the relationship between species abundance and site characteristics. The site characteristics were the same as described above, and the year of sampling was used as a covariate (ter Braak 1995). Forward-stepping multiple regression was used to select the variables that had a significant correlation with species abundance patterns. Rare species were downweighted in the analysis.

## Endemic Species

Systematic monitoring of endemic species began in 1991. Three different approaches were used: general searches, estimates of cover and/or density in plots, and focused monitoring of five species highly restricted in distribution and/or abundance. General searches for all endemic species were conducted in 1991, 1992, 1995, and 1996. The number of observations of each species in each of 190 x 1 km<sup>2</sup> blocks was noted each year. Because only half the blocks were surveyed each year, the searches were divided into two time periods: 1991–1992, and 1995–1996. Changes in the frequency of the total number of occurrences between time periods of all endemic species were analysed with Chi-square tests.

The density and/or cover of the more-widely distributed and abundant endemic species were estimated from 1991 to 1995. One hundred plots were located from near the eastern end of TNC's property to the west end of the island. The plots were 30 m x 2 m in dimension, and cov-

ered all of the island's major geographic subdivisions except the north-west side. Sixty-one plots were initially established in the spring of 1991, but following a preliminary sample size analysis another 39 were added during the spring of 1992. Plots were stratified proportionally by the area of the five major plant communities (Minnich 1980).

Most plot locations were picked by randomly selecting a starting point on the eastern end of TNC property, then stopping every 0.8 km along a road and picking a random compass bearing and distance within 150 m from the road. This system allowed for randomness but also let field staff have a consistent reference distance to begin searching for plots. Seven plots were located along trails; a random compass bearing and distance were used to select these locations, but distance between location markers varied.

All species (endemic and non-endemic) occurring in a 2 m wide belt (1 m on either side of the tape) along the tape were recorded. The number of shrubs and trees rooted within the 2 m wide belt were counted, and cover was estimated with the point-intercept method (Bonham 1989). Cover estimates were made by vertically extending a thin metal rod at 100 points spaced equidistantly along the tape. All species of plant the rod intercepted were recorded, and the height of the tallest species intercepted by the point was also recorded. Sampling occurred from March to May each year from 1991 to 1995.

Five endemic plant species with highly restricted distribution and/or abundance were surveyed annually from 1991 to 1998. *Arabis hoffmannii* Rollins (Brassicaceae) is a herbaceous perennial with only three known populations on SCI. One population of *A. hoffmannii* is also known to occur on Santa Rosa Island. *Berberis pinnata* Lagasca subsp. *insularis* Munz (Berbericidae) is a woody perennial species that occurs on SCI and Anacapa Island. It is known to occur in three areas of SCI. *Dudleya nesiotica* A. Berger (Crassulaceae), *Malacothamnus fasciculatus* Greene subsp. *nesitoicus* Kearney (Malvaceae), and *Thysanocarpus conchuliferus* Greene (Brassicaceae) occur only on SCI. *M. fasciculatus* subsp. *nesioticus* is a woody perennial that had only one known population on the island. *T. conchuliferus* is a herbaceous annual with 14 historic locations on the island. *D. nesiotica* is a perennial succulent restricted to a 100 ha area on the western tip of SCI. Historically it had been reported to be relatively abundant within its range (Hochberg *et al.* 1980).

All individuals of both *A. hoffmannii* and *M. fasciculatus* subsp. *nesioticus* were marked, and measurements of height and counts of the number of stems, flowers and/or fruits and were made annually. Searches were made of known locations of *B. pinnata* and *T. conchuliferus*, and presence/absence noted in each location. Counts and estimates of cover of *D. nesiotica* were made in 30 x 0.25 m<sup>2</sup> quadrats from 1991 to 1995, and 70 quadrats from 1995 – 1998. Least-squares regression was used to analyse changes in stem number and/or flowers and fruits for *D. nesiotica*, *A. hoffmannii* and *M. fasciculatus* subsp. *nesioticus*.

Analyses of contingency tables and regression analyses were done with Systat 8. Canoco 4 was used to conduct the CCA (ter Braak and Smilauer 1998). All statistical tests were considered significant if  $p < 0.05$ . If  $0.10 > p > 0.05$ , the test was considered to be marginally significant.

Nomenclature follows Junak *et al.* 1995.

## RESULTS

### Grassland community

A total of 161 species occurred in the plots (Table 3). Based on the percent of all species recorded in the plots, native

**Table 3 Relative frequency of occurrence of five different guilds of plants in relation to the number and percentage of species within each guild on Santa Cruz Island, California, 1984-93.**

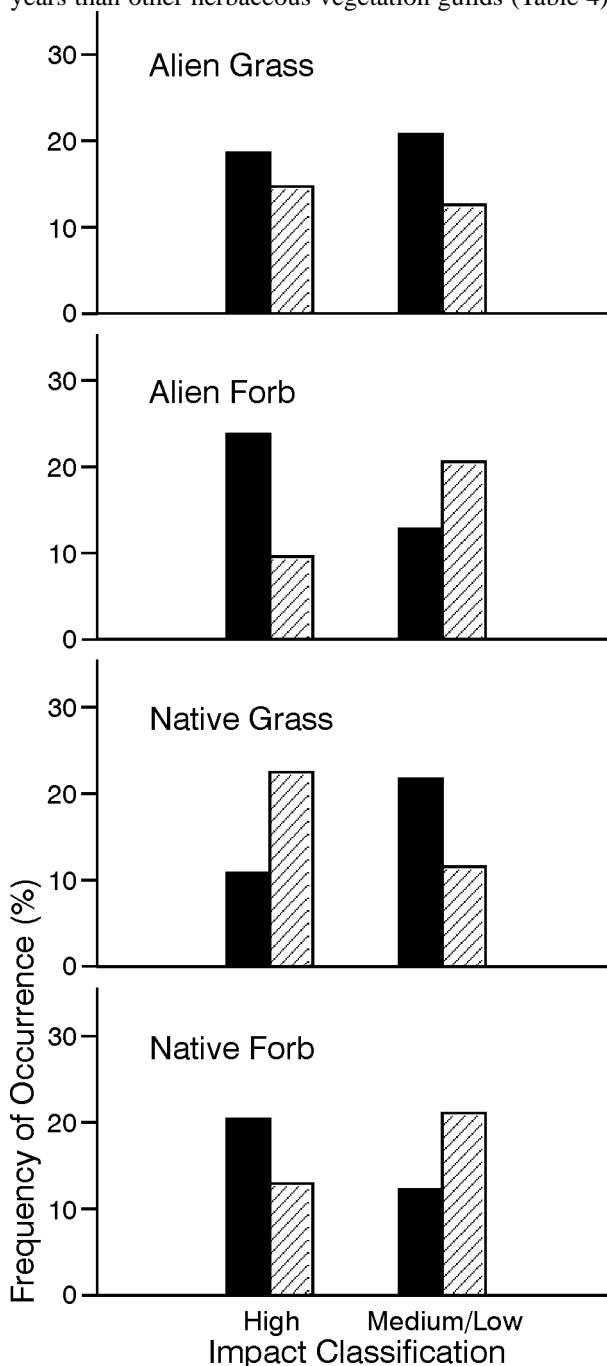
Guild	Species (N)	Species (%)	Frequency (%)
Native Forb	85	52.7	26.5
Native Grass	10	6.2	3.9
Shrubs	15	9.3	1.5
Alien Forb	34	21.1	28.5
Alien Grass	17	10.7	39.6

**Table 4 The frequency of occurrence (%) for species in four guilds of herbaceous vegetation in areas with different impacts from feral sheep on Santa Cruz Island, California. Frequency of occurrence was summed across nest sizes of 25 cm<sup>2</sup>, 625 cm<sup>2</sup>, 1250 cm<sup>2</sup> and 2500 cm<sup>2</sup> within 2500 cm<sup>2</sup> quadrats for each species in each guild. Values are the percentage of occurrences for each combination of guild, impact, and year divided by the total for the entire study.**

Year	Alien Forb	Alien Grass	Native Forb	Native Grass	Total
<b>High Impact</b>					
1984	4.2	17.6	1.5	0.1	23.5
1985	7.0	12.9	4.5	0.1	24.5
1989	2.6	7.8	1.0	0.0	11.3
1991	1.3	4.4	0.3	0.0	6.0
1992	3.7	18.9	3.9	0.5	27.0
1993	0.6	6.9	0.2	0.1	7.7
Total	19.3	68.4	11.4	0.9	100.0
<b>Medium/Low Impact</b>					
1984	1.4	20.7	0.2	0.5	22.7
1985	5.1	16.6	1.8	0.6	24.0
1989	1.4	7.5	0.2	0.1	9.2
1991	5.8	7.2	1.3	0.0	14.2
1992	6.5	13.4	2.0	0.5	22.3
1993	0.4	6.7	0.3	0.1	7.5
Total	20.4	72.0	5.7	1.8	100.0

species occurred disproportionately less than would have been expected ( $p < 0.0001$ ). Although they made up  $< 32\%$  of the species, alien forbs and grass accounted for  $>68\%$  of the frequency of occurrence of all species in the quadrats ( $p < 0.0001$ ).

Alien annual grass had significantly greater frequency of occurrence in all combinations of impact category and years than other herbaceous vegetation guilds (Table 4).



**Fig. 2 Frequency of occurrence of species within four herbaceous vegetation guilds between areas of different impact classification from feral sheep on Santa Cruz Island, California, 1984-1993. Percentage of occurrences is the percentage of all occurrences for all species within a guild across years. Black bars represent the period 1984-1989 and hatched bars the period 1991-1993.**

The frequency of occurrence of native forbs in high-impact areas was significantly less than alien forbs in all years except 1992 (Table 4). In medium/low-impact areas alien forbs had significantly greater frequency of occurrence than native forbs in all years except 1993 (Table 4). Native grass had the lowest frequency of occurrence of all vegetation categories in the high-impact areas, while in the medium/low-impact areas they had the lowest values in all years except 1984 (Table 4).

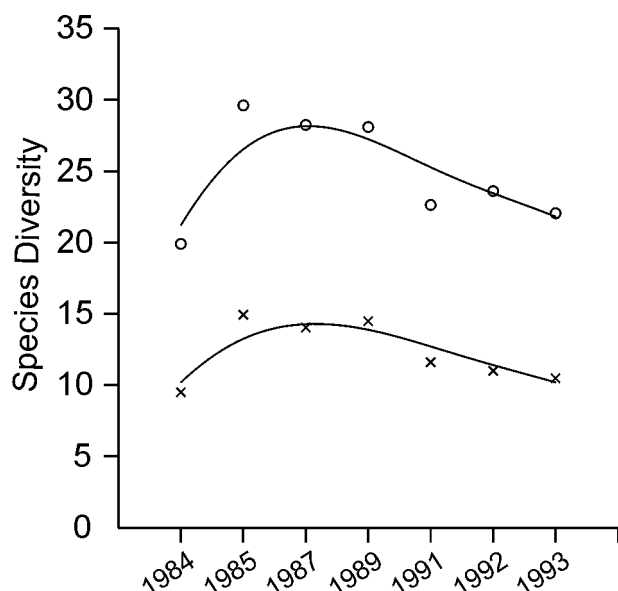
From 1984 to 1989 the frequency of occurrence of native and alien forbs was significantly greater in the high-impact than medium/low-impact class, but from 1991 to 1993 frequency of occurrence was significantly greater in the medium/low-impact class for both guilds (Fig. 2). In con-

trast, the frequency of occurrence of native and alien grass was significantly greater in the medium/low-impact class than high-impact class from 1984 to 1989, but from 1991 to 1993 frequency of occurrence was significantly greater in the high-impact class for both guilds (Fig. 2).

There were significant second-order patterns for alpha diversity from 1984 to 1993 (Fig. 3). Species richness ( $r = 0.38$ ,  $df = 2,105$ ,  $p < 0.0001$ ) and species diversity ( $N_2$ ;  $r = 0.42$ ,  $df = 2,105$ ,  $p < 0.0001$ ) reached their maximum values from 1985 to 1989, then declined steadily through 1993. Species evenness showed a similar pattern ( $r = 0.26$ ,  $df = 2,104$ ,  $p = 0.026$ ), but mean values for E only ranged from 0.81 and 0.89, so ecologically this pattern was trivial.

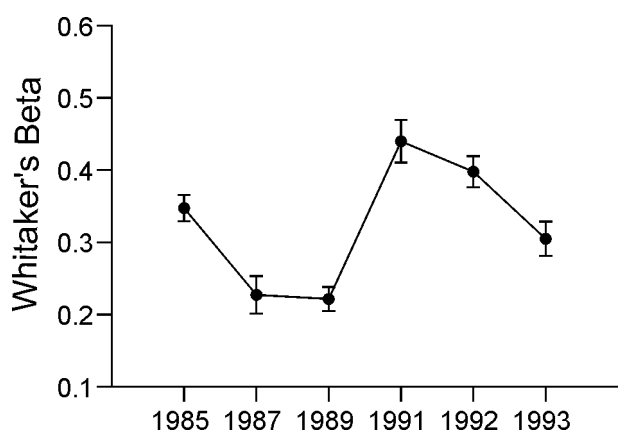
**Table 5 Multiple regression statistics for the relationship of eight site characteristic variables with species diversity indices and species richness and frequency of occurrence of herbaceous vegetation in grassland plots before and after the eradication of feral sheep from Santa Cruz Island, California, 1984 – 1993. The site characteristic variables were density of feral sheep in the year of sampling (density), the density of feral sheep prior to eradication (pre-density), years post-eradication (ype), % organic litter cover (litter), % vegetation cover (cover), elevation, slope, and aspect. Semipartial correlation coefficient = *Sr*, t-test statistics = *t*, and probability values = *p* for multiple regression analyses.**

Independent Variable	<i>Sr</i>	<i>t</i>	<i>P</i>	Independent Variable	<i>Sr</i>	<i>t</i>	<i>P</i>
<b>Species Richness;</b> R=0.54, df=8,99, p<0.0001				<b>Mean Native Grass Frequency;</b> R=0.51, df=8,99 p<0.0001			
Aspect	.279	3.12	0.002	Elevation	-.462	4.43	<0.0001
Elevation	-.454	4.43	<0.0001	Litter	-.313	1.92	0.058
Vegetation Cover	-.397	2.16	0.034	<b>Native Grass Species Richness;</b> R=0.51, df=8,98 p<0.0001			
<b>Species Diversity (N<sub>2</sub>);</b> R=0.61, df=8,99, p<0.0001				Slope			
Aspect	.235	2.79	0.006	Elevation	-.384	3.67	<0.0001
Elevation	-.393	4.09	<0.0001	Vegetation Cover	-.437	2.28	0.025
Vegetation Cover	-.645	3.73	<0.0001	<b>Mean Alien Forb Frequency;</b> R=0.42, df=8,99 p=0.011			
Pre-Density	.220	2.19	0.031	Ype	.251	2.02	0.046
<b>Species Evenness (E);</b> R=0.52, df=8,97 p<0.0001				Slope			
Pre-Density	.235	2.15	0.034	Elevation	-.222	2.01	0.047
Ype	.426	3.60	0.001	Vegetation Cover	-.397	2.00	0.048
Vegetation Cover	-.614	3.29	0.001	<b>Alien Forb Species Richness;</b> R=0.48, df=8,98, p=0.001			
Elevation	-.201	1.91	0.060	Aspect	.254	2.70	0.008
<b>Mean Native Forb Frequency;</b> R=0.53, df=8,99 p<0.0001				Elevation			
Pre-Density	.272	2.52	0.013	Pre-Density	.205	1.84	0.069
Slope	.216	2.17	0.032	<b>Mean Alien Grass Frequency;</b> R=0.54, df=8,98 p<0.0001			
<b>Native Forb Species Richness;</b> R=0.53, df=8,98 p<0.0001				Elevation			
Pre-Density	.223	2.07	0.041	Litter	.462	2.89	0.005
Slope	.249	2.47	0.015	Vegetation Cover	.578	3.14	0.002
Elevation	-.269	2.60	0.011	<b>Alien Grass Species Richness;</b> R=0.43, df=8,99 p<0.007			
Vegetation Cover	-.355	1.92	0.058	Ype	-.251	2.03	0.045
Aspect	.161	1.78	0.079	Elevation	-.195	1.78	0.077

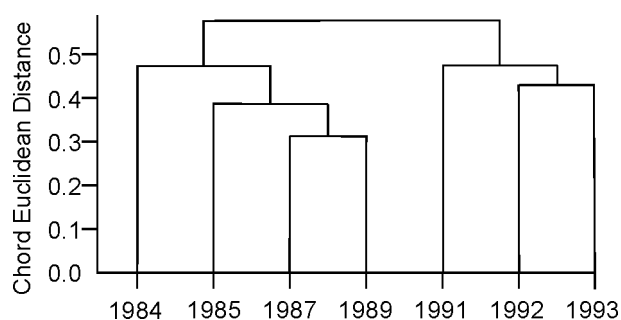


**Fig. 3** Species richness (S; shown as open circles) and diversity (N2; shown as X) of herbaceous vegetation during and after eradication of feral sheep from Santa Cruz Island, California, 1984-1993. The eradication programme occurred from 1981-1988.

Species richness was negatively correlated with two site variables and positively correlated with one site variable (Table 5). Species richness increased on low, relatively dry slopes with lower values of vegetation cover. Species diversity (N2) showed the same pattern as species richness, but was also positively correlated with higher sheep density prior to eradication (Table 5). Species evenness was positively correlated with higher sheep density prior to eradication and the number of years after eradication, and negatively correlated with vegetation cover and elevation (Table 5).



**Fig. 4** Turnover of species (Whitaker's beta) of herbaceous vegetation during and after eradication of feral sheep from Santa Cruz Island, California, 1984-1993. The eradication programme occurred from 1981-1988. Error bars are +/- one standard error of the mean.



**Fig. 5** Dendrogram of similarity (chord Euclidean distance) of herbaceous vegetation during and after eradication of feral sheep from Santa Cruz Island, California, 1984-1993. The eradication programme occurred from 1981-1988. Average linkage was used to construct the dendrogram.

There was a weak negative correlation between species richness and rainfall ( $r = 0.25$ ,  $df = 1,106$ ,  $p = 0.010$ ), and species diversity (N2) and rainfall ( $r = 0.31$ ,  $df = 1,106$ ,  $p = 0.001$ ). There was no correlation between species evenness and rainfall.

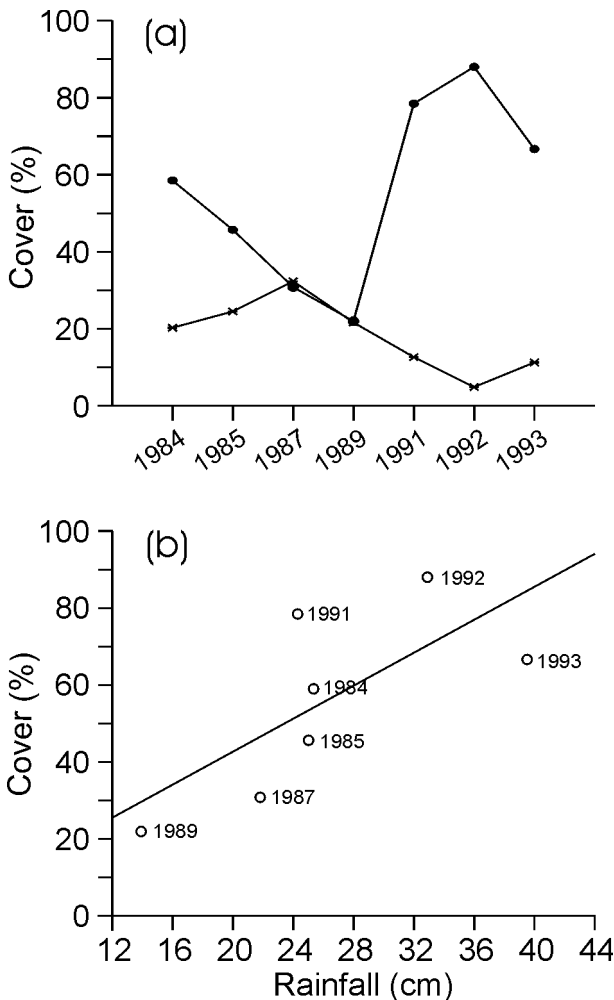
The turnover of species within plots was greatest between 1984 and 1985, and between 1989 and 1991 (Fig. 4). Cluster analysis indicated that there were two periods with the greatest difference in species composition: 1984 to 1989, and 1991 to 1993 (Fig. 5). The mean coefficient of similarity for 1984-1989 was 0.90, and for 1991-1993 was 0.88. The mean coefficient of similarity between the years from 1984 to 1989 and the years from 1991 to 1993 was 0.81. There was a significant difference among years in the rank order of the 10 most abundant species (Kendall Coefficient of Concordance = 0.264,  $df = 6$ ,  $p = 0.015$ ). Two species were primarily responsible for the change in rank abundance. The alien grass *Vulpia myuros* C.C. Gmel declined in rank abundance from 1989 to 1992, then increased in 1993. The native forb *Eremocarpus setigerus* Benth. declined in rank abundance after 1991. Nine of the 10 species with the greatest frequency of occurrence were nonnative.

The percentage cover of herbaceous vegetation did not linearly increase between 1984 and 1993 (Fig. 6a). However, there was a positive correlation between cover and rainfall ( $r = 0.54$ ,  $df = 1,106$ ,  $p < 0.0001$ ) (Fig. 6b), so mean cover in the period from 1991 to 1993 was 37% greater than the period from 1984 to 1989. There was a significant negative correlation between rainfall and S ( $r = 0.25$ ,  $df = 1,106$ ,  $p = 0.010$ ) and N2 ( $r = 0.31$ ,  $df = 1,106$ ,  $p = 0.005$ ). Beta diversity had a marginally significant positive relationship with rainfall ( $r = 0.20$ ,  $df = 1,106$ ,  $p = 0.061$ ).

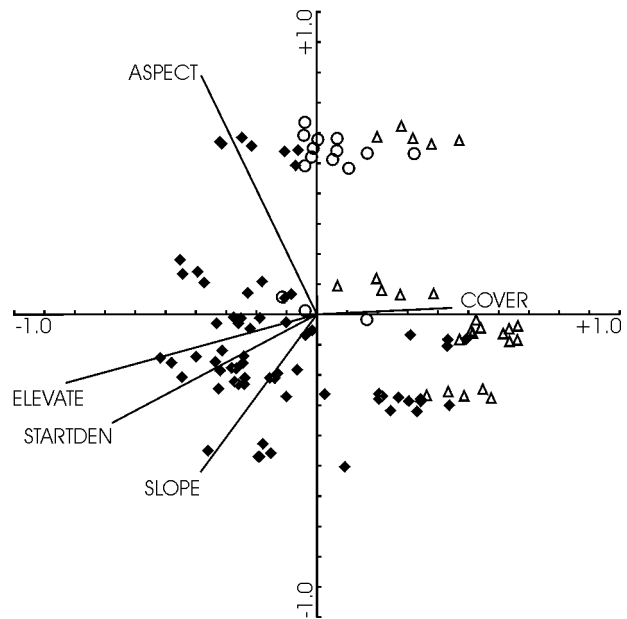
Five environmental variables were retained for the Canonical Correspondence Analysis (CCA); the density of sheep in an area prior to eradication, slope, aspect, elevation, and cover of vegetation. Sheep density in the year of sam-

pling and litter cover did not contribute significantly to the CCA, and years post-eradication and bare ground were not included because of their strong correlation with vegetation cover ( $r > 0.73$ ). The first two CCA axes had clear ecological interpretation, and indicated that distribution and abundance patterns of herbaceous species in grasslands were correlated with topographic features as well as sheep impacts. The first CCA axis was a sheep impact and elevation gradient, with species distribution and abundance patterns varying from high elevation areas with low vegetation cover to low elevation areas with higher vegetation cover (Fig. 7). The second axis was a topography gradient, with slope and aspect having the primary influence on species composition (Fig. 7). The first axis accounted for >50% of the variation in the species abundance data, and the second axis for 22% of the variation in the species abundance data.

There was a significant positive correlation of the mean frequency score of native forbs with slope and density of sheep in an area prior to eradication (Table 5). Species richness of native forbs had significant positive correla-



**Fig. 6** (a) Change in percentage cover of bare ground (shown as X) and herbaceous vegetation (shown as closed circle) and, (b) the relationship between rainfall and vegetation during and after eradication of feral sheep from Santa Cruz Island, California, 1984-1993. The eradication programme was from 1981-1988.



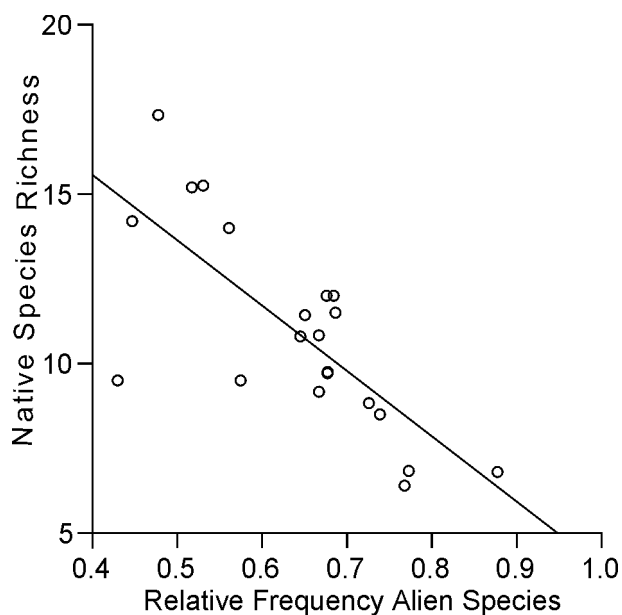
**Fig. 7** Canonical Correspondence Analysis biplot of the relationship between five environmental variables and plant species composition in plots with different impacts from feral sheep on Santa Cruz Island, California, 1984-1993. Solid black diamonds are plots categorised as high impact areas, open circles are plots categorised as medium impact areas, and open triangles are plots categorised as low impact areas. Startden is the density of sheep prior to eradication and Cover is percent total herbaceous vegetation cover. Aspect, Elevate, and Slope are geographic attributes of the plots.

tion with slope, elevation, and density of sheep in an area prior to eradication (Table 5). Species richness of native forbs also had a marginally significant negative relationship with percentage cover of vegetation and a marginally significant positive relationship with aspect (Table 5). The mean frequency of native grass had significant negative correlation with litter and elevation, while species richness of native grass had significant negative relationships with slope, elevation and the percentage cover of vegetation (Table 5).

The mean frequency of alien forbs had significant negative correlation with slope, elevation, and percentage cover of vegetation, and a significant positive correlation with the number of years post-eradication (Table 5). Species richness of alien forbs had a significant positive correlation with aspect and a significant negative correlation with elevation (Table 5). The density of sheep in an area prior to eradication had a marginally significant positive correlation with species richness of alien forbs (Table 5).

There was a significant positive correlation between the mean frequency of alien grass and elevation, litter, and vegetation cover (Table 5). Species richness of alien grass had a significant negative correlation with the number of years post eradication and a marginally significant negative correlation with elevation (Table 5).





**Fig. 8** The relationship between species richness of native grasses and forbs and the relative frequency of alien grasses and forbs during and after eradication of feral sheep from Santa Cruz Island, California, 1984-1993. The eradication programme was from 1981-1988.

There was no significant relationship between species richness of native and alien species. However, there was a significant negative correlation between native species and the mean frequency of aliens ( $r = 0.745$ ,  $df = 1,19$ ,  $p < 0.0001$ ) (Fig. 8).

### Endemic Species

The distribution of endemic species increased from 47.5% of the km<sup>2</sup> units during the 1991-1992 survey period to 52.5% in the 1995-1996 survey period ( $X^2=6.66$ ,  $df=1$ ,  $p=0.01$ ). Of the 43 endemic species, 33 were observed in more km<sup>2</sup> units during the 1995-1996 survey. Four of the species occurred less frequently in the 1995-1996 survey than during the 1991-1992 survey, and two species, *Malacothrix squalida* Greene (Asteraceae) and *Erysimum insulare* Greene (Brassicaceae) were not observed in either of the survey periods (Table 6).

Twenty-four of the 250 species (9.6%) recorded on the transects from 1991-1995 were endemic. There was a significant linear increase in the percentage of plots that nine of the species occurred in, and none decreased in distribution or abundance. The six species that had a significant linear increase in density were all shrubs (Table 6).

Of the five endemic species that were monitored most intensively, the abundance of one species remained unchanged, two increased in population size, and two had serious declines. No new populations of *Berberis pinnata* were found, and the populations that were known from previous surveys showed no indication that they were expanding their range or increasing in abundance.

**Table 6** Change in distribution of 43 endemic vascular plant species between 1991 and 1995 on Santa Cruz Island, California. Surveys are for 190 x 1 km<sup>2</sup> units checked in two periods: 1991-1992 and 1995-1996. Transects are for one hundred 30m x 2m transects surveyed annually from 1991-1995. In the Survey column the symbols '+', '0', and '-' indicate an increase, no change, or decrease (respectively) in the number of units the species was observed in between survey periods. In the Transect column: the symbols '+', '0', and '-' indicate a linear increase, no change, or decrease in the percentage of transects the species occurred in; an '\*' indicates that that species had a significant linear increase in density and/or cover; no symbol indicates that the species was not observed in the transects.

Species	Surveys	Transects
<i>Arabis hoffmannii</i>	+	
<i>Arctostaphylos insularis</i>	+	0*
<i>Arctostaphylos tomentosa</i> subsp. <i>insulicola</i>	+	0
<i>Arctostaphylos viridissima</i>	+	0
<i>Astragalus miguelensis</i>	+	
<i>Berberis pinnata</i> <i>insularis</i>	+	
<i>Calystegia macrostegia</i> subsp. <i>macrostegia</i>	-	0
<i>Castilleja lanata</i> subsp. <i>hololeuca</i>	+	+
<i>Ceanothus arboreus</i>	+	0
<i>Ceanothus megacarpus</i> subsp. <i>insularis</i>	+	+*
<i>Chorizanthe wheeleri</i>	+	0
<i>Dendromecon rigida</i> subsp. <i>harfordii</i>	+	
<i>Dudleya candelabrum</i>	+	
<i>Dudleya greenii</i>	+	
<i>Dudleya nesiotica</i>	0	
<i>Eriogonum arborescens</i>	+	0*
<i>Eriogonum grande</i> subsp. <i>grande</i>	+	0*
<i>Eriogonum grande</i> subsp. <i>rubescens</i>	+	
<i>Erysimum insulare</i>	0	
<i>Escholzia ramosa</i>	+	
<i>Galium angustifolium</i> subsp. <i>foliosum</i>	+	0
<i>Galium buxifolium</i>	-	
<i>Galium nuttallii</i> subsp. <i>insulare</i>	+	0
<i>Gilia nevini</i>	-	0
<i>Hazardia detonsa</i>	+	
<i>Helianthemum greenii</i>	+	0
<i>Hemizonia clementina</i>	+	
<i>Heuchera maxima</i>	+	+
<i>Jepsonia malvifolia</i>	+	+
<i>Lotus argophyllus</i> subsp. <i>niveus</i>	+	
<i>Lotus dendroideus</i> subsp. <i>dendroideus</i>	+	+*
<i>Lyonothamnus floribundus</i> subsp. <i>aspleniifolius</i>	0	
<i>Malacothamnus fasciculatus</i> subsp. <i>nesioticus</i>	+	
<i>Malacothrix indecora</i>	0	
<i>Malacothrix saxatilis</i> subsp. <i>implicata</i>	+	+
<i>Malacothrix squalida</i>	0	
<i>Mimulus flemingii</i>	+	+*
<i>Quercus pacifica</i>	+	0
<i>Quercus tomentella</i>	0	+
<i>Rhamnus pirifolia</i>	+	0
<i>Ribes thacherianum</i>	+	0
<i>Solanum clokeyi</i>	+	+
<i>Thysanocarpus conchuliferus</i>	-	

One new population of *Arabis hoffmannii* was discovered, but two of the known populations were severely impacted by feral pigs. In 1993, rooting by feral pigs reduced the size of the largest population from 32 stems to 19 stems. The population rebounded the next year to 78 stems, and reached a maximum of 110 stems in 1996. In 1997 the population decreased to 98 stems, but flower and seed production remained high. Intense hunting in the surrounding area eliminated feral pig impacts to the population. In 1995 feral pigs destroyed a second population on an isolated cliff on the north side of the island. This population had been comprised of 15 stems, and no recruitment was occurring. No stems were seen after 1995. The third population fluctuated between 11 and 81 stems from its discovery in 1995 and the last year of surveys in 1998.

Two previously-unknown populations of *Malacothamnus fasciculatus* subsp. *nesioticus* were found. A population discovered in 1992 increased annually from 16 to 27 stems through 1997, and a population discovered in 1997 was comprised of 87 stems and appeared to have been increasing for a number of years. The number of stems from the previously-known population increased annually from six in 1991 to 48 in 1997.

The two endemic species that declined were *Dudleya nesiotica* and *Thysanocarpus conchuliferus*. The density of *D. nesiotica* initially increased between 1991 and 1993, but it declined from a mean of 30.6 stems/m<sup>2</sup> in 1993 to 3.6 stems/m<sup>2</sup> in 1998. The decline was strongly correlated with habitat alteration as a result of an increase in cover of alien grasses and forbs and a related buildup of organic litter (R. Klinger, *in review*). *Thysanocarpus conchuliferus* was found at 11 of the 14 historically-known populations in 1991. In the ensuing seven years only one of these populations continued to persist. Feral pigs had rooted five of the sites, and the habitat at all locations had been heavily modified by an increase in cover of alien annual grass. There were <56 individuals at the remaining known population.

## DISCUSSION

It is often assumed that removing nonnative grazers from islands will lead to recovery of native species (Temple 1990; Halvorson 1992, 1994). This assumption can be justified to a certain degree (Ritchie 1970; Meurk 1982; Wodzicki and Wright 1984), but as a general expectation it is probably overly simplistic (Cunningham 1970; Usher 1989; Maunder *et al.* 1998). As the patterns showed on SCI, removing feral animals from islands will lead to a range of complex effects, many of which will be beneficial to native species and many of which may not.

The net effect on species diversity following the eradication of feral sheep from SCI has been relatively minor. Species richness, diversity, and evenness were all related to site characteristics other than just sheep impact. The increase in herbaceous cover and decrease in bare ground that occurred after the sheep were eradicated actually resulted in lower levels of alpha diversity, at least within

grasslands. Indeed, there was some indication that alpha diversity might be decreasing as a result of the dominance of alien grasses.

Turnover of species within plots appeared to be most related to the end of the drought and the elimination of the sheep. Changes in turnover at local scales will likely be small, and more a result of changes in the relative abundance of species than changes in species richness itself. Even years that were most dissimilar in composition shared about 85% of the species. Island wide, beta diversity will not be likely to change unless there are major invasion or extinction events on SCI, which seems unlikely.

Reflecting the lack of major changes in alpha diversity, there was no unambiguous change in gamma diversity. Twenty-two species of vascular plants that were never previously recorded on SCI or were considered extirpated have been found since 1987, and no species have been known to go extinct since the sheep were eradicated. It is important to note that 14 of these species that have been recently found are alien (S. Junak, Santa Barbara Botanic Garden, pers. comm.). But, it is unknown whether these species represent new invasions or had simply been on the island and then increased in abundance to detectable levels after the sheep were eradicated.

The relative abundance of native species in grasslands on SCI was determined primarily by an interaction between grazing intensity, competition with alien species, rainfall patterns, and site characteristics. All of these factors had effects on guilds of herbaceous species, and site characteristics had strong effects at the species level. Other studies on the relationship between grazing pressure, species composition, and species diversity have reported similar patterns (Noy-Meir *et al.* 1989; Cornelius and Schultka 1997; Oliva *et al.* 1998).

Rainfall was an important factor affecting the increase of vegetation cover, but the increase in cover did not lead to an increase in the number or relative frequency of native species. Surprisingly, relatively more native species occurred in open areas where sheep impacts had been severe, albeit at low abundance. These tended to be higher and steeper sites with lower frequency of alien annual grass.

Species composition in grasslands was dominated by alien species in all years, and alien annual grasses were the dominant group in all areas, regardless of site characteristics or rainfall patterns. But they were less abundant in high impact areas than low and medium-impact areas prior to the completion of eradication, which in all likelihood was a result of heavy grazing by the sheep. In the five years after completion of the eradication programme and the end of the drought, alien grasses increased in frequency in the high-impact areas relative to the medium and low-impact areas. This pattern has been noted in other studies on SCI. Klinger and Messer (*in press*) reported a strong correlation between rainfall and cover of alien annual grass in grassland areas where prescribed burns had been conducted.

Both native and alien forbs had greater relative frequency of occurrence in high impact areas than medium and low-impact areas prior to and just after completion of the eradication programme. In the wetter years after the end of the eradication, they decreased in frequency in the high-impact areas, which reflected the increase in frequency of the alien grasses in these areas.

The frequency of native grasses was lower in areas of high impact than medium and low-impact areas prior to the end of the eradication programme. After the end of the eradication programme the frequency of native grasses increased in the high-impact areas. Studies on the relationship between native grasses and grazing in California have noted that they are intolerant of continuous, high intensity grazing (Heady 1977; Bartolome and Gemmill 1981; Mack 1989; Dyer *et al.* 1996). When grazing pressure was removed, native grasses on SCI increased in frequency. But frequency of native grass decreased with increasing amounts of litter, and build-up of litter is characteristic of grasslands in California dominated by non-native annual grasses.

Native species were not displaced by new non-native species invading an area, but by an increase in cover from nonnative species already present in an area. There was no relationship between species richness of alien species and species richness of native species, but the number of native species tended to be lower in areas where the relative frequency of aliens was high. This pattern probably reflects the historical effect of sheep grazing; the levels of species diversity, composition, and cover had been established decades earlier, and ongoing grazing did not change them in any significant manner. After the sheep were removed and environmental conditions became favourable (increased rainfall) the vegetation had a chance to recover. Annual grasses increased most rapidly, especially in the high-impact areas, resulting in the displacement of native species.

An evaluation of how the eradication affected diversity patterns, species composition, and vegetation structure in communities other than grasslands must be made cautiously. Although grasslands comprise almost half the area of SCI, there are several lines of evidence indicating both shrub communities and shrub species are recovering. A study of the Bishop pine *Pinus muricata* community on the north side of the island showed that diversity has increased since the eradication (Wehtje 1994). An analysis of diversity patterns from the 100 transects located throughout the island also showed that levels of alpha and beta diversity in communities dominated by shrubs and trees are greater than in grasslands, and a relatively high proportion of this diversity is comprised of native species (Klinger unpubl. data). There has been no decline in abundance of woody endemic species, and a number of endemic shrubs increased both in distribution and abundance.

Regardless of whether it was dominated by alien species or not, the increase in cover undoubtedly reduced erosion

and helped restore natural hydrologic regimes. Ongoing degradation of these ecosystem processes would have made future restoration projects more challenging and expensive, if not impossible (Maunder *et al.* 1998). Besides reducing soil loss and improving watershed quality, another desirable outcome since completion of the eradication programme was the overall increase in distribution and abundance of endemic species. This was long considered one of the most important reasons for eradicating sheep from SCI (Hochberg *et al.* 1980), and in most cases appears to have had a high payoff. It is interesting to note that of the 23 species that showed a positive response to the removal, 20 were woody shrubs or trees. This may be due in part to them being less prone to competitive effects of alien species, most of which are herbaceous. A number of woody alien species occur on SCI, but they tend not to be particularly invasive or still only occur in very small, discrete patches (Junak *et al.* 1995; Klinger unpubl. data).

However, it is telling that the two endemic species that showed negative responses to the eradication were two of the rarest species. Although their impact may be less obvious, alien plants can have many of the same detrimental effects to natural communities as feral animals (D'Antonio and Vitousek 1992; Halvorson 1994). This certainly appeared to be the case with both *Dudleya nesiotica* and *Thysanocarpus conchuliferus*. Both were apparently being affected negatively by alien annual grass, and while a well designed habitat management programme could improve conditions for *Dudleya nesiotica*, an *ex situ* propagation programme will probably be required to preserve *Thysanocarpus conchuliferus*. While it is not unlikely that other populations of *Thysanocarpus conchuliferus* will be found on SCI, it is clear that it is in a precarious demographic position.

In summary, there was no single, consistent community-wide pattern that manifested itself in grasslands on SCI once grazing pressure was eliminated. Diversity patterns and species composition following the eradication of feral sheep were determined by complex interactions between rainfall, topography, and the historical severity of grazing. Alien annual grasses tended to dominate most grassland areas, but this was not a result of new invasions but rather by proliferation of species already occurring in the community. Endemic species as a group appeared to show a favourable response to eradication of the sheep, but declines in at least some of the endemic species were associated with the increase in cover of alien annual grasses. Ten years ago it may have been possible to argue that these patterns and others observed on SCI following eradication of grazers (Brenton and Klinger 1994) were isolated events. But ecologists are developing a greater understanding of ecosystem responses to control and eradication programmes (Zavaleta *et al.* 2001, Zavaleta 2002), and it appears likely that the patterns on SCI are representative of the complex responses that can be expected to occur on both island and mainland areas.

## CONSERVATION IMPLICATIONS

It is important to recognise that eradication programmes should only be considered a first step for protecting and restoring native species diversity. It is likely that environmental factors influencing the response of plant and animal species to eradication programmes will vary unpredictably, resulting in some succession patterns that are relatively undesirable for native species. Management activities will likely be needed to prevent unwanted outcomes from eradicating feral animals, such as the displacement of native herbaceous species by alien grasses and forbs that has occurred on Santa Cruz Island.

The necessity of eradication programmes will usually be obvious, but it is critical that conservation scientists and land managers understand the likely outcome of these programmes. Simplistic hopes must be replaced with realistic expectations that many outcomes will be unpredictable, and some will be undesirable. The important strategy will be to try to predict the types of undesirable outcomes that may occur, and while it may be unrealistic to predict exactly what species will be involved, resources and plans can be developed for beginning the process of mitigating these events.

Schuyler (1993) noted that four processes needed to be monitored to document how the Santa Cruz Island ecosystem responded to the removal of feral sheep: (1) changes in vertebrate populations, (2) changes in alien plants, (3) changes in hydrologic regimes, and, (4) changes in erosion processes and soil formation. Of these, only changes in alien herbaceous plants were adequately monitored during the Santa Cruz Island sheep eradication. If the other processes had been monitored as Schuyler (1993) suggested, a more comprehensive evaluation of the ecosystem's response to the eradication could have been made.

Feral animal eradication programmes are underway or planned on many islands throughout the world. By designing extensive monitoring protocols as an integral part of any eradication programme, conservation scientists will be able to better react to some of the unwanted outcomes that will inevitably occur after completion of an eradication programme. A number of different ecosystem parameters should be monitored; monitoring should be initiated before eradication begins; and sampling should continue consistently throughout the eradication phase and at least several years beyond.

It has only been 15 years since sheep were eradicated on the western 90% of SCI, and response from the effects of overgrazing will be ongoing for decades. Succession patterns will vary among communities, and some of those patterns will favour native species. Nevertheless, situations like those of *Dudleya nesiotica* and *Thysanocarpus conchuliferus* are reminders that our lack of understanding of how ecosystems function can lead to unintended outcomes that imperil the species and communities we are trying to protect and restore. Ultimately, we will not judge

the success of eradication programmes in terms of the number of nonnative organisms we destroy, but rather the number of native species whose populations we preserve.

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**Appendix 1 Estimated sheep density (#/km<sup>2</sup>) on Santa Cruz Island, California. After 1987 no sheep occurred on the western 90% of the island.**

Pasture	1982	1983	1984	1985	1986	1987
<b>Light Impact</b>						
La Punta	26.0	0.0	0.0	0.0	0.0	0.0
Cabrillo	43.5	43.5	43.5	0.0	0.0	0.0
Portezuela	12.0	12.0	12.0	12.0	0.9	0.9
<b>Medium Impact</b>						
Alberts	64.2	5.7	14.2	0.0	2.2	4.7
Pozo/Sauces	131.8	131.8	131.8	131.8	76.5	0.4
<b>Heavy Impact</b>						
Dos Cuevas	200.9	74.7	3.2	1.2	0.0	0.0
North Shore	287.6	198.3	198.3	5.5	0.9	1.7
Laguna	291.2	291.2	291.2	291.2	225.8	1.7
Willows	265.6	265.6	265.6	265.6	199.5	1.1