

RESEARCH ARTICLE

Passive Recovery of Vegetation after Herbivore Eradication on Santa Cruz Island, California

Roxanne S. Beltran,^{1,2,3} Nissa Kreidler,¹ Dirk H. Van Vuren,⁴ Scott A. Morrison,⁵ Erika S. Zavaleta,⁶ Kelly Newton,¹ Bernie R. Tershy,¹ and Donald A. Croll¹

Abstract

Understanding how insular ecosystems recover or are restructured after the eradication of an invasive species is crucial in evaluating conservation success and prioritizing island conservation efforts. Globally, herbivores have been removed from 762 islands, most with limited active restoration actions following eradication. Few studies have documented the effects of invasive herbivore removal after multiple decades of passive recovery. Here we evaluate recovery of vegetation on Santa Cruz Island, California, after the removal of feral sheep (*Ovis aries*) in 1984. We repeat a study conducted in 1980, and examine vegetation changes 28 years after the eradication. Before eradication, grazed areas were characterized by reduced plant cover, high exposure of bare ground, and erosion. After 28 years of passive recovery, transect data showed a 23% increase in woody overstory, whereas analysis of photographs from landscapes photographed pre- and post-eradication showed

a 26% increase in woody vegetation. Whole island vegetation maps similarly showed a transition from grass/bare ground (74.3% of cover) to woody plants (77.2% of cover), indicating the transition away from predominantly exotic annual grassland toward a community similar to the overstory of coastal scrubland but with an understory dominated by non-native annual grasses. We estimate that replacement of grasses/bare ground by native woody vegetation has led to 70 and 17% increases in the stored carbon and nitrogen pools on the island, respectively. Our results demonstrate that these island ecosystems can experience significant recovery of native floral communities without intensive post-eradication restoration, and results of recovery may take decades to be realized.

Key words: biodiversity conservation, carbon sequestration, introduced species, island, restoration, Santa Cruz Island.

Introduction

Invasive alien animals are one of the most significant threats to biodiversity and have extensive impacts on ecological function and community composition across a wide range of systems (Mooney & Hobbs 2000). Invasive predators and herbivores often occur at extremely high densities on islands (Terborgh 2001) and have particularly destructive effects on island ecosystems (e.g. extinction or imperilment). Native island species tend to have smaller population sizes and smaller ranges (MacArthur & Wilson 1967), less genetic diversity (Frankham 2010), and lack behavioral (Curio 1966; Blumstein & Daniel 2005), life

history (Köhler & Moyà-Solà 2009) and morphological (Bowen & Van Vuren 1997; Boyer & Jetz 2010) defenses against invasive predators. In response to these detrimental impacts, conservation practitioners have eradicated over 1,000 invasive alien animal populations on islands globally (Database of Island Invasive Species Eradications, <http://diise.islandconservation.org>).

Following invasive animal eradication, native ecosystems may be sufficiently resilient to recover unaided. However, recovery can be limited, have unintended consequences (Zavaleta et al. 2001; Morrison 2007), or take exceptionally large timescales after the removal of human disturbance (Holl & Aide 2011). Ultimately, the degree of recovery is likely dependent on both severity and duration of the impacts as well as the nature of the disturbed ecosystem (Jones & Schmitz 2009). Thus, removal of introduced animals is necessary, but not always sufficient to reach conservation goals (Simberloff 1990). Given the large expense in cost and labor of active restoration at large spatial scales, there is considerable debate about the necessity for active (management to accelerate the succession to recovery) versus passive (natural or unassisted recovery) restoration subsequent to removal of human disturbance (DellaSala et al. 2003; Prach & Hobbs 2008;

¹Department of Ecology & Evolutionary Biology, University of California, 100 Shaffer Road, Santa Cruz, CA 95060, U.S.A.

²Address correspondence to R. S. Beltran. email roxanne.beltran@gmail.com

³Present address: Department of Biological Sciences, University of Alaska, 3101 Science Circle, Anchorage, AK 99508, U.S.A.

⁴Department of Wildlife, Fish, & Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616, U.S.A.

⁵The Nature Conservancy, 201 Mission St., 4th Floor, San Francisco, CA 94105, U.S.A.

⁶Department of Environmental Studies, University of California, 1156 High St., Santa Cruz, CA 95064, U.S.A.

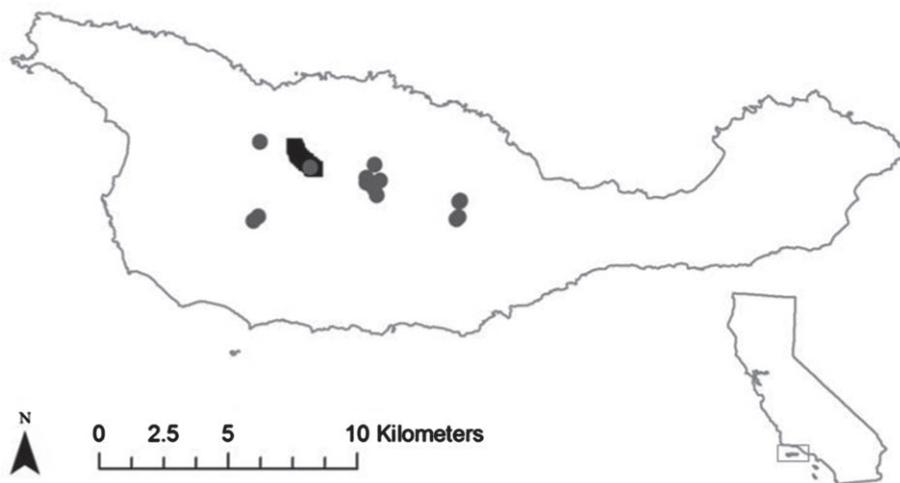


Figure 1. Santa Cruz Island study location. Location of vegetation transects are depicted as squares, photo monitoring stations as circles. Inset shows location of the island in the state of California.

Clewell & McDonald 2009; Benayas et al. 2009; Holl & Aide 2011).

To better predict the potential for post-eradication recovery, long-term monitoring or resampling studies are required. Few post-eradication studies have had sufficient time to evaluate decade-scale outcomes of passive recovery from the eradication of invasives (Simberloff 1990; Jones & Schmitz 2009). Here we evaluate passive recovery of vegetation on Santa Cruz Island, California, 28 years after removal of feral sheep (*Ovis aries*) and cattle (*Bos primigenius*) across most (90%), and eventually all of the island. Prospects for passive recovery from the long-term impacts of these herbivores were particularly problematic due to the secondary impacts of herbivores on erosion and soil nutrient characteristics (Corry 2006) and the rapid increase in non-native herbaceous plants soon after herbivores were removed (Klinger et al. 1994).

Introduced herbivores are particularly destructive to island plant communities. Documented impacts include reduction of native and total plant cover and diversity, increased spread of non-native plants, increased erosion, and changes in native animal composition, abundance, and diversity (Donlan et al. 2002; Chapuis 2004). Sheep were introduced to Santa Cruz Island over 150 years ago and became feral by the late 1920s (Bowen & Van Vuren 1997). Horses (*Equus ferus*), cattle (*B. primigenius*), and feral pigs (*Sus scrofa*) were also introduced to the island as ranching activities expanded (Parkes et al. 2010; Morrison 2007). These vertebrates resulted in heavy grazing and trampling of native plant communities and caused changes in plant community composition, reduced herbaceous cover, altered community structure, decreased litter, and increased erosion rates, all of which were evident by the early 1980s (Minnich 1980; Van Vuren & Coblentz 1987). In particular, Van Vuren and Coblentz (1987) documented direct impacts of grazing ungulates, including a shift from the native, coastal sage, chaparral and oak woodland communities (Brumbaugh et al. 1982; Junak et al. 1995) to exotic annual grasslands with high erosion rates (Bowen & Van Vuren 1997). Introduced

ungulate eradication programs were initiated in 1981 (Klinger et al. 2002). Sheep, cattle, and horses were eliminated from 90% of the island by 1989, and islandwide by 1999 (Faulkner & Kessler 2011). Feral pigs were eradicated between 2005 and 2007 (Parkes et al. 2010). The goals of the eradication program as defined by the island managers (The Nature Conservancy and National Park Service) were to “preserve and to protect in perpetuity and enhance the natural ecosystems, the unique natural flora and fauna of the island, the hydrologic features and the natural esthetic values of the island” (Schuyler 1993). Consistent with this goal, a metric of floral recovery was an increase in native-dominated vegetation (Klinger et al. 1994).

Here, we assess the long-term (almost three decade) passive recovery of plant community structure based on resampled vegetation transect data, photo monitoring, and islandwide vegetation maps pre- and post eradication. Because there is ongoing economic demand for land-based carbon sinks, we also estimate potential changes in sequestered carbon pools on Santa Cruz Island resulting from decades of passive recovery.

Methods

Study Site

Santa Cruz Island (34°00'N, 119°43'W), California, United States, is located 30 km off the coast of California, 40 km south of Santa Barbara, and at 250 km², is the largest California Channel Island (Fig. 1). Two east–west oriented ridges transect the island longitudinally along a geologic fault and form a 20 km long Central Valley. The island’s climate is maritime Mediterranean with wet, cool winters and dry, hot summers (Junak et al. 1995). Santa Cruz Island is home to more than 625 plant species, 198 bird species, and 12 native species of reptiles, amphibians, and mammals (Junak et al. 1995; Cohen et al. 2009). The island is co-owned and managed by The Nature Conservancy and the U.S. National Park Service. In the 1980s, The Nature Conservancy owned 90% of the island, and all

introduced ungulates except feral pigs were removed from that portion of the island between 1981 and 1989 (Schuyler 1993; Klinger et al. 2002). Because the post-eradication sampling occurred during different years, we report different recovery times for each of the following methodologies.

Transects

In 1980, Van Vuren and Coblenz (1987) conducted a series of vegetation transects on the south-facing slopes of Picacho Diablo. The site is located in rugged topography with an elevation ranging from 380 to 492 m, and includes grassland, coastal scrub, and chaparral communities. Dominant vegetation in the area consisted of shrubs such as *Quercus dumosa*, *Ceanothus megacarpus*, *Senecio flaccidus*, *Heteromeles arbutifolia*, *Cercocarpus betuloides*, *Diplacus longiflorus*, *Adenostoma fasciculatum*, and *Prunus ilicifolia* as well as grasses *Avena* spp., *Bromus* spp., *Festuca megalura*, *Hordeum* spp., and *Lamarckia aurea*. Transect sampling was aimed at quantitatively characterizing the plant community overstory. Understory was not measured.

In 2012, we replicated Van Vuren and Coblenz's study, 28 years after non-native sheep had been fully eradicated from the site in 1984 (P. T. Schuyler, formerly The Nature Conservancy, personal communication). We relocated 16 original reference points used in the initial 1980 study that were set at random distances along a 1,450 m fence (Fig. 1). Using these original reference points from the 1980 study we conducted 30 m point-intercept transects perpendicular to the fence, beginning 10 m from the fence to avoid fence effects (Fig. 1). Sheep had been continuously present in the area from their introduction circa 1850 to their eradication in 1984 and were at high densities (approximately 2 sheep/ha) in 1980 (Van Vuren & Coblenz 1987). At 1 m intervals along each transect, we identified the overstory plant species and form of the tallest vegetation. We classified vegetation type as shrub, tree, grass, forb, succulent, or thatch. Additionally, we classified substrate as soil/rock, if it was moveable by hand, or outcrop if it was not. Sampling occurred during July 2012 for recent data, and during March 1980 in the initial survey (Van Vuren & Coblenz 1987).

To avoid seasonal effects on vegetation sampling, we combined plant vegetation forms (grasses, forbs, thatch, etc.) into three plant classification categories distinguishable regardless of seasonal wet and dry periods: (1) bare, consisting of soil/rock and outcrop; (2) herbaceous, consisting of forbs, grasses, and thatch; and (3) woody, consisting of trees, shrubs, and succulents. We conducted pairwise *t* tests using JMP (JMP, Version 9, SAS Institute Inc., Cary, NC, U.S.A., 1989–2012) to determine the differences in form cover between 1980 and 2012. Alpha level of 0.05 was used for all tests.

Historic Photoanalysis

To examine long-term changes in plant community structure, we compared photos taken in 1979/1980 (pre-eradication) with photos taken from the same vantage point in 2009 (20 years after removal of exotic grazing ungulates in 1989). Single pre- and post-eradication photographs were taken in the same

direction using landmarks and compass bearings at 17 sites near Picacho Diablo and adjacent hills (Fig. 2). We used ImageJ (NIH, <http://rsb.info.nih.gov/ij>) public domain photo analysis software to trace the area of vegetation types in the photos, then calculated percent cover of overstory woody vegetation before and after sheep eradication. We performed a paired sample *t* test to compare woody vegetation percent cover between landscape photographs taken pre- (1980) and post- (2009) eradication.

Aerial Imagery

Cohen et al. (2009) compared vegetation maps generated from aerial photographs taken in 1985 and 2005 to examine long-term changes in Santa Cruz Island overstory vegetation cover. Understory vegetation was not examined. We aggregated their vegetation classifications to compare broad changes in relative cover of grass/bare ground and woody vegetation between 1985 and 2005. Cohen et al. (2009) cross-classified vegetation maps generated from aerial images taken in November 2005 (1:12,000 scale) and compared them with vegetation maps generated from aerial images taken in July 1985 (1:24,000 scale) by Jones et al. (1993) (detailed methodology in Cohen et al. 2009). We used estimates of area cover from Cohen et al. (2009) to compare percent cover changes from 1985 to 2005 in nine vegetation classifications (grasses, coastal sage scrub, chaparral, oaks, island ironwoods, pines, riparian, woody exotics, and barren) (Table 2). In addition, we aggregated these estimates of vegetation cover into two classifications: grasses/bare ground (Cohen et al.'s grass and barren classifications) and woody vegetation (Cohen et al.'s coastal sage scrub, chaparral, oaks, island ironwoods, pines, riparian, and woody exotics classifications). We used aggregated GIS shape files to generate vegetation maps for 1985 and 2005 (pre- vs. post-herbivore eradication).

Carbon Sequestration

As woody vegetation has recovered and replaced non-native annual grasses and bare ground, there have also likely been changes in stored carbon and nitrogen pools on the island. We used estimates of aerial changes in vegetation cover from 1985 to 2005 (Cohen et al. 2009), and estimates of carbon sequestration aboveground and belowground at sites vegetated with grassland versus woody shrub vegetation in coastal California (6,353 g/m² in grassland vs. 15,400 g/m² in restored woody scrub; Zavaleta & Kettley 2006) to estimate changes in insular carbon and nitrogen pools resulting from changes in the relative cover of grasses versus woody scrub vegetation (coastal sage scrub and chaparral).

Results

Transects

Resurvey of pre-eradication transects revealed that 28 years after removal of introduced sheep, bare ground cover decreased 30%, $t_{(25.6)} = 6.60$, $p < 0.0001$, whereas woody overstory cover

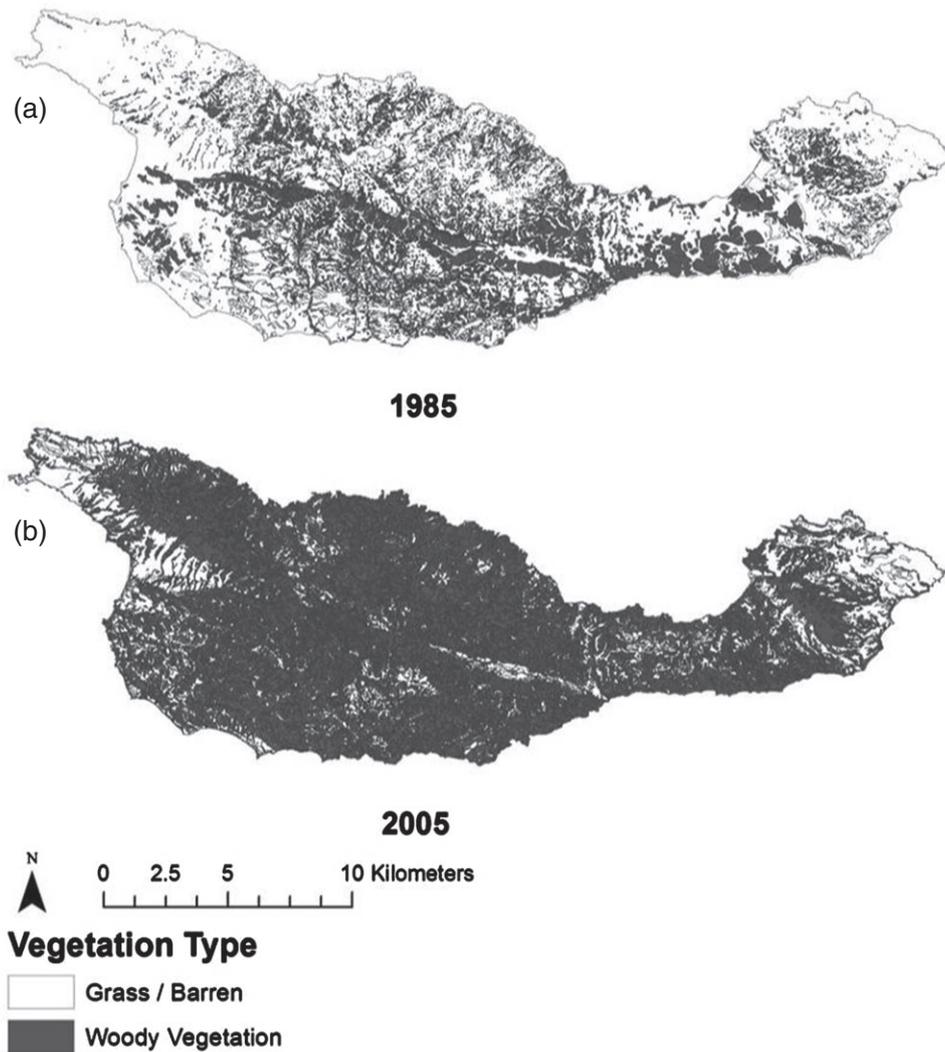


Figure 2. Overstory vegetation change on Santa Cruz Island, California, pre- and 20 years post-invasive ungulate eradication. Distribution of grassland/barren ground (white) and woody vegetation (black) in 1985 (a) and 2005 (b). Figures adapted from vegetation maps generated by Jones et al. (1993) and Cohen et al. (2009).

increased 23%, $t_{(16.4)} = 6.01$, $p < 0.0001$ (Fig. 3). Herbaceous cover was unchanged.

Woody overstory vegetation was composed entirely of native species, whereas 84% of post-eradication herbaceous vegetation was non-native (*Avena* spp. and *Bromus* spp.) (Table 1). Native woody species were dominated by *Eriogonum arborescens* (an island endemic) and *Artemisia californica* (79 and 5% of sampled woody vegetation post-eradication, respectively) (Table 1). Herbaceous cover was comprised mainly of invasive grasses (*Avena* spp. and *Bromus* spp.) in post-eradication sampling periods as well, but some native grass (*Stipa* spp.) was also found (Van Vuren & Coblenz 1987).

Historic Photoanalysis

Mean woody overstory plant cover increased 26% from 1980 to 2009 in repeat photographs of 17 sites (from $26.9 \pm 4.5\%$,

$N = 17$ in 1980 to $52.9 \pm 4.2\%$, $N = 17$ in 2009), $t_{(16)} = 6.89$, $p < 0.0001$ (Fig. 3).

Aerial Imagery

Between 1985 and 2005, woody vegetation increased 51.5% on Santa Cruz Island (Table 2; Fig. 1a & 1b). This resulted from an increase in coastal sage scrub and chaparral of 45.1 and 6.4%, respectively (Table 2). In contrast, non-native grassland cover decreased 47% whereas barren ground decreased 4.5%. Other classes of woody vegetation showed less dramatic changes: oaks, pines, riparian, and woody exotic vegetation all changed by less than 3% over 20 years.

Carbon Sequestration

We estimate that post-eradication vegetation changes resulted in a 97% increase in total aboveground and belowground

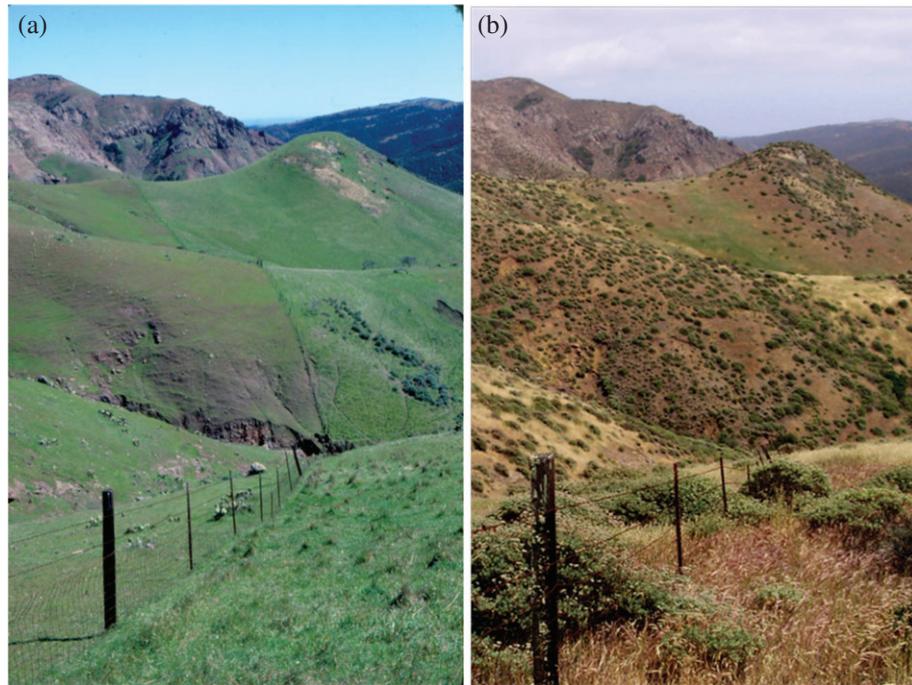


Figure 3. Landscape vegetation changes on Santa Cruz Island, California from historical photographs taken pre- (March 1980) (a) and 19 years post-eradication (May 2008) (b) of invasive ungulates. Note change from grassland (a) to woodland (b).

Table 1. Species, form, mean percent cover, longevity, and provenance of each plant species encountered along vegetation transects in 2012.

Species	Vegetation Form	Mean % of Total Sampled	Mean % of Vegetation Form Sampled	Longevity	Provenance
<i>Avena</i> spp.	Herbaceous	31	70	Annual	Non-native
<i>Bromus</i> spp.	Herbaceous	6	14	Annual	Non-native
<i>Aristida</i> spp.	Herbaceous	3	7	Perennial	Native
<i>Stipa</i> spp.	Herbaceous	3	7	Annual	Native
<i>Acmispon argophyllus</i>	Herbaceous	1	2	Perennial	Native
<i>Eriogonum arborescens</i>	Woody	44	79	Perennial	Native
<i>Salix</i> spp.	Woody	3	5	Perennial	Native
<i>Prunus ilicifolia</i>	Woody	3	5	Perennial	Native
<i>Artemisia californica</i>	Woody	3	5	Perennial	Native
<i>Baccharis pilularis</i>	Woody	1	2	Perennial	Native
<i>Lupinus albifrons</i>	Woody	1	2	Perennial	Native
<i>Quercus pacifica</i>	Woody	1	2	Perennial	Native

carbon storage (1.73 vs. 3.41 Tg C pre- vs. post-eradication, 1 Tg = 10^{12} g). Similarly, we estimate that the stored aboveground and belowground nitrogen pool increased by 17% (132,000 vs. 155,000 mt N pre- vs. post-eradication) with the shift toward woody vegetation (using values of 603 g/m² in grassland and 729 g/m² in mature woody scrub; Zavaleta & Kettley 2006).

Discussion

Historical accounts, photographs, and field evidence indicate that the native grassland, riparian, coastal scrub, chaparral, oak woodland, and conifer communities on Santa Cruz Island underwent notable change with the onset of introduced vertebrate herbivory (Brumbaugh et al. 1982). Junak et al.

(1995) hypothesized that, with the onset of grazing, native coastal sage scrub-dominated communities were replaced by non-native-dominated grasslands. Studies conducted soon after herbivore removal on Santa Cruz Island noted some increases in not only native woody vegetation (Klinger et al. 1994) but also non-native grass and forb cover (Klinger et al. 2002; Ogden & Rejmanek 2005; Morrison 2007; Cohen et al. 2009). Studies conducted within the first decade of herbivore removal noted that, rather than an increase in native-dominated shrub cover, the primary response of the plant community was a decrease in bare ground as it was invaded by non-native herbaceous vegetation (Klinger et al. 1994). However, the recovery of the island plant community over the long term has not been examined in detail.

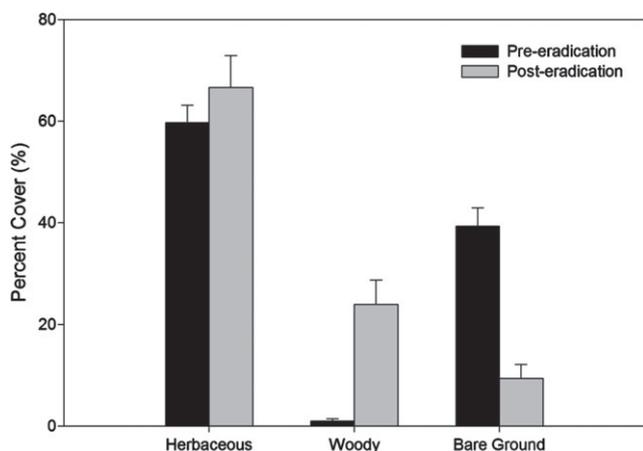


Figure 4. Changes (mean ± SE) in overstory vegetation cover on Santa Cruz Island, California pre- (1980) versus 20 years post-eradication (2012) of invasive ungulates measured using point-intercept transects. Herbaceous includes forbs, grasses, and thatch; woody includes shrubs and trees; bare ground includes soil/rock and outcrop. Data from 1980 from Van Vuren and Coblenz (1987).

Table 2. Changes in overstory vegetation cover pre- (1985) versus 20 years post-eradication (2005) of grazing ungulates from Santa Cruz, Island, California.

Vegetation Type (Jones et al. 1993)	Percent Cover 1985	Percent Cover 2005	Difference
Grasses	67.5	20.5	-47.0
Coastal sage scrub	3.3	48.5	45.2
Chaparral	14.6	21.0	6.4
Oaks	4.2	2.7	-1.5
Island ironwood	0.4	0.7	0.3
Pines	1.2	2.7	1.5
Riparian	1.9	1.5	-0.4
Woody exotics	0.1	0.1	0
Barren	6.8	2.3	-4.5
Aggregated vegetation type			
Grasses/barren	74.3	22.8	-51.5
Woody vegetation	25.7	77.2	51.5

Data from aerial images modified from Jones et al. (1993) and Cohen et al. (2009).

Our analyses demonstrate that since the cessation of introduced ungulate grazing, Santa Cruz Island has experienced a dramatic, unassisted recovery from an overstory plant community dominated by non-native, herbaceous vegetation toward an overstory community dominated by native woody vegetation, indicating that this system had sufficient resilience to recover much of its previous plant structure through 20–28 years of unassisted restoration. Our results suggest that even while initial post-eradication studies on Santa Cruz Island showed that communities responded to invasive herbivore removal with a surge in exotic grasslands (Klinger et al. 2002), long-term recovery toward a native dominated woody overstory is occurring in the absence of active restoration efforts.

Key to discussions of recovery is how it is defined. In this case, the goal of island managers was not recovery of “pristine” conditions (i.e. vegetation consisting exclusively of diverse,

non-native plants). Instead, the a priori definition included increased cover of native-dominated vegetation (Schuyler 1993), implicitly recognizing that Santa Cruz Island vegetation will likely continue to include an understory dominated by non-native annual grasses and that vegetation diversity may be less than pre-eradication levels. This could persist in an alternate stable state, influencing fire regimes, erosion rates, and animal habitats. Using this definition, recovery is occurring across Santa Cruz Island, as indicated by the consistency of intensive vegetation transect data and larger-scale data from landscape photographs and aerial imagery. Broad recovery of overstory native woody plant communities is occurring, with over 51% of the island’s overstory vegetation cover shifting to native coastal scrub and chaparral communities. Corry (2006) documented similar plant community recovery across widespread sampling locations on San Miguel and Santa Barbara Islands following invasive herbivore removal. This further reinforces the likelihood that the recovery we documented at our Picacho Diablo site is occurring across much of Santa Cruz Island.

There are several sources of potential bias that may affect conclusions drawn from transect data. First, some of the herbaceous cover had likely disappeared by our sampling in July leading to classification of herbaceous cover as bare ground. This bias is likely not significant because we focus our analyses on changes in woody vegetation overstory that is perennially present. Second, point-intercept sampling is biased toward the most abundant species in a community, which would lead to an over-representation of certain species in our analysis (e.g. *Eriogonum* spp., *Avena* spp.). Finally, transects, photoanalysis, and aerial surveys do not account for understory that lies beneath woody vegetation. For this reason our analyses are restricted to describing changes in plant overstory across all sampling methodologies.

Invasive herbivore-induced disturbance of vegetation is widespread in the Mediterranean-type climate ecosystems of California (Fleischner 1994; Vila & Sardans 1999; Corry 2006). Historically, Santa Cruz Island has been subjected to a variety of invasive herbivore species (cattle, pigs, sheep, horses) and a mosaic of grazing intensities (Van Vuren & Coblenz 1987). It is likely that recovery may occur at different rates across the island, depending upon grazing history, local soil conditions, and microclimate differences (Klinger et al. 2002; Ghorbani et al. 2007). Other factors such as slope steepness and aspect, exposure to fog (Brumbaugh et al. 1982; Gutierrez et al. 2000), and the presence of animal seed dispersers (Morrison et al. 2011) will likely influence the recovery rate and composition of Channel Island plant communities. Specifically, the portions of the island that are less steep and have deeper soils may follow different recovery trajectories than the steeper areas with more shallow soils. A comparative study of Santa Cruz Island and other islands that experience the same general climatic conditions, such as Guadalupe Island (240 km from mainland Baja California, Mexico) that has recently been released from grazing pressure by the eradication of feral goats (*Capra hircus*); (Campbell & Donlan 2005), would improve our ability to predict the importance of microclimates, soils, slopes, and

seed dispersal to unaided recovery following invasive herbivore eradication.

Important increases in ecosystem services have occurred due to non-native herbivore removal. Vegetation maps show that bare ground was reduced by 4.5%. Much of the bare ground cover pre-eradication consisted of sheep trails and landslides, which likely resulted in significant gully erosion, slope failures, and soil loss (Pinter & Vestal 2005). This loss may be exacerbated during high rainfall events such as those occurring during El Niño (Pinter & Vestal 2005). Van Vuren et al. (2001) found that reduction in bare ground on Santa Cruz Island has resulted in decreased surface run-off rates and reduced soil erosion rates. In addition, increased soil stability has likely resulted from increased woody vegetation cover. Perhaps most significantly, we estimated that invasive herbivore eradication resulted in a near doubling of stored C and a 17% increase in stored N. This is likely a conservative estimate of changes in important greenhouse gasses, because the roughly 2,000 cattle, 45,000 sheep, and 5,000 pigs removed from the island (Morrison 2007) were also a constant annual source of methane production until their removal. Continuing vegetation recovery will likely only further increase sequestration of these gasses and affect subsequent recruitment of other vegetation types. This has important implications for the role that invasive herbivore removal from island ecosystems can play in mitigating anthropogenic greenhouse gas production. At the same time, greenhouse gas sequestration can become an innovative mechanism to finance island forest reestablishment (Bekessy & Wintle 2008), including islandwide eradications of introduced herbivores.

Simberloff (1990) suggests that restoration is successful if it results in a system whose structure and function are no different than those of the system in a natural, unperturbed state. Islands have been severely altered by invasive species (Croll et al. 2005; Kurle et al. 2008; Keitt et al. 2011) and the eradication of those species is being used more frequently as a tool for island restoration, with 762 herbivore eradications, including 215 ungulate eradications, attempted to date (Keitt et al. 2011). Few of these efforts have been monitored as the ecosystem recovers, so it is not clear whether recovery occurs, at what rate, and to what extent. Jones and Schmitz (2009) conducted a meta-analysis on recovery of ecosystems from a range of human impacts. While they found that recovery from the impacts of invasive species generally required less than a decade, the recovery of terrestrial ecosystems from human impacts requires an average of approximately 20 years. In a world with limited resources to apply toward ecosystem recovery, it is important to direct efforts toward strategies likely to deliver the highest conservation return (Holl & Aide 2011). It is also important to understand the timeframe required for restoration to occur so as to set realistic expectations for managers, stakeholders, and funders. Our results illustrate how long-term post-eradication monitoring can inform where passive restoration may be adequate and where active intervention may be necessary. Perhaps most importantly, our results provide encouraging support to the notion that native vegetation on Santa Cruz Island is on a positive recovery trajectory.

Implications for Practice

- Transects, historical photographs, and vegetation maps revealed a conversion from bare ground to native, woody cover after two decades of post-eradication passive recovery.
- Total carbon sequestered on the island nearly doubled with recovery of native woody vegetation after eradication.
- Long-term post-eradication monitoring can inform where passive restoration may be adequate and where active intervention may be necessary.

Acknowledgments

Our research was completed at the University of California Natural Reserve System Santa Cruz Island Reserve on property owned and managed by The Nature Conservancy. The authors express gratitude to the UCSC BIOE151 field course participants; to M. Tang, Z. Wedel, and J. Anderson-Huxley for help in the field; to G. Dayton, A. Borker, and D. Spatz for helpful feedback; to L. Laughrin for logistical assistance; to P. Raimondi for aid in statistical analysis; to B. Cohen, C. Boser, and C. Cory from The Nature Conservancy for access to vegetation map data and input on study design; and to the UCSC Ecology and Evolutionary Department, UC LEADS, and the UC Natural Reserve System Student Travel Fund for funding this research. Additional support was provided by funding from the Packard and National Fish and Wildlife Foundations.

LITERATURE CITED

- Bekessy, S. A., and B. A. Wintle. 2008. Using carbon investment to grow the biodiversity bank. *Conservation Biology* **22**:510–513.
- Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* **325**:1121–1124.
- Blumstein, D. T., and J. C. Daniel. 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences* **272**:1663–1668.
- Bowen, L., and D. Van Vuren. 1997. Insular endemic plants lack defenses against herbivores. *Conservation Biology* **11**:1249–1254.
- Boyer, A. G., and W. Jetz. 2010. Biogeography of body size in Pacific island birds. *Ecography* **33**:369–379, DOI: 10.1111/j.1600-0587.2010.06315.x.
- Brumbaugh, R. W., W. H. Renwick, and L. L. Loeher. 1982. Effects of vegetation change on shallow landsliding, Santa Cruz Island, California. General Technical Report PSW, No. 58, 397–402. Berkeley, CA.
- Campbell, K., and C. J. Donlan. 2005. Feral goat eradications on islands. *Conservation Biology* **19**:1362–1374.
- Chapuis, J. 2004. Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate change. *Biological Conservation* **117**:167–179.
- Clewell, A., and T. McDonald. 2009. Relevance of natural recovery to ecological restoration. *Ecological Restoration* **27**:122–124.
- Cohen, B., C. Cory, J. Menke, and A. Hepburn. 2009. A spatial database of Santa Cruz Island vegetation. Pages 229–244 in C. C. Damiani and D. K. Garcelon, editors. *Proceedings of the 7th California Islands Symposium*, Institute for Wildlife Studies, Arcata, California.
- Corry, P. M. 2006. Vegetation dynamics following grazing cessation on the Channel Islands, California. Dissertation, University of North Carolina at Chapel Hill.

- Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**:1959–1961.
- Curio, E. 1966. How finches react to predators. *Animals* **9**:142–143.
- DellaSala, D., A. Martin, R. Spivak, T. Schulke, B. Bird, M. Criley, C. vanDaalen, J. Kreilick, R. Brown, and G. Aplet. 2003. A citizen's call for ecological forest restoration: forest restoration principles and criteria. *Ecological Restoration* **21**:14–23.
- Donlan, C. J., B. R. Tershy, and D. A. Croll. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. *Journal of Applied Ecology* **39**:235–246.
- Faulkner, K. R., and C. C. Kessler. 2011. Pages 295–299 in Live capture and removal of feral sheep from eastern Santa Cruz Island, California. IUCN, Gland, Switzerland.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in Western North America. *Conservation Biology* **8**:629–644.
- Frankham, R. 2010. Challenges and opportunities of genetic approaches to biological conservation. *Biological Conservation* **143**:1919–1927.
- Ghorbani, J., M. G. Le Duc, H. A. McAllister, R. J. Pakeman, and R. H. Marrs. 2007. Temporal responses of propagule banks during ecological restoration in the United Kingdom. *Restoration Ecology* **15**:103–117.
- Gutierrez, J. R., G. Arancio, and F. M. Jaksic. 2000. Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. *Journal of Vegetation Science* **11**:641–648.
- Holl, K. D., and T. M. Aide. 2011. When and where to actively restore ecosystems? *Forest Ecology and Management* **261**:1558–1563.
- Jones, H. P., and O. J. Schmitz. 2009. Rapid recovery of damaged ecosystems. *PLoS ONE* **4**:e5653.
- Jones, J. A., S. A. Junak, and R. J. Paul. 1993. Progress in mapping vegetation on Santa Cruz Island and a preliminary analysis of relationships with environmental factors. Pages 97–104 in Proceedings of the 3rd California Islands Symposium, Santa Barbara, California.
- Junak, S., T. Ayers, R. Scott, D. Wilken, and D. Young. 1995. A flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, California.
- Keitt, B., K. Campbell, A. Saunders, M. Clout, Y. Wang, R. Heinz, K. Newton, and B. Tershy. 2011. The global islands invasive vertebrate eradication database: a tool to improve and facilitate restoration of island ecosystems. Pages 74–77 in C. R. Veitch, M. N. Clout and D. R. Towns, editors. *Island invasives: eradication and management*. IUCN, Gland, Switzerland.
- Klinger, R. C., P. T. Schuyler, and J. D. Sterner. 1994. Vegetation response to the removal of feral sheep from Santa Cruz Island. Pages 341–350. The Fourth California Islands Symposium, Santa Barbara, California.
- Klinger, R. C., P. T. Schuyler, and J. D. Sterner. 2002. The response of herbaceous vegetation and endemic plant species to the removal of feral sheep from Santa Cruz Island, California. Pages 141–154 in C. R. Veitch and M. N. Clout, editors. *Turning the tide: the eradication of invasive species*. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, United Kingdom.
- Köhler, M., and S. Moyà-Solà. 2009. Physiological and life history strategies of a fossil large mammal in a resource-limited environment. *Proceedings of the National Academy of Sciences of the United States of America* **106**:20354–20358.
- Kurle, C. M., D. A. Croll, and B. R. Tershy. 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. *Proceedings of the National Academy of Sciences of the United States of America* **105**:3800–3804.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Vol 1. Princeton University Press, Princeton, New Jersey.
- Minnich, R. A. 1980. Vegetation of Santa Cruz and Santa Catalina Islands. Pages 123–138 in *The California Islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, California.
- Mooney, H. A., and R. J. Hobbs. 2000. *Invasive species in a changing world*. Island Press, Washington, DC.
- Morrison, S. A. 2007. Reducing risk and enhancing efficiency in non-native vertebrate removal efforts on islands: a 25-year multi-taxa retrospective from Santa Cruz Island, California. Pages 398–409. *Managing vertebrate invasive species: proceedings of an International Symposium*, USDA/APHIS/WS, National Wildlife Research Center, Fort Collins, Colorado, USA. USDA National Wildlife Research Center Symposia.
- Morrison, S. A., T. S. Sillett, C. K. Ghalambor, J. W. Fitzpatrick, D. M. Graber, V. J. Bakker, et al. 2011. Proactive conservation management of an island-endemic bird species in the face of global change. *BioScience* **61**:1013–1021.
- Ogden, J. A. E., and M. Rejmanek. 2005. Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: implications for management. *Biological Conservation* **125**:427–439.
- Parkes, J. P., D. S. L. Ramsey, N. Macdonald, K. Walker, S. McKnight, B. S. Cohen, and S. A. Morrison. 2010. Rapid eradication of feral pigs (*Sus scrofa*) from Santa Cruz Island, California. *Biological Conservation* **143**:634–641.
- Pinter, N., and W. D. Vestal. 2005. El Niño-driven landsliding and postgrazing vegetative recovery, Santa Cruz Island, California. *Journal of Geophysical Research* **110**:F02003.
- Prach, K., and R. J. Hobbs. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology* **16**:363–366.
- Schuyler, P. 1993. Control of feral sheep (*Ovis aries*) on Santa Cruz island, California. Pages 443–452 in *The Third California Islands Symposium: recent advances in research on the California Islands*. Santa Barbara, California.
- Simberloff, D. 1990. Community effects of biological introductions and their implications for restoration. Pages 128–136 in D. R. Towns, C. H. Daugherty, and I. A. E. Atkinson, editors. *Ecological restoration of New Zealand islands*. Conservation Sciences Publication No. 2 Department of Conservation, Wellington, New Zealand.
- Terborgh, J. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923–1926.
- Van Vuren, D., and B. E. Coblenz. 1987. Some ecological effects of feral sheep on Santa Cruz Island, California, USA. *Biological Conservation* **41**:253–268.
- Van Vuren, D., M. L. Johnson, and L. Bowen. 2001. Impacts of feral livestock on island watersheds. *Pacific Science* **55**:285–289.
- Vila, M., and J. Sardans. 1999. Plant competition in Mediterranean-type vegetation. *Journal of Vegetation Science* **10**:281–294.
- Zavaleta, E. S., and L. S. Kettley. 2006. Ecosystem change along a woody invasion chronosequence in a California grassland. *Journal of Arid Environments* **66**:290–306.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution* **16**:454–459.