Vegetation change following rabbit eradication on Lehua Island, Hawaiian Islands

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Abstract Lehua Island is a 112 ha tuff crater that lies 1.2 km north of Niihau in the Hawaiian Islands. This island hosts ten species of nesting seabird and is the second largest seabird colony in the main Hawaiian Islands. The first biological survey of the island was conducted in 1935 when European rabbits (*Oryctolagus cuniculus*) were already established on the island. A few years later Pacific rats (*Rattus exulans*) were detected. There are no historical data to indicate when these species were introduced and their impacts on the island community remain largely unknown. Fossil pollen and seabird bones indicate that there have been remarkable changes on the island. In an attempt to restore the island, rabbits were eradicated in November 2005. A series of transects were used to monitor vegetation change three years before and three years after rabbit eradication. A significant increase in vegetation cover and species diversity was immediately evident after rabbit eradication. The majority of this new biomass was largely due to the spectacular spread of the introduced grass *Setaria verticillata* in addition to introduced shrubs. Although plant cover of some native species increased, overall native plant cover declined. Of concern was the establishment of *Verbesina encelioides* (Asteraceae). This non-native herb has caused devastating changes to native plant communities and seabird habitat elsewhere in Hawaii. Rabbit removal in isolation does not appear to be beneficial for the conservation of Lehua Island. In such a highly invaded system, a successful restoration programme should incorporate concurrent control of non-native plants and non-native herbivores.

Keywords: Invasive species eradication, island restoration, *Oryctolagus cuniculus*, *Rattus exulans*, herbivory, introduced species, secondary effect

INTRODUCTION

The accidental or intentional introduction of alien species is one of the most serious threats faced by island ecosystems (Vitousek 1988). Rabbits (*Oryctolagus* sp.) have been released on more than 800 islands worldwide (Flux and Fullager 1983), often with devastating consequences. For example, rabbits introduced to Laysan Island in the Northwest Hawaiian Islands denuded the island within 20 years resulting in the loss of 22 species of plants and the extinction of three species of endemic landbirds (Watson 1961).

Introduced mammalian herbivores affect ecosystems in several ways. Through browsing, grazing, and trampling, they may cause the population decline of palatable plant species by decreasing their survival, growth, or fitness (Crawley 1997; Chapuis *et al*. 2004). At the community level, these effects can lead to drastic changes in diversity and species composition (Gilham 1961; North *et al*. 1994). Herbivore actions can lead to extensive erosion (Watson 1961; Kessler 2002) and stimulate cascading changes in entire ecosystems (Holmgren 2002; Maron *et al*. 2006).

Introduced herbivores can have devastating effects on those island plant communities without a history of vertebrate herbivory. Plants evolve defences in direct proportion to the risk of herbivory, and because defences are costly, production decreases when herbivore pressure is absent (Marquis 1991). Consequently, insular endemic plants that evolved in the absence of vertebrate herbivores typically lack defences against herbivory making them more palatable and susceptible to extirpation (Bowen and Van Vuren 1997).

Recent advances in techniques for removing introduced mammals from islands have made it an increasingly used management option. However, research has shown that species removal in isolation can also result in unexpected changes to other ecosystem components (North *et al*. 1994; Courchamp *et al*. 1999; Bergstrom *et al*. 2009). Furthermore, the secondary effects of alien removal become more likely as the number of interacting invaders increases in ecosystems and as aliens in late stages of invasion assume the functional roles of native species (Zavaleta *et al*. 2001).

Lehua Island is considered a priority site for conservation work by the Offshore Islet Restoration Committee (OIRC), which aims to preserve and restore Hawaiian offshore islets. There are no native terrestrial mammals presently or historically on the island, but two non-native mammals have been introduced. European rabbits (*Oryctolagus cuniculus*) were detected during the first survey of the island's flora and fauna in 1936 (Caum 1936) and the Coast Guard reported Pacific rats (*Rattus exulans*) in 1940 (Bishop Museum, vertebrate collection). The OIRC planned for the eradication of all non-native mammals from the island starting with a rabbit eradication programme in November 2005.

There is little historical data on the long-term effects of rats and rabbits on the Lehua island community. However, paleoecological studies indicate that there have been major changes on the island. Fossil pollen types identified on Lehua are typical of dry lowland forests, among the most endangered of all ecosystems in the Hawaiian archipelago. The following tree and shrub genera have been identified: *Psydrax, Pritchardia, Cordia, Thespesia, Rauvolfia, Zanthoxylum, Pittosporum, Dodonaea* and *Chenopodium* (OIRC, unpublished data). This contrasts with grassland/shrubland that was described during the first botanical survey of the island in 1936 (Caum 1936). Further altering the system is the introduction of 28 non-native species, which have become naturalised during the past 70 years (ca 56 total species present) and form a dominant component of the grassland/shrubland (Wood *et al*. 2004).

The goals of this study were to use the rabbit eradication as an opportunity to evaluate the secondary effects of herbivore removal in a highly altered ecosystem and to aid managers by identifying early invasions of non-native plant species.

METHODS

Study site and history

Lehua Island is an uninhabited tuff crater 1.2 km north of Niihau and 31 km west of Kauai, Hawaii (22°01'N, 160°06'W). The crater is highly eroded and nearly half submerged, forming a steep, crescent-shaped island of 112 ha with a maximum elevation of 213 m (Palmer 1936). The environment is harsh with highly seasonal precipitation and intense solar radiation. Annual rainfall is less than 600 mm with the majority falling during intense winter storms (Giambelluca *et al*. 1986). Lehua is the second

Pages 290-294 In: Veitch, C. R.; Clout, M. N. and Towns, D. R. (eds.). 2011. Island invasives: eradication and management. IUCN, Gland, Switzerland.

largest seabird colony in the main Hawaiian islands, with 10 species nesting in large numbers (VanderWerf *et al*. 2007) and is protected as part of the Hawaii State Seabird Sanctuary. Nutrient input by seabirds significantly enriches soils and plants on the island (unpublished data).

As part of a Lehua restoration plan, it was hoped that the combined removal of rats and rabbits would reduce soil erosion, encourage colonization by small, rare seabird species and allow for an extensive planting effort. The rabbit eradication programme began in November 2005. Approximately 95% of the rabbits were killed within the first 10 days of hunting and the remainder were eradicated in January 2006 (Island Conservation, unpublished data). Logistical difficulties delayed the rat eradication until 2008.

Pacific rats were present on Lehua throughout the study period. Surveys and incidental observations indicate that the rat population increased after rabbit eradication. A rodent survey conducted before rabbit eradication in April 2004 detected no rats or rat activity in 154 trap nights (R. Doratt, unpublished data). Surveys conducted after rabbit eradication in June and September 2007 detected 137 rats in 500 trap nights and 39 rats in 223 trap nights respectively (R. Doratt, unpublished data). Incidental observations are consistent with these results as rats were increasingly commonly seen after rabbit eradication. Rats were observed regularly during the day and night, whereas prior to eradication such observations were extremely rare.

Vegetation monitoring

Vegetation monitoring began in September 2003, three years before rabbit eradication (effectively December 2005) and continued twice annually until April 2008. Sampling periods corresponded with the end of the wet season in April or May and the end of the dry season in September or October. Sampling focused on the most accessible, vegetated portions of the island. On the inner crescent, seven 100 m transects were randomly established in an east-west direction following the contours of the crescent. On the outer crescent, 15 x 50 m transects were randomly established along the lower ridges in a north-south direction with 1-3 transects on each ridge.

Point-intercept sampling (Mueller-Dombois and Ellenberg 1974) was used along these transects to estimate plant cover and species diversity (inverse of Simpson's index) for each transect during the sampling period. Sampling points were monitored at 1 m intervals noting species present at each point. Transect ends were marked with steel rods fitted with a PVC pipe for greater visibility and recorded with GPS. Plant cover was estimated by dividing the number of targets "hit" by the number of potential targets. To evaluate relative changes in the abundance of individual species, growth forms (forb, grass, shrub) or status (native, non-native), 2 x 2 chi-square contingency tables were used. To assess whether rabbit eradication affected total plant cover or mean species diversity, two-sample T-tests were used on the combined pre-eradication and post-eradication data. Statistical analyses were calculated using Minitab 15.

RESULTS

Two months after rabbit eradication, heavy rain (over twice the historical average) fell on Lehua from February 2006 to April 2006 (Fig. 1). Vegetation sampling in April 2006 showed a 53% increase in vegetation cover and a 71% increase in species diversity from the previous sample in October 2005.

Rabbit eradication was followed by a 59.7% increase in vegetation cover ($t = 5.54$, $p < 0.001$; Table 1; Fig. 2) that resulted from significant increases in non-native grasses and shrubs (Table 1). Cover by grasses increased by 83.3% (Chi-square value = 455.5, $p < 0.001$), predominantly from a rapid expansion of *Setaria verticillata*, and shrubs increased by 79.0% (Chi-square value = 25.0, $p < 0.001$). There was no significant change in forb cover. Overall, there was a 112.8% increase (Chi-square value = 751.0, $p < 0.001$) in cover by non-native species compared with a 33.9% decrease in the cover of native species (Chi-square value = 62.5, $p < 0.001$).

Plant diversity increased by 31.7% after rabbit eradication ($t = 4.12$, $p < 0.001$; Fig. 2). Ten new species were recorded in the study area. One was an indigenous forb, *Solanum americanum*. The remainder were non-native forbs (*Bidens pilosa, Boerhavia coccinea*, *Chenopodium carinatum, Conyza bonariensis, Crotalaria pallida, Emilia fosbergii, Sonchus oleraceus*) and grasses (*Chloris barbata, Digitaria* spp*., Paspalum conjugatum*). Although not detected in the study area, *Verbesina encelioides* became locally abundant after rabbit eradication and has since spread to different parts of the island.

DISCUSSION

Vegetation change following rabbit eradication

Vegetation on Lehua responds to winter rains with increases in cover and diversity, followed by a period of senescence during the dry season. The period of high rainfall coupled with rabbit removal in 2005 may have synergistically facilitated vegetation change. However, the effects were not due to rainfall alone as the increased vegetation cover and diversity remained significantly higher once rainfall levels returned to normal (Fig. 1).

The removal of rabbits from Lehua was followed by a remarkable increase in vegetative cover and a corresponding decrease in bare ground. This may have positive effects

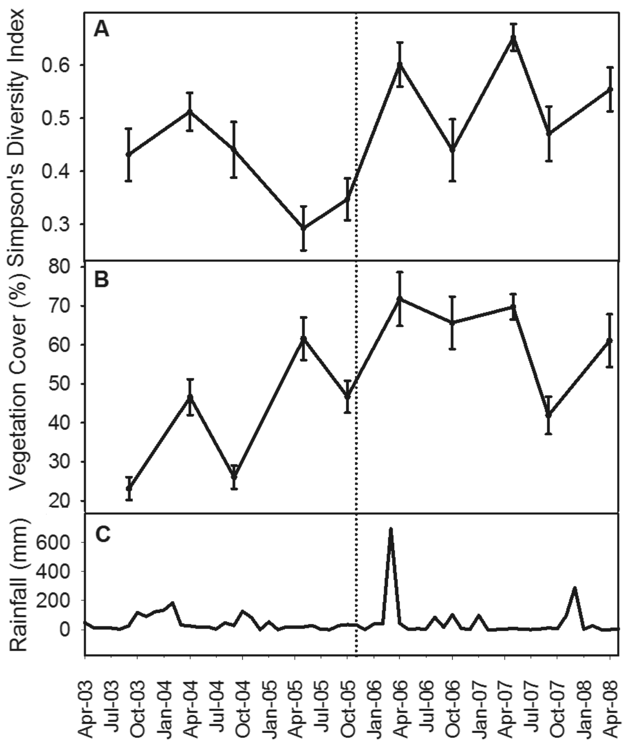

Fig. 1 A. Changes in species diversity with SE bars; B. Changes in vegetative cover with SE bars; and C. Rainfall between 2003 and 2008. The dashed line indicates when rabbits were effectively removed from Lehua. No weather station exists on Lehua. Monthly precipitation data were obtained from the closest weather station most resembling conditions on the island: Waimea rain gauge on Kauai's south shore (National Climatic Data Center).

Table 1 Frequency of occurrence and change in vegetative cover (%) after rabbit eradication. Chi-square analysis is not applicable to very small values; these species are indicated in gray. Native species are indicated with a (+). Bold text represents significant changes in vegetation cover when pre- and post-eradication of rabbits was compared.

Species	Frequency of occurrence pre eradication	Frequency of occurrence post eradication	Change in veg. cover (%)	Chi-square value
Grasses				
Cenchrus ciliaris	13.11	13.43	2.43	0.22
Cenchrus echinatus	0.37	1.66	**349.83**	41.98***
Chloris barbata	0.00	0.23	N/A	
Digitaria spp.	0.00	0.72	N/A	
Eragrostis amabilis	0.02	0.13	557.45	
Panicum torridum+	5.05	4.43	-12.34	2.11
Paspalum conjugatum	0.00	0.06	N/A	
Setaria verticillata	5.98	24.36	**307.35**	660.23***
Forbs				
Ageratum conyzoides	1.30	0.47	-64.02	19.04***
Bidens pilosa	0.00	0.02	N/A	
Conyza bonariensis	0.00	0.04	N/A	
Emilia fosbergii	0.00	0.09	N/A	
Gamochaeta purpurea	0.04	0.00	-100.00	
Sonchus oleraceus	0.02	0.02	9.57	
Chenopodium carinatum	0.00	0.19	N/A	
Jacquemontia ovalifolia+	10.33	5.57	**-46.04**	74.99***
Sicyos maximowiczii+	0.31	0.83	**167.09**	11.93***
Chamaesyce hirta	0.02	0.04	119.15	
Crotalaria pallida	0.00	0.02	N/A	
Waltheria indica+	0.33	1.85	**460.76**	54.42***
Boerhavia coccinea	0.00	0.21	N/A	
Boerhavia repens+	0.04	0.06	64.36	
Portulaca oleracea	0.02	1.98	10090.43	
Portulaca pilosa	0.21	0.06	-70.12	
Anagallis arvensis	0.17	0.11	-39.13	
Solanum americanum+	0.00	0.13	N/A	
Unknown forb	0.06	0.02	-63.48	
Shrubs				
Pluchea carolinensis	0.06	0.11	82.62	
Pluchea indica	1.03	1.53	48.86	4.96*
Abutilon grandifolium	1.09	2.26	**107.41**	20.72***
Combined values				
Bare ground	60.74	39.11	**-35.61**	459.97***
Grass	24.52	44.96	**83.32**	455.45***
Forb	12.91	11.89	-7.89	2.35
Shrub	2.17	3.89	**79.04**	24.99***
Native species	16.06	10.62	**-33.88**	62.45***
Non-native species	23.55	50.13	**112.83**	751.08***

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

on the ecosystem through decreased erosion and increased burrow stability for nesting seabirds. However, the increased plant cover came from the release of non-native plants, primarily grasses and shrubs. These changes may seem counterintuitive as grasses and shrubs dominated the vegetation community before rabbit removal, but there are two factors at work to determine the effects of herbivory on plant community composition and structure. Herbivores directly affect vegetation through 1) feeding selectivity, and 2) recovery capacity of plants fed upon (see review by Augustine and McNaughton 1998). As such, the non-native grasses and shrubs must have been highly palatable (shown by their increase after rabbit removal), but also highly tolerant of tissue loss relative to other species, allowing them to achieve dominance under browsing pressure.

Two species of native plants increased in abundance (*Sicyos maximowiczii* and *Waltheria indica*; both browsed by rabbits) after rabbit eradication, but there was an overall decline in native plant cover. The native species that declined were likely less palatable to rabbits (no evidence of browsing damage), giving these natives a competitive advantage compared to highly palatable species. This advantage allowed the natives to co-dominate with competitive, fast-growing grasses. When released from herbivory, the grasses increased in range and density to the exclusion of these formerly abundant natives. Furthermore, the grasses have formed impenetrable mats in some areas precluding the germination of additional species. Similar trends have been observed following rabbit eradications elsewhere (e.g., Chapuis *et al.* 2004; North *et al.* 1994).

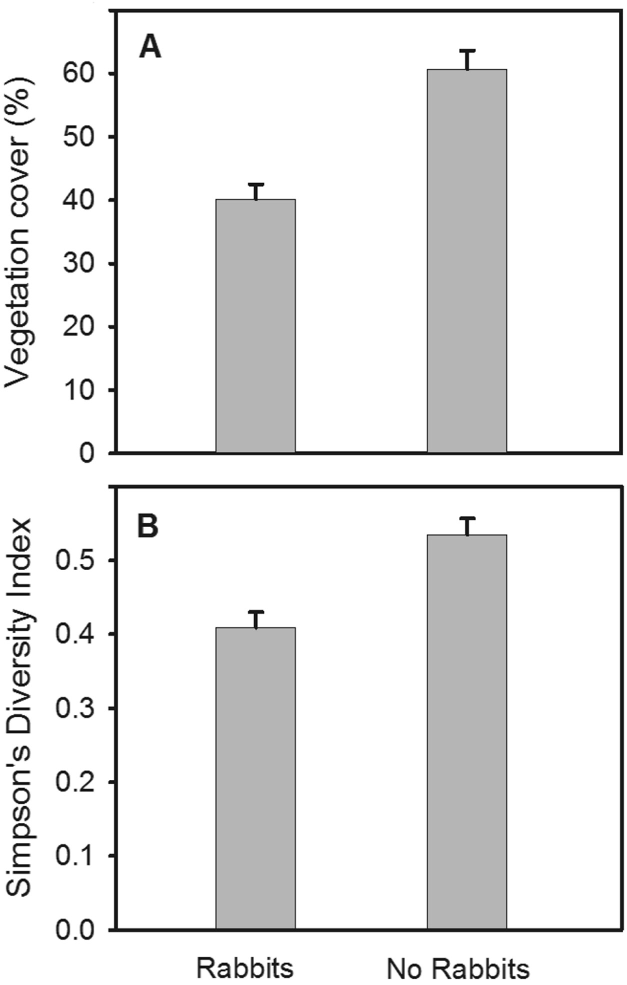

Fig. 2 Average change in vegetative cover A. and species diversity B. before and after rabbit eradication with SE bars. Both were statistically significant with $p < 0.001$.

Along with the increase in vegetation cover there was a significant increase in the mean number of plant species. This included ten species previously undetected in the study area, nine of which were non-native. Other incipient invasions of non-native species were found outside the study area including *Verbesina encelioides*, an invasive plant in the sunflower family that has caused devastating changes to native plant communities and seabird habitat elsewhere in Hawaii (Feenstra and Clements 2008). *Verbesina* has been reported on Lehua in the past but did not become established until rabbits were eradicated. This observation supports the theory that herbivores may suppress new plant invasions (Becerra and Bustamante 2007).

Rat influence

An attempted rat eradication, delayed until January 2008, was unsuccessful. After the rabbits were eradicated the rat population appeared to expand in response to an increase in available resources. Rats are omnivores that can alter vegetation composition, structure and dynamics through selective herbivory and granivory (Allen *et al*. 1994; Campbell and Atkinson 1999; Towns *et al*. 2006). They also contribute to recruitment depression through destruction of flowers, fruits, seeds, seedlings and plant parts (eg. Cuddihy and Stone 1990; Allen *et al*. 1994; Campbell and Atkinson 1999). This makes inferences about vegetation change following rabbit eradication challenging as herbivory by the increased rat population may be affecting plant community composition.

Effects of long-term herbivory

The premise behind the removal of rabbits and rats from Lehua Island was that because introduced herbivores target palatable species of plants their effects would be greatest on insular endemic species. In reality, the situation was more complex and involved links between introduced plants, rats and rabbits, plant palatability, tolerance to herbivory and competitive ability. Long-term suppression by herbivores, and subsequent depletion of the seed bank, results in a decline of preferred species which have low herbivory tolerance (Hunt 2001) and in some situations these changes can lead to alternate ecosystem states (Mack and D'Antonio 1998; Maron *et al*. 2006). Introduced rats and rabbits were present on Lehua for at least 70 years during which the ecosystem appears to have changed from a coastal dry forest to coastal dry grassland/shrubland. Of nine genera historically on the island, four are regarded as highly palatable to rats including *Pritchardia* (Athens *et al*. 2002; Perez *et al*. 2008), *Pittosporum* (Stone 1985; Cuddihy and Stone 1990), *Psydrax* (Medeiros *et al*. 1986) and *Zanthoxylum* (Cuddihy and Stone 1990). An additional genus is woody with large, fleshy fruits (*Rauvolfia*), which is also a characteristic favoured by rats (Meyer and Butaud

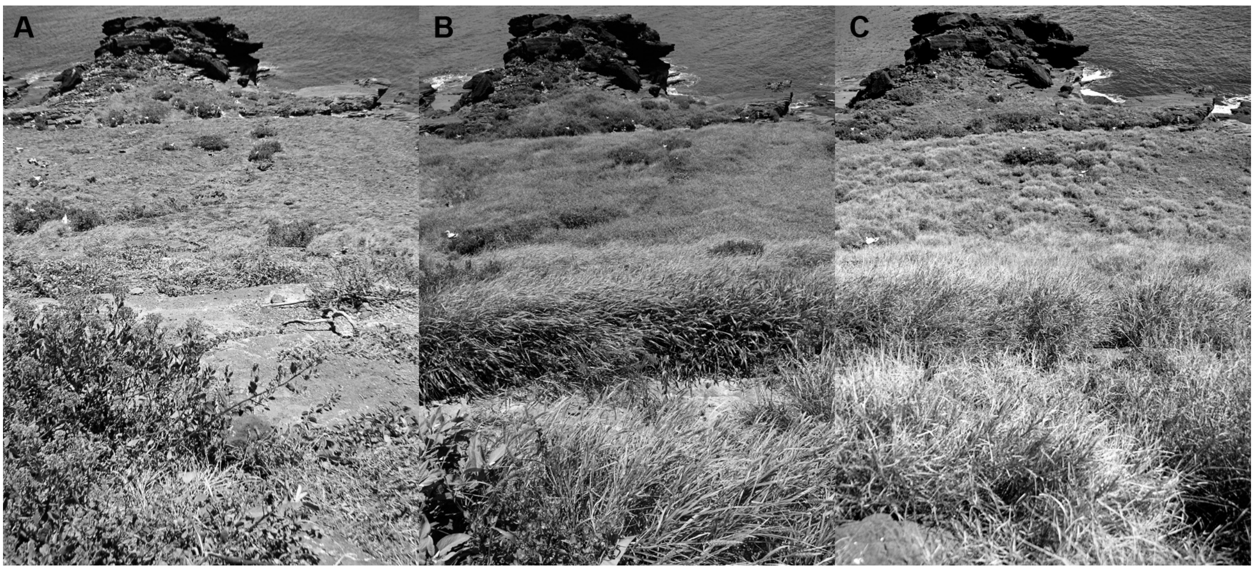

Fig. 3 Photo comparisons of transects on the outer crescent monitored in A. April 2004, before to rabbit eradication; B. April 2006, after rabbit eradication and an extremely wet season; and C. April 2008, more than two years after rabbit eradication.

2009). More recently, extirpated native species such as the succulents *Scaevola sericea* and *Portulaca villosa* may have been targeted by both rats and rabbits.

Conservation implications

The removal of non-native herbivores is presumed to have beneficial effects for native plant communities, especially since herbivore-induced changes can be reversible in some situations (eg. Copson and Whinam 1998; Donlan *et al*. 2002). However, when ecosystems experience multiple, or long-term invasions, the situation can become increasingly complicated and chances of successful reversal may be less likely (Zavaleta 2002; Courchamp *et al*., 2003). The adverse effects caused by the long-term presence of rabbits and rats on Lehua in combination with introduced plant species has resulted in a highly altered ecosystem. In this new system, introduced rabbits suppressed non-native plants and the removal of rabbits in isolation resulted in an increase of non-native plant cover, a corresponding decrease in native plant cover, and an increase in the abundance of rats. A problem for restoration of this seabird sanctuary is the increased rat population that followed rabbit removal. This may be increasing predation pressure on nesting birds. Additionally, short-term management of the island in the presence of rats means efforts to replace non-native plant species with native species must be delayed as native species are sensitive to rat damage. In situations like Lehua a restoration programme should address concurrent control of all non-native plants and animals.

ACKNOWLEDGEMENTS

I thank Holoholo Charters for generously providing transport to and from Lehua, the Hawai'i Division of Forestry and Wildlife for logistical assistance and granting landing permits, the U.S. Coast Guard for granting landing permits, Rogelio Doratt and Laura Driscoll of the U.S. Department of Agriculture for conducting rodent surveys. I would also like to thank the wonderful people that provided logistical and field assistance including Maya LeGrande, Ken Wood, Jaap Eijzenga, Chris Swenson, Adonia Henry, Lindsay Young, Kim Morishige and Bongo Lee. Valuable comments on the manuscript were made by Aaron Shiels and David Duffy. Funding for this project was made possible by the Offshore Islet Restoration Committee.

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