RESEARCH ARTICLE

Increase in Wedge-tailed Shearwaters and Changes in Soil Nutrients following Removal of Alien Mammalian Predators and Nitrogen-fixing Plants at Kaena Point, Hawaii

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Abstract

A predator-proof fence was built at Kaena Point Natural Area Reserve, Hawaii in 2010 as part of an ecosystem restoration project. All non-native mammalian predators were removed and are now excluded. Non-native plants are being removed and native species are being outplanted. We monitored abundance and reproduction of *Puffinus pacificus* (wedge-tailed shearwaters), collected soil samples before and after fence construction, and examined the relationship between changes in shearwater numbers and soil nutrients. Shearwater numbers increased over time, from 11 young produced in 1994 to 3,274 in 2012. The average number of shearwaters produced during the 3 years before and after fence construction increased from 614 ± 249 to $2,359 \pm 802$ (384% increase). The average number of shearwater pairs attempting to nest also increased during the same periods, from $3,265 \pm 827$ to $4,726 \pm 826$ (45% increase). Soil samples from 2010 to 2013 showed an overall decline in concentration of ammonium (NH_4^+) and no change in concentration of nitrate (NO_3^-) or orthophosphate (PO_4^{3-}). However, there was a positive relationship between changes in shearwater numbers and changes in ammonium. Examination of spatial patterns in nutrient abundance showed that the highest nutrient concentrations occurred in areas dominated by the non-native nitrogen-fixing plants *Leucaena leucocephala* and *Prosopis pallida*. Removal of these plants caused local nutrient declines, but increases in shearwater numbers have countered this at some points. We anticipate that shearwaters and other seabirds will replace non-native plants as the dominant source of nitrogen and phosphorous and facilitate recovery of a native-dominated plant assemblage.

Key words: island restoration, predator fence, predator removal, *Puffinus pacificus*, seabirds.

Introduction

Oceanic islands provide extreme examples of both the importance of birds in transporting nutrients from the marine environment and of the perturbations that alien species can cause to native species and ecosystem nutrient dynamics (Blackburn et al. 2004; Croll et al. 2005; Maron et al. 2006; Wardle et al.

2009). Seabirds strongly influence nutrient dynamics on islands because of their abundance, large body size, mobility, and, frequently, the absence of other nutrient sources. Seabirds can transport nitrogen (N) and phosphorus (P) thousands of miles across the ocean and deposit it on islands in their guano, eggs, and carcasses of their dead (Fukami et al. 2006; Sekercioglu 2006). These nutrients, in turn, support vegetation that provides structural stability to soil for burrows, food for arthropods and other invertebrates, and shade and protection to seabird chicks (Mulder et al. 2009).

The abundance of many seabirds has been greatly reduced recently as a result of predation by non-native animals (Steadman 1995; Jones et al. 2008), diminishing their role as nutrient links and limiting productivity of some island ecosystems (Sekercioglu et al. 2004). Oceanic islands often lacked native land mammals or large predators of any kind, so the species present on such islands are often naïve to predators and thus vulnerable to extinction when predators are introduced by humans

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(VanderWerf 2012). The effects of predator introductions on native species and the trophic cascades that often result have been well described (Croll et al. 2005; Fukami et al. 2006; Mulder et al. 2009; Wardle et al. 2009), and the ability of invasive alien species, both plant and animal, to modify ecosystems and alter nutrient dynamics has received considerable attention recently (Croll et al. 2005).

Predators have been removed from many islands (Nogales et al. 2004; Howald et al. 2007; Phillips 2010; Keitt et al. 2011), which in many cases helped to restore seabirds and more natural ecosystem function (Mulder et al. 2009; Smith et al. 2010). On continents and larger, inhabited islands, eradicating predators and restoring seabird populations has been more difficult. Creation of "mainland islands" with fences to exclude predators is one way of increasing seabird numbers and restoring input of marine nutrients in cases where predators cannot be completely eradicated (Saunders 2001).

Kaena Point Natural Area Reserve is located at the northwestern tip of the island of Oahu and contains one of the best remaining examples of a native coastal ecosystem in Hawaii. Kaena Point also hosts one of the largest seabird colonies in the inhabited Hawaiian Islands, as well as three species of endangered plants. Exclusion of off-road vehicles from the reserve in the early 1990s allowed habitat recovery to begin and encouraged two species of seabirds, *Phoebastria immutabilis* (Laysan albatross) and *Puffinus pacificus* (wedge-tailed shearwater), to breed there. Nesting success of both species was low until regular predator control began in 2000 (Young et al. 2013). Despite regular predator control, up to 15% of albatross nests failed each year because of predators, hundreds of shearwaters were periodically killed, and native plants and their seeds were under constant threat (Young et al. 2009; Lohr et al. 2013).

To end the chronic, and sometimes catastrophic, effects of predation at Kaena Point, a peninsula-style predator fence capable of excluding all mammalian predators was constructed around a 20-ha portion of the reserve in 2011 (Fig. 1; Young et al. 2013). As part of the restoration process, some non-native plants have been removed and native species have been out-planted; both activities continue today. We expected that the restoration efforts, including the predator fence, might have two effects on plant available nutrients. First, we expected an increase in nutrients as a result of increased bird density and reproductive success. Second, we expected the removal of invasive N-fixing plant species *Leucaena leucocephala* (koa haole) and *Prosopis pallida* (kiawe), could reduce nutrients, whereas concurrent plantings of the native N-fixing plant species *Sesbania tomentosa* (ohai) would provide some replacement of those inputs. However, the overall net effect of these activities on plant available nutrients was unknown. Here, we report on the increase in abundance and reproductive success of wedge-tailed shearwaters after fence construction, and we examine associated changes in soil nutrients over time.

We focused on wedge-tailed shearwaters because they are much more numerous and more widely distributed at Kaena Point than Laysan albatrosses. Wedge-tailed shearwaters are widespread in the tropical Pacific and Indian oceans (Onley & Scofield 2007); however, they are largely restricted to
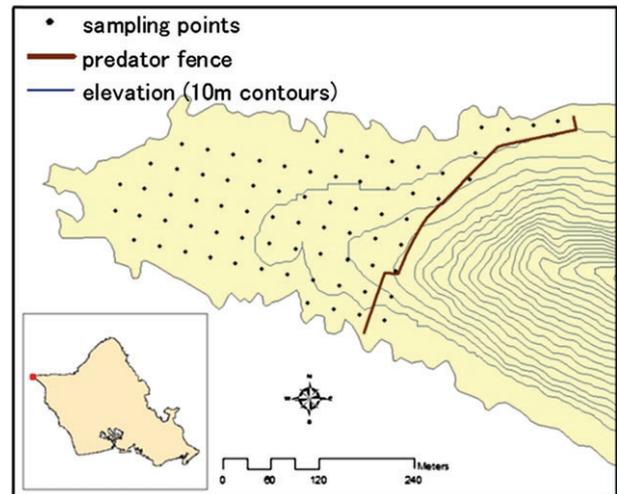
Figure 1. Map of study site at Kaena Point Natural Area Reserve, Hawaii.

predator-free islands. Because of their ground-nesting habits, wedge-tailed shearwaters are vulnerable to predation by a variety of non-native mammals, such as *Canis familiaris* (feral dogs), *Felis cattus* (feral cats), *Herpestes auropunctatus* (small Indian mongooses), and *Rattus* spp. (rats); (Smith et al. 2002, 2006). In Hawaii, wedge-tailed shearwaters are abundant on some of the uninhabited Northwestern Hawaiian Islands and also some small islets off the southeastern Hawaiian Islands, but few nesting colonies exist on the larger islands inhabited by people because of the abundance of alien predators (Harrison 1990; Smith et al. 2002; Smith et al. 2006; Marie et al. 2014).

Methods

Shearwater Monitoring

Wedge-tailed shearwaters in Hawaii nest in underground burrows, rock crevices, or occasionally on the surface under vegetation (Whittow 1997; VanderWerf et al. 2007). They lay a single egg in late May or June, which is incubated for about 53 days by both parents in alternating shifts lasting several days (Byrd et al. 1983; Floyd & Swanson 1983). Chicks hatch in late July or August and fledge in November or December (Byrd et al. 1983; Whittow 1997; Hyrenbach 2011). We measured reproduction of wedge-tailed shearwaters at Kaena Point in late October or early November from 1994 to 2013, just before chicks fledged, using two methods. From 1994 to 2008, we censused the number of chicks by searching the entire reserve, and we also censused the number of empty nests in which shearwaters attempted to reproduce but failed, as indicated by the absence of a chick and the presence of fresh digging, feathers, droppings, or foot prints. We added the numbers of chicks and empty nests to obtain the total number of nesting attempts. We estimated nest success as the proportion of all nests in which there was a chick. It is possible that some empty nests with droppings and so forth were made by pre-breeders prospecting for a nest site, which would result

in an underestimate of nest success. The total number of nesting attempts was not counted in 1994, and no surveys of any kind were conducted in 2004 or 2005.

In 2008, when the growing number of birds made a census less practical, we began using a plot-based method to estimate the number of chicks and nests. In the plot method, we counted the numbers of chicks and nests within 60 circular plots distributed uniformly across the reserve (Fig. 1). We started with plots of different sizes (4, 5, 6, and 8 m in radius), and we compared the results from each plot size to a census done concurrently to determine which plot size produced the most accurate results, which we then used in all subsequent years.

Soil Sampling and Nutrient Analysis

We collected soil samples in March 2010 (8 months before fence construction) and October 2013 (3 years after fence construction) at 45 points that formed the center of the same plots used to monitor shearwaters. If a point fell on rocky substrate that prevented soil collection, we collected the sample from a point 30 cm to the west, or as close as possible. We collected samples with a small trowel inserted 10 cm into the soil. Air-dried samples were stored in sealed plastic bags at room temperature until analysis, which is standard practice (Sparks et al. 1996).

We prepared soil samples for plant available nutrient extraction by passing them through a 2 mm sieve and lightly grinding them with a mortar and pestle to achieve homogeneity. Inorganic forms of nitrogen, that is, nitrate (NO_3^-) and ammonium (NH_4^+), were extracted using an aerobic inorganic method combining soil and 2 M KCl in a 1:10 ratio and shaken for 1 hour (Sparks et al. 1996). Orthophosphate (PO_4^{3-}) was extracted using Olsen's Method (Olsen et al. 1954). For each sample, 2 g of soil was combined with 40 mL of 0.5 M sodium bicarbonate ($NaHCO_3$) at pH 8.5 and shaken for 30 minutes. All samples were filtered and stored frozen in 50 mL Falcon tubes until analysis on a QuikChem 8500 Series 2 flow injection analysis system (Lachat Instruments, Loveland, CO, U.S.A.). Nutrient concentrations were quantified using colorimetric determination, with either QuikChem Method 12-207-04-1-F (NO_3^- and NH_4^+) or QuikChem Method 12-115-01-1-B (PO_4^{3-}) (Lachat Instruments 2008). For every 15 samples, we re-extracted a subsample to confirm repeatability.

Data Analysis

We examined temporal patterns in shearwater abundance and reproduction using regression, with year as the independent variable and number of nests, number of chicks, or nest success as the dependent variable. We compared average concentrations of NO_3^-, NH_4^+, and PO_4^{3-} in samples from 2010 to 2013 using paired *t* tests. We examined the relationship between shearwater numbers and soil nutrients using regression analysis, with change in number of shearwaters before and after the fence as the independent variable and change in NO_3^-, NH_4^+, or PO_4^{3-} concentration as the dependent variable. To remove some of the annual variation in changes in shearwater numbers,

Table 1. Summary statistics from cross validation of interpolations for bird density data (total nests and chick number) and plant available nutrients (NO_3^-, NH_4^+, and PO_4^{3-}).

	2010			2013		
	Mean Error	*RMS*	*RMSS*	*Mean Error*	*RMS*	*RMSS*
Total nests	−0.01	6.71	1.10	−0.03	10.16	1.01
Chick number	−0.001	1.69	1.09	−0.08	5.67	0.99
NO_3^-	0.18	43.46	0.92	−0.11	21.43	1.03
NH_4^+	0.14	48.13	0.92	−0.24	30.11	1.17
PO_4^{3-}	−0.06	45.35	1.05	−1.00	28.64	0.98

RMS, root mean square error; RMSS, root mean square standardized error.

we averaged the number of shearwaters over the 3 years before and after fence construction.

We employed ordinary kriging in ArcGIS 10.3 to further examine the spatial distribution of bird density (i.e., nests and chicks) and plant available nutrients (i.e., NO_3^-, NH_4^+, and PO_4^{3-}) over the entire reserve. Interpolation results were cross-validated and then assessed with mean error, root mean square (RMS) error, and root mean square standardized (RMSS) (Table 1). Mean error is the averaged difference between the observed and predicted values, RMS reflects how close the predicted and observed values are (the smaller value the better with respect to the magnitude of measurement values), and RMSS estimates the prediction variability (a valid interpolation will have a value close to 1.0). RMS error estimates for the predicted nutrient data were larger than those for the bird density. In particular, the nutrient data in 2010 had high RMS errors; however, all RMSS errors were near 1.0, indicating a valid interpolation. High variability in the observed versus predicted values is logical, given the high heterogeneity of the data (see Results Section). The high density of grid sampling within the experimental design gives strength and validity (i.e., RMSS near to 1.0) to the interpolated results even when high RMS error exists.

Results

Shearwater Monitoring

In 2008, the 8-m radius plots resulted in more accurate estimates than any of the smaller plots. Compared to the known values from the census, 4- and 5-m radius plots underestimated the number of chicks, and 4-, 5-, and 6-m radius plots overestimated the number of nests (Fig. 2). We therefore used only 8-m radius plots in all subsequent surveys from 2009 to 2013.

The number of wedge-tailed shearwater chicks produced at Kaena Point increased over time, from 11 in 1994 to 3,274 in 2012 (Fig. 3; $F_{[1,16]} = 26.37$, $p < 0.001$, $R^2 = 62.2\%$). The total number of shearwater nests at Kaena Point also increased over time (Fig. 3; $F_{[1,15]} = 130.55$, $p < 0.001$, $R^2 = 89.7\%$). Shearwater nest success showed a generally increasing trend, but there was considerable annual variation and the overall pattern was not significant (Fig. 3; $F_{[1,15]} = 2.27$, $p = 0.15$, $R^2 = 13.1\%$). However, average nest success was higher from 2000 to 2013 (38% ± 5%), when predators were either controlled or excluded,
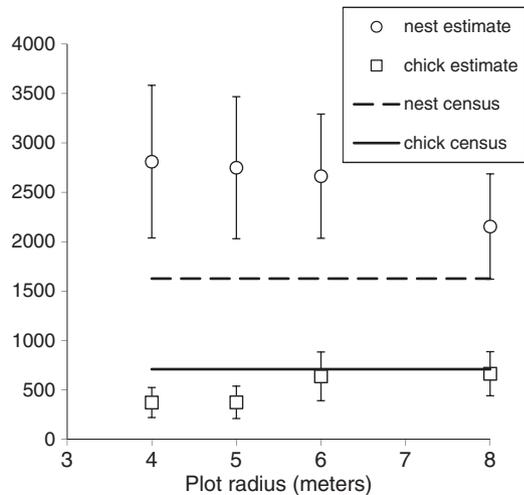
Figure 2. Accuracy of estimates of numbers of wedge-tailed shearwater chicks and nests from different plot sizes compared to actual values from a census. Error bars are standard error.
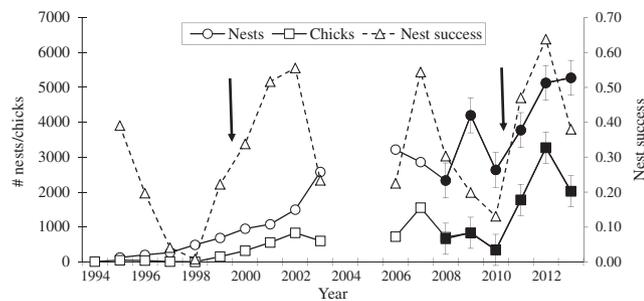
Figure 3. Numbers of wedge-tailed shearwater nests, chicks, and nest success at Kaena Point from 1994 to 2013. For numbers of nests and chicks, solid symbols with error bars (SE) are plot-based estimates, open symbols without error bars are censuses. No counts were conducted in 2004 or 2005. Predator control began in 2000 and predators were excluded with a fence in early 2011 (indicated by arrows).

than from 1994 to 1999, when nests were not protected from predators (17% ± 7%; Mann–Whitney $W = 127.5$, $p = 0.045$). Similarly, nest success was higher after the fence was built (50% ± 8%) than during the 3 years before the fence was built (21 ± 5%). The average number of shearwater chicks produced during the 3 years before and after fence construction increased from 614 ± 249 to 2,359 ± 802, an increase of 384%. The average number of shearwater pairs attempting to nest also increased during the same periods, from 3,265 ± 827 to 4,726 ± 826 (45% increase).

In addition to increasing in number, the distribution of wedge-tailed shearwaters expanded (Fig. 4). Most of the shearwater increase occurred in a band through the center of the reserve, but they also began to expand eastward and westward.

Soil Nutrients

Soil samples collected in 2010 and 2013 showed an overall decrease in concentration of NH_4^+, from 17.6 ± 7.6 μg/g

of soil in 2010 to 7.7 ± 3.3 μg/g of soil in 2013 ($t = 1.98$, $p = 0.05$). There was no overall change in concentration of NO_3^- (27.9 ± 7.1 versus 19.2 ± 3.1 μg/g of soil; $t = 1.26$, $p = 0.21$) or PO_4^{3-} (49.6 ± 6.7 versus 45.0 ± 4.7 μg/g of soil; $t = 0.70$, $p = 0.49$) over the same period.

However, at some sampling points there was an increase in NH_4^+ that was associated with an increase in bird density; regression of changes in NH_4^+ concentration on changes in number of shearwater chicks showed a significant positive relationship (Fig. 5; $F_{[1,44]} = 4.60$, $p = 0.04$). The relationship between NH_4^+ and shearwater numbers was not as strong if the total number of nests was used in the regression instead of the number of chicks ($F_{[1,44]} = 2.53$, $p = 0.12$). Regressions of changes in concentration of NO_3^- and PO_4^{3-} on changes in number of shearwater chicks were not significant (Fig. 5; $F_{[1,44]} = 0.17$ and 0.00, $p = 0.68$ and 0.99, respectively).

Examination of interpolated nutrient concentrations showed geospatially explicit patterns of gains and losses (Fig. 6). All three nutrients showed similar spatial patterns, with higher concentrations in the southeastern corner of the reserve, a rocky area with no shearwaters, where the vegetation is dominated by non-native nitrogen-fixing plants (*Leucaena leucocephala* and *Prosopis pallida*). The nutrient concentrations were generally higher in 2010, but similar spatial pattern persisted in 2013 at a reduced level. Much of the overall decline in nutrients appeared to be associated with removal of non-native nitrogen fixing plants. Since 2010, 18,495 *Leucaena* plants and two patches of *Prosopis* have been removed or treated with herbicide. All individuals of these plants were removed from a portion of the reserve, though there has been some regrowth. The southeastern portion of the reserve, which supported the highest density of *Leucaena* and *Prosopis*, has received some weeding effort but still contains significant numbers of these plants (Fig. 6).

Some areas showed nutrient increases, primarily in areas where shearwater numbers increased, and to a lesser extent where native N-fixing *Sesbania* seedlings were planted in 2012 and 2013. In particular, NH_4^+ increased in the northeastern and north-central portion of the reserve, where some of the largest shearwater increases occurred. Similarly, plant-available PO_4^{3-} increased substantially from 2010 to 2013 in the north-central area of the reserve where shearwater numbers also increased. Intermediate levels of PO_4^{3-} were maintained in the south-central portion of reserve where bird density increased and *Sesbania* were planted.

Discussion

The number of wedge-tailed shearwaters nesting at Kaena Point and their nesting success increased after various management actions were implemented in the early 1990s. Exclusion of off-road vehicles was the first step that allowed seabirds to colonize the site. Control of feral dogs, feral cats, and mongooses from 2000 to 2010 resulted in increased but variable nest success. Removal and exclusion of all predators, including cats, mongooses, rats, and mice, with a predator fence in 2011 resulted in a dramatic improvement in nest success and reduced
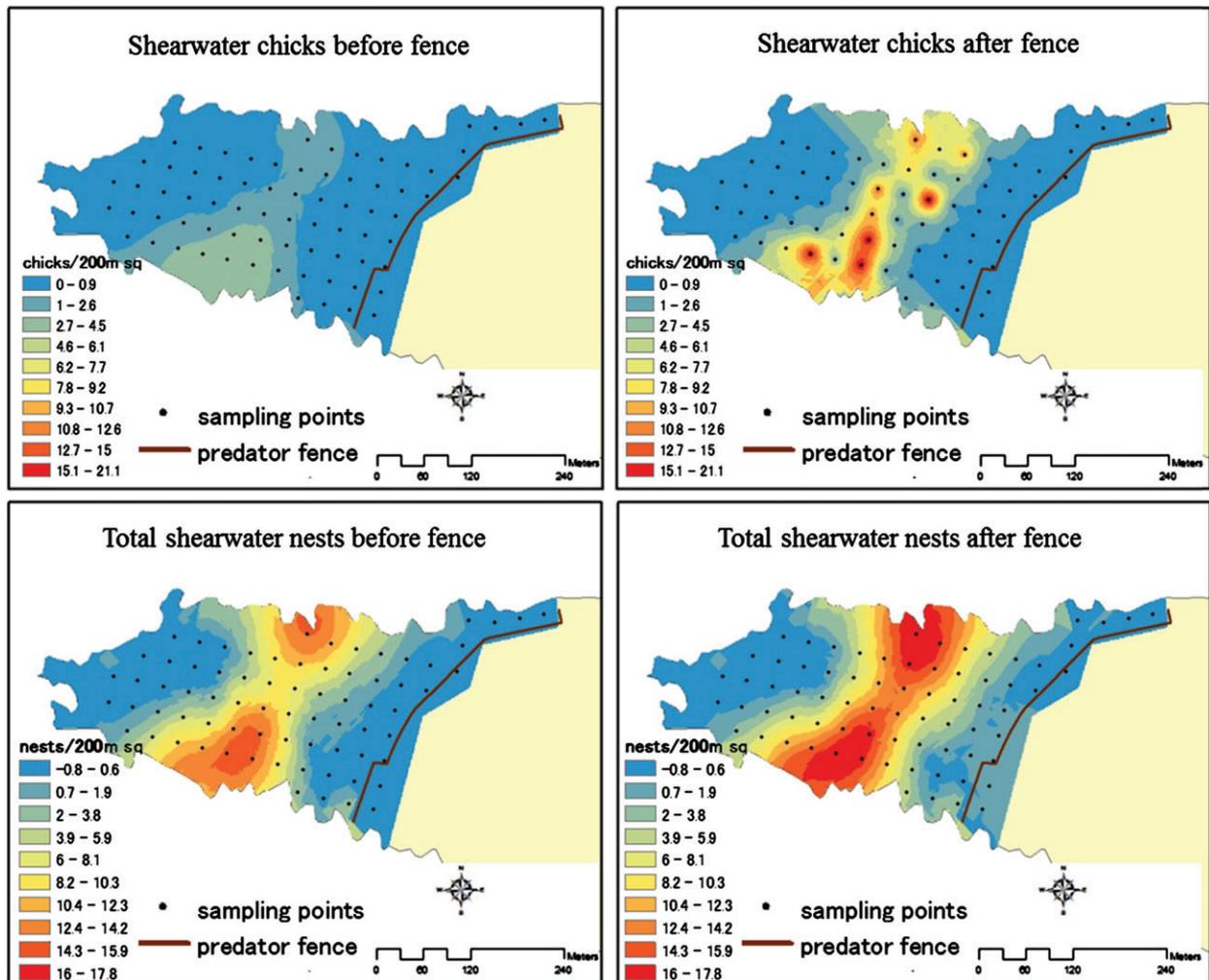
Figure 4. Interpolated spatial abundance of wedge-tailed shearwater chicks and nests at Kaena Point before (2010) and after (2013) completion of a predator fence in 2011.

annual variation. Other studies have documented increases in wedge-tailed shearwater numbers and nesting success following rat eradication (Smith et al. 2002; Marie et al. 2014), and similar increases have been seen in *Calonectris diomedea* (Cory's shearwater) and *Puffinis iherminieri* (Audubon's shearwater) after rat eradications (Igual et al. 2006; Pascal et al. 2008). There will continue to be some natural variation in nesting success of wedge-tailed shearwaters caused by inter-annual variation in oceanographic conditions (Hyrenbach 2011), but we anticipate that the number of shearwaters nesting at Kaena Point will continue to increase, and possibly accelerate, as the larger cohorts produced after fence construction begin to return and breed.

The soil at Kaena Point was generally of poor quality, with low nutrient concentrations similar to those in other simple, sandy, tropical soils. Similar concentrations of NO_3^-, NH_4^+, and P were measured on Palmyra Atoll, a low, sandy island 1,550 km south of Oahu, where nutrient concentrations were higher in areas with native vegetation (100.74 ± 26.10 µg/g

of soil, 65.09 ± 5.23 µg/g of soil, 6.06 ± 0.90 µg/g of soil, respectively) than in areas dominated by non-native *Cocos nucifera* (coconut palms; 8.04 ± 2.31 µg/g of soil, 39.59 ± 6.21 µg/g of soil, 1.63 ± 0.31 µg/g of soil, respectively) (Young et al. 2010). In another similar environment, Mulder and Keall (2001) found that on a small, partially forested island in New Zealand with abundant nesting seabirds, the concentration of NH_4^+ averaged 22.8 ± 55.4 µg/g of soil and that of NO_3^- averaged 148.8 ± 93.2 µg/g of soil. The sandy soil at Kaena Point has low inherent fertility, making inputs from seabirds and plant detritus important drivers of soil fertility and ecosystem health in this system.

Allochthonous marine nutrients are important inputs to nutrient-poor coastal ecosystems such as at Kaena Point and the presence or introduction of predators can interrupt this flow. Furthermore, the removal or absence of seabird predators from islands often results in cascading ecosystem effects on bird populations and soil nutrients. For example, on forested islands in New Zealand where rats were absent and seabirds abundant,

Nitrate

Ammonium
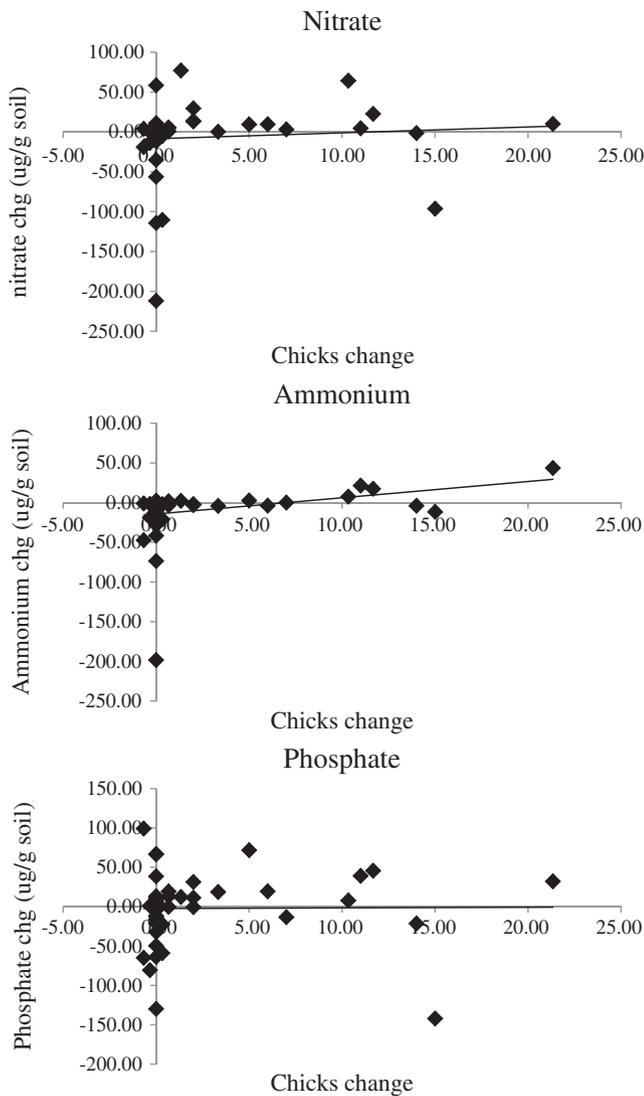
Phosphate

Figure 5. Relationships between changes from 2010 to 2013 in number of wedge-tailed shearwater chicks and concentration of nitrate, ammonium, and orthophosphate in soil samples from Kaena Point.

soil N and P concentrations were greater than on similar islands with rats but without seabirds (Fukami et al. 2006). Similarly, the concentration of P was four times greater on arctic islands in Alaska that were free of invasive foxes and where birds were abundant than on fox-infested, bird-free islands (Croll et al. 2005).

Invasive, non-native plants also alter soil nutrient dynamics, and species capable of biological nitrogen fixation may cause profound ecological shifts (Ehrenfeld 2003, 2010). Plant litter is an important factor in soil nutrient status, particularly in the presence of N-fixing species, whether a native or non-native (Allison & Vitousek 2004). Nitrogen limitation is the most common nutrient deficiency in terrestrial ecosystems and the leaf tissue of N-fixing species is more concentrated in N than non-N-fixing species (McKey 1994). For example, soil inorganic N concentration was four times higher in soils under a

stand of the invasive N-fixing tree, *Myrica faya*, than under native, non N-fixing *Metrosideros polymorpha* (ohia) trees on the Island of Hawaii (Vitousek et al. 1987). There also may be indirect effects of non N-fixing species of invasive trees on soil nutrients. In a coastal system similar to this study, the introduction of coconut palms indirectly reduced the abundance of soil nutrients because birds avoided nesting and roosting in them, thereby interrupting the input of marine nutrients (Young et al. 2010).

As a result of the combination of restoration activities at Kaena Point, there was an overall decline the concentration of NH_4^+, a fundamental plant macronutrient. However, within that overall pattern of decline driven by the removal of dense, invasive plant species, the increase in number of wedge-tailed shearwaters was associated with local increases or maintenance of soil NH_4^+ concentration, presumably caused by the accumulation of their guano. Because the 2013 sampling took place during a dry period at Kaena Point, NH_4^+ and not NO_3^- was more responsive to bird density. If the soil had been sampled during the rainier winter months, the availability of water likely would have promoted nitrification and the production of NO_3^- and the relationship may have shifted (Stark & Firestone 1995).

Although shearwaters have increased in number and range, they still occupy only a fraction of the reserve, and the time scale over which we measured changes in soil nutrients was short. Most studies examining the effects of seabird nutrient input and effects of invasive predators on island ecosystems have compared islands on which predators have been established (and thus seabirds reduced) for several decades (Fukami et al. 2006; Maron et al. 2006). We anticipate that the concentration of NH_4^+ will continue to increase over more of the reserve as shearwaters become more widespread, and that perhaps NO_3^- and PO_4^{3-} will follow.

The number of shearwater chicks produced in a plot was a better predictor of NH_4^+ concentration than was total number of nests. This result is important because it indicates that the presence of a chick for several months was required to cause a significant change in soil nutrients; adults visiting and attempting to nest but failing did not have a significant effect. The greater importance of chicks is not surprising, because adults are present for a shorter time during failed nesting attempts, developing chicks defecate more often, and adults may defecate at sea.

Although the overall relationship between bird density and P was not significant, the geospatial association of bird density and PO_4^{3-} in the northern central area of the reserve suggests that there was a link between increasing seabird numbers and soil P. The lack of a closer relationship between PO_4^{3-} or NO_3^- and bird numbers was caused by only one or two outlying points with atypical results. Native outplantings involved very local application of fertilizer, and it is possible that these outlying points were the result of large, temporary changes in nutrient abundance caused by fertilization.

Individually, each component of the Kaena Point restoration project, including predator removal, increased seabird numbers, removal of non-native N-fixing plants, and planting of
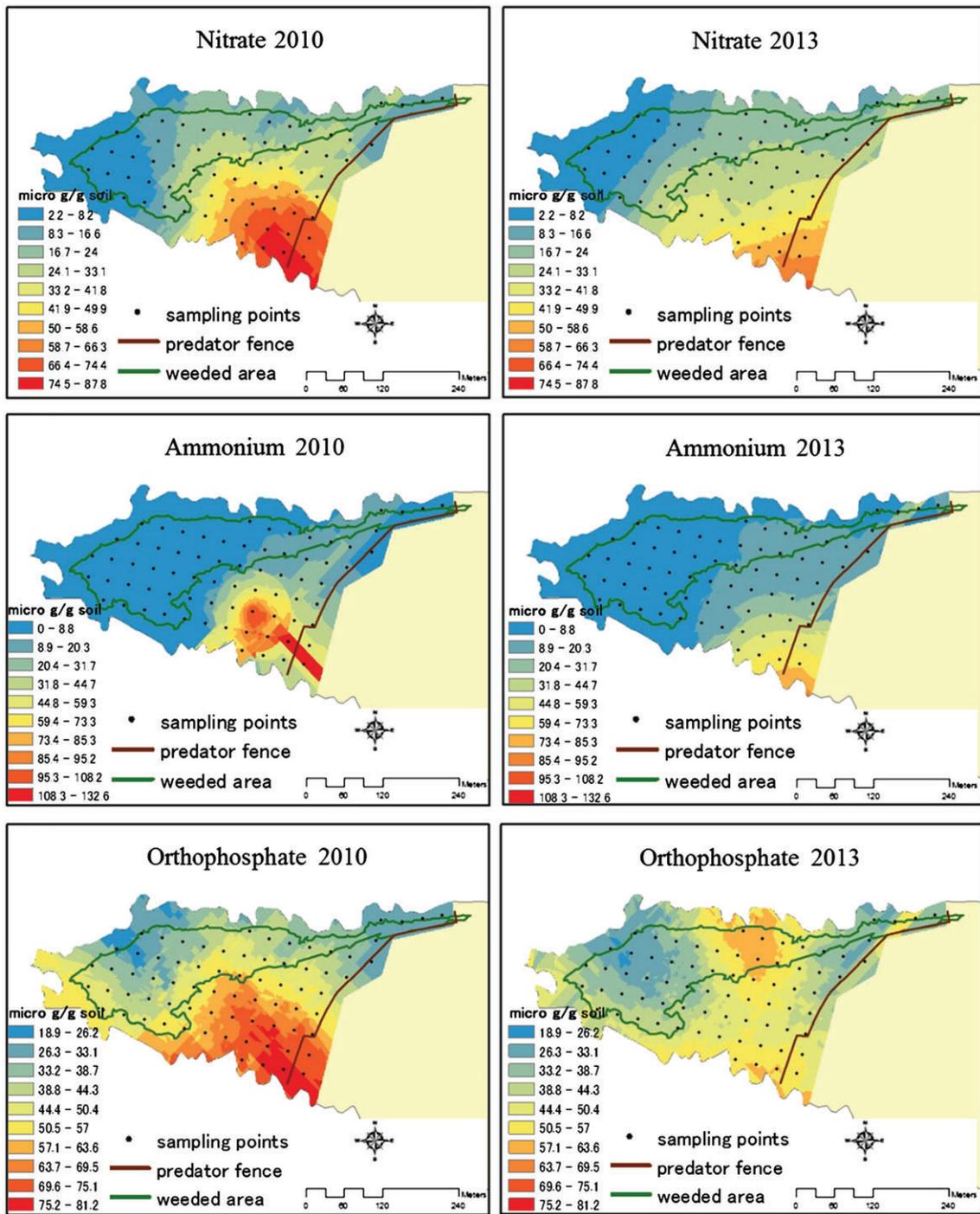
Figure 6. Spatial distribution of nitrate, ammonium, and orthophosphate in soil samples at Kaena Point before (2010) and after (2013) completion of a predator fence in 2011. Non-native nitrogen-fixing plants were removed primarily within the "weeded area."

native N-fixing species, affected soil nutrient status. Collectively, these restoration activities created a dynamic environment where losses of nutrient input through an anthropogenic process is being replaced through a shift to other, natural mechanisms. The overall losses of nutrients associated with removal of N-fixing plant species and their high nutrient inputs of leaf litter, woody debris, and root turnover drove the overall patterns in nutrient change from 2010 to 2013. This overall loss was countered in some areas by gains in nutrient input from seabird nesting and through planting of native N-fixing species. We anticipate that, over time, seabirds and native plants will replace non-native plants as the dominant source of nutrients

in the restored ecosystem at Kaena Point. These findings highlight the importance of considering nutrient inputs into a system when conducting restoration.

Implications for Practice

- Predator fencing can provide a high level of protection that facilitates seabird restoration.
- Soil nutrient concentrations may change slowly as a result of increasing seabird numbers.
- Removing invasive non-native nitrogen-fixing plants can affect soil nutrient dynamics and should be considered in designing a restoration strategy.
- Restoration and management efforts should encompass multiple species and consider the effects of natural and anthropogenic nutrient inputs.

Acknowledgements

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