

A 400-year isotopic record of seabird response to eastern tropical Pacific productivity

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Seabirds play an important role in coastal environments, serving as key indicators of marine ecosystem variability as well as biovectors that influence terrestrial productivity and carbon storage. Long-term estimates of seabird populations remain rare, but lakes that support large seabird populations in their watersheds can archive a history of seabird activity in their sediment records. Here we present a seabird guano-influenced sediment record from Genovesa Crater Lake, Galápagos Islands, home to the world's largest reported colony of red-footed boobies (*Sula sula*) and smaller populations of other species. Influx of seabird guano into Genovesa Crater Lake produces high sedimentary $\delta^{15}\text{N}$ values, and temporal variability in sediment $\delta^{15}\text{N}$ primarily reflects changes in guano influx through time. Two abrupt increases in sedimentary $\delta^{15}\text{N}$ occurred at 1835 AD and 1965 AD, and variance increased following the 1965 AD shift. The largest of these abrupt shifts at 1835 AD coincided, within age model error, with an abrupt increase in marine productivity indicators in sediment records off the coast of Perú and Chile. In the latter part of the twentieth century, $\delta^{15}\text{N}$ values increased during periods of higher landings of Peruvian anchoveta and sardines. We hypothesise that seabird presence and activity on Genovesa increased during periods of higher regional marine productivity. Enhanced variance in Genovesa $\delta^{15}\text{N}$ following the 1965 AD shift may reflect a modern population more susceptible to climate and environmental variability than at any other time in the last 400 years.

Key words guano; seabird; tropical Pacific; nitrogen; productivity

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Introduction

Seabirds provide a valuable gauge of marine ecosystem health (Palczyński *et al.* 2015), and also transport nutrients and contaminants from ocean to land (Anderson and Polis 1999; Caut *et al.* 2012), influencing greenhouse gas emissions (Riddick *et al.* 2012 2014), terrestrial productivity (Ellis 2005; Stapp *et al.* 1999), and carbon storage (Leblans *et al.* 2014; Wardle *et al.* 2007). In regions where seabird colonies are associated with lakes, seabird guano influences lake chemistry, ecology, and productivity (Goodman 1972; Griffiths *et al.* 2010; Keatley *et al.* 2011; Kienel *et al.* 2013; Michelutti *et al.* 2009 2010). The sediment records from such lakes archive variability in guano influx,

particularly via changes in the stable isotopic composition of nitrogen ($\delta^{15}\text{N}$) as well as other geochemical variables (Brimble *et al.* 2009; Liu *et al.* 2006a 2006b; Michelutti *et al.* 2009). Guano $\delta^{15}\text{N}$ values reflect the $\delta^{15}\text{N}$ of metabolised nitrogen in guano (Mizutani and Wada 1988) and scale with trophic level (Hobson *et al.* 1994). Thus, higher sediment $\delta^{15}\text{N}$ values in seabird-influenced lake sediments have been interpreted as reflecting past increases in guano influx and larger seabird populations within lake watersheds (Michelutti *et al.* 2009 2010). However, to date, such sediment investigations have mainly focused on high-latitude lakes. Although there have been some recent studies of guanotrophic lakes and their sediments in the western Pacific and off the southwest coast of Mexico (Kienel

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et al. 2013; Liu *et al.* 2006a), no seabird-influenced paleolimnological records exist in the eastern equatorial Pacific. In this region, seabird census work shows interannual and decadal population variability, including a recent decline in some species, coincident with ocean–atmosphere variability, namely, the El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Anchundia *et al.* 2014; Anderson 1989; Barber and Chavez 1983; Chavez *et al.* 2003). Such variability, with implications for conservation, biodiversity and ecotourism, suggests that a longer temporal record of seabird activity would be valuable, especially in terms of understanding the relationship between seabirds, terrestrial productivity, regional biologic regime shifts and decadal to centennial variability in regional marine productivity.

Here we present a seabird-influenced sediment record from Genovesa Crater Lake, Genovesa Island, Galápagos (Figure 1). The Galápagos are located in a region that experiences a large biologic response to changes in ocean–atmosphere variability on interannual to multidecadal timescales (Barber and Chavez 1983; Chavez *et al.* 2003). The small, uninhabited island of Genovesa is located in the northeastern Galápagos archipelago (0.33° N, 89.96° W). In 1964, 140 000 pairs of red-footed boobies (*Sula sula*, henceforth RFBO), a pelagic seabird, were estimated to inhabit Genovesa (Nelson 1978), and at present, numerous RFBOs nest around the lake, along with a population of great frigatebirds (*Fregata minor*). Guano deposits are copious within Genovesa Crater (Figure 2), and RFBOs have been established as an important biovector for Genovesa Crater Lake, transporting nutrients into the lake system via guano deposition in the lake watershed (Howmiller 1969; Nelson 1978). In the following sections, we introduce the Genovesa sedimentary record

and present new organic $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, carbon, nitrogen and pollen data spanning the last 400 years. We demonstrate that variability in sedimentary $\delta^{15}\text{N}$ values reflects past variability in island seabird activity, which in turn exerts an influence on lake productivity and mangroves in the Genovesa watershed. Most importantly, we find that temporally, $\delta^{15}\text{N}$ variability is coincident with large-scale changes in eastern tropical Pacific productivity.

Study site and methodology

The crater near the centre of Genovesa Island holds a 27.5 m deep hypersaline lake that sits at sea level, at the base of steep, 60 m cliffs [Figure 1(a)]. Red mangroves (*Rhizophora mangle*) line the shore, with a beach area of fine calcium carbonate and organic guano-derived sediment in the northeastern quadrant (Goodman 1972). The sediment record from Genovesa consists of alternating mm to sub-mm scale laminations of organic and carbonate-rich sediments (Colinvaux 1969; Conroy *et al.* 2014; Goodman 1972). Occasional layers of siliceous ooze (composed primarily of the diatom *Chaetocerus* sp.) and tephra are also present throughout the sediment record, as is microscopic ornithogenic matter, including partially dissolved or digested fish bones. Despite the sparse vegetation and steep slopes, there is minimal terrigenous input into the lake from erosion of the crater walls, due to the filtering effect of the mangroves lining the lakeshore. One sediment trap study, coupled with limnologic and weather station data from the island, suggests that more calcium carbonate is precipitated when lake water is more saline (Conroy *et al.* 2014).

Sediment cores analysed in this study were collected from the deepest part of the lake in 2004, 2007 and

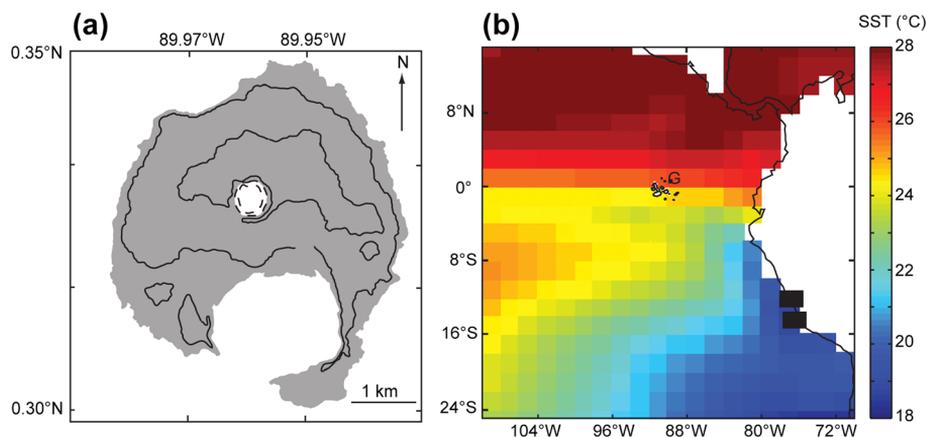


Figure 1 Maps of study region. (a) Genovesa Island. The crater lake is located in the centre of island. Grey shading indicates land, contours denote 100 m elevation. (b) Mean annual SST in the eastern tropical Pacific, 1950–2013 (Smith *et al.* 2008). ‘G’ denotes location of Genovesa. Black rectangles indicate locations of marine sediment records with a nineteenth century $\delta^{15}\text{N}$ shift coincident with the abrupt shift in Genovesa $\delta^{15}\text{N}$ (Gutierrez *et al.* 2009; Salvatteci *et al.* 2014)

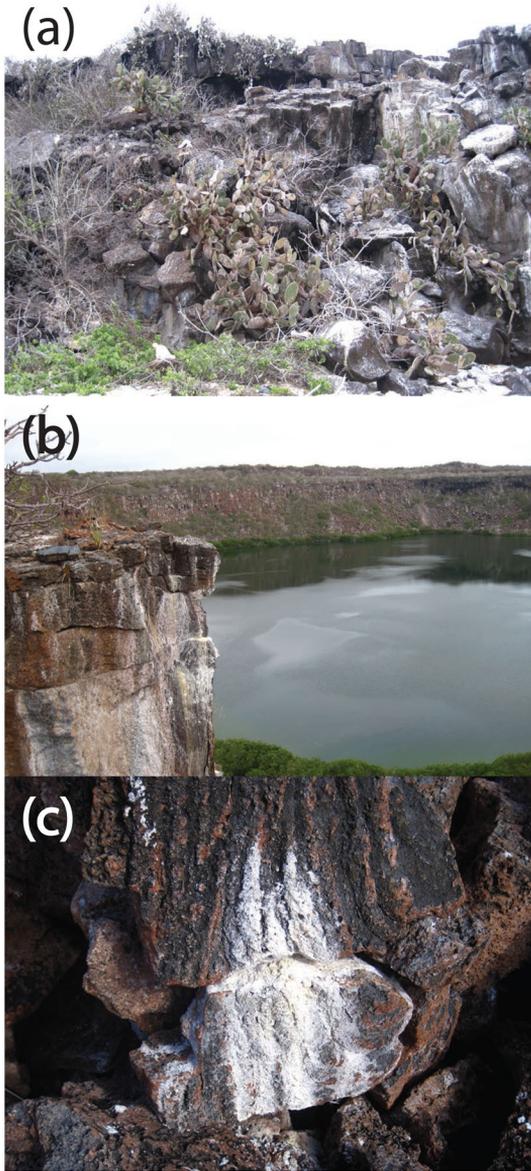


Figure 2 Images of study site, showing copious guano deposits on vegetation (a), crater walls (b), and bedrock (c) of Genovesa

2009. Due to the watery nature of the upper sediments, the upper parts of these cores were extruded in the field at 0.25 cm intervals. The sediment age model is based on ^{210}Pb -estimated ages, using a constant rate of supply model, as well as radiocarbon ages on mangrove leaves collected from a near-shore core that is correlated with cores from deeper waters (Conroy *et al.* 2014). The age model was constructed with the *bacon 2.2* program (Blaauw and Christen 2011) for the upper 54 cm of the Genovesa sediment core (Figure S1), and indicates a mean sedimentation rate of 0.12 cm/year from 1600

to 2004 AD. During the twentieth century, the sedimentation rate was 0.17 cm/year. Age model error (1σ) is approximately multidecadal from 1600 to 1900 AD (± 54 years), and interannual from 1900 to 2004 AD (± 6.5 years, ± 4 years 1960–2004 AD).

We measured organic carbon and nitrogen abundance as well as carbon and nitrogen stable isotope ratios from recent guano samples taken from the crater, extruded core sediment at 0.25 cm intervals, and core material at 0.5 cm intervals. To remove carbonates we pretreated the dried, pulverised sediment samples with 6% sulfurous acid in silver capsules and dried them in a 60°C oven following the procedure outlined by Verardo *et al.* (1990). A subset of untreated samples was also measured to assess any potential treatment effects on the elemental and stable isotopic values. Carbon and nitrogen abundance and stable isotope ratios were measured in the Environmental Isotope Laboratory at the University of Arizona using a Costech elemental analyser (Valencia, California) coupled with a continuous flow gas-ratio mass spectrometer (Finnegan DeltaPlusXL (Bremen, Germany)). Standardisation of elemental analysis is based on acetanilide with a precision of 0.15%. Carbon and nitrogen isotope ratios are reported in δ notation ($R_{\text{sample}}/R_{\text{standard}} - 1 \times 1000$) relative to Vienna Pee Dee Belemnite (VPDB) and air standards, respectively. Analytical precision for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is based on repeated internal standards and is $<0.30\text{‰}$. We found no significant difference in $\delta^{15}\text{N}$ values between treated samples (median $\delta^{15}\text{N}=19.9\text{‰}$, $N=15$) and untreated samples (median $\delta^{15}\text{N}=20.1\text{‰}$, $N=15$); the difference is below analytical precision of 0.30‰ . $\delta^{13}\text{C}$ values are corrected for the Suess effect following procedures discussed in Schelske and Hodell (1995).

Pollen measurements were made in the Department of Biological Sciences at Florida Institute of Technology. The 2004 and 2007 cores were correlated stratigraphically, and sediment samples used for pollen analysis were collected from the top 10.3 cm of the extruded portion of the 2004 core ($n=26$) and from 14–46 cm of the 2007 core ($n=63$), yielding a 43.5 cm pollen record from 2004 to 1600 AD. Sediment samples were spiked with styrene microspheres to quantify pollen concentration and treated with standard pollen preparation protocols (Battarbee and Kneen 1982; Faegri and Iversen 1989). Pollen types were recorded until 300 non-*Rhizophora* grains or 2000 microspheres were counted. *Rhizophora* pollen concentration was calculated in grains/cm³.

Results

Genovesa sediments contain 7–15% organic carbon and 0.6–1.5% nitrogen. Bulk $\delta^{15}\text{N}$ values range from 11.3 to 28.4‰ and $\delta^{13}\text{C}$ values range from -21.4 to -11.8‰ . Median $\delta^{15}\text{N}$ values of the Genovesa sediment samples are 20‰ higher than median $\delta^{15}\text{N}$ values of sediment

from El Junco, a Galápagos highland lake that does not have a seabird colony or substantial guano input [Figure 3(a)]. The median $\delta^{15}\text{N}$ value of Genovesa sediment is 5‰ higher than the median $\delta^{15}\text{N}$ value of Genovesa guano samples taken in 2004 and 2009 [Figure 3(a)]. Genovesa sediment $\delta^{13}\text{C}$ values overlap $\delta^{13}\text{C}$ values of guano samples as well as two samples of algae taken from submerged mangrove roots, but many sediment samples have higher $\delta^{13}\text{C}$ values than the measured algae and guano. The lowest $\delta^{13}\text{C}$ values measured from the Genovesa watershed are *R. mangle* leaves taken from the shoreline of the lake; these median mangrove $\delta^{13}\text{C}$ values are 10‰ lower than median lake sediment $\delta^{13}\text{C}$ values [Figure 3(b)].

Organic carbon and nitrogen abundance covary positively (Pearson's $r=0.53$, $N=105$, $p<0.001$). Sediment N abundance is positively correlated with sediment $\delta^{15}\text{N}$ values (Pearson's $r=0.43$, $N=99$, $p<0.001$) and $\delta^{13}\text{C}$ values are negatively correlated with $\delta^{15}\text{N}$ values (Pearson's $r=-0.49$, $N=107$, $p<0.001$). Two abrupt shifts in mean lake sediment $\delta^{15}\text{N}$ values are clearly apparent in the time series. To test whether these shifts in mean $\delta^{15}\text{N}$ are statistically significant, we used the regime shift detection algorithm of Rodionov (2004) on interpolated, 10-year moving windows of $\delta^{15}\text{N}$ values, from 1605 to 2004 AD, after accounting for autocorrelation by prewhitening the time series using the ordinary least squares method (Rodionov 2006; Seddon *et al.* 2014). We find statistically significant increases in the mean at 1835 AD ($p<0.001$) and 1965 AD ($p<0.001$) [Figure 4(C)]. Following the second regime shift, variance is greater in the $\delta^{15}\text{N}$ time series (Table I). A large increase in C and N also occurs at the 1965 AD regime shift [Figure 4(a,b)], as well as an increase in the concentration of *R. mangle* pollen and a large decrease in $\delta^{13}\text{C}$ values (Figure 5).

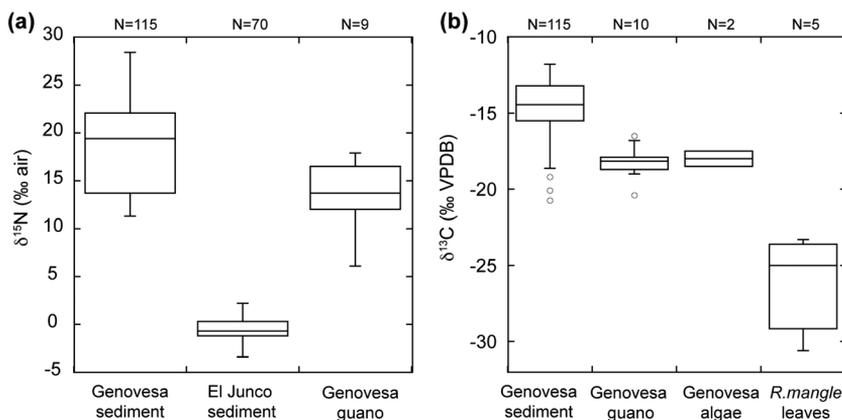


Figure 3 Box and whisker plots of (a) $\delta^{15}\text{N}$ values (‰ air) from El Junco and Genovesa lake sediment, guano. (b) $\delta^{13}\text{C}$ values (‰ VPDB) from mangrove leaves, Genovesa sediment, guano, and algae. Box boundaries are 25th and 75th percentiles, line in box indicates median value, whiskers indicate 90th and 10th percentiles, circles indicate values >90 th and <10 th percentile

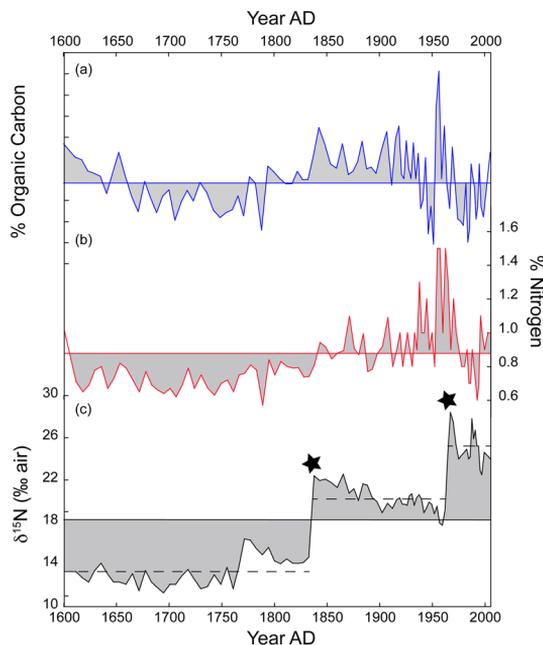


Figure 4 Averaged time series of (a) %C, (b) %N and (c) $\delta^{15}\text{N}$ (‰ air) from three Genovesa sediment cores (plotted individually in Figure S2). Solid line indicates long-term mean of datasets, stars indicate the two detected regime shifts (Rodionov 2004), dashed lines indicate regime-mean $\delta^{15}\text{N}$ values

Discussion

Guano influence on sedimentary $\delta^{15}\text{N}$

Previous studies have shown that guano exerts an influence on Genovesa water chemistry and productivity (Colinvaux 1968; Goodman 1972; Howmiller 1969).

Table 1 Average age model error (1 σ), N , mean and variance of Genovesa $\delta^{15}\text{N}$ for the three distinct 'regimes' determined using the regime detection algorithm of Rodionov (2004; 2006)

	1600–1830 AD	1830–1960 AD	1960–2004 AD
$\pm 1\sigma$ age error	61	24	4
N	39	36	19
Mean $\delta^{15}\text{N}$ (‰ air)	13.3	20.2	25.1
Variance $\delta^{15}\text{N}$ (‰ air)	1.3	1.4	2.5

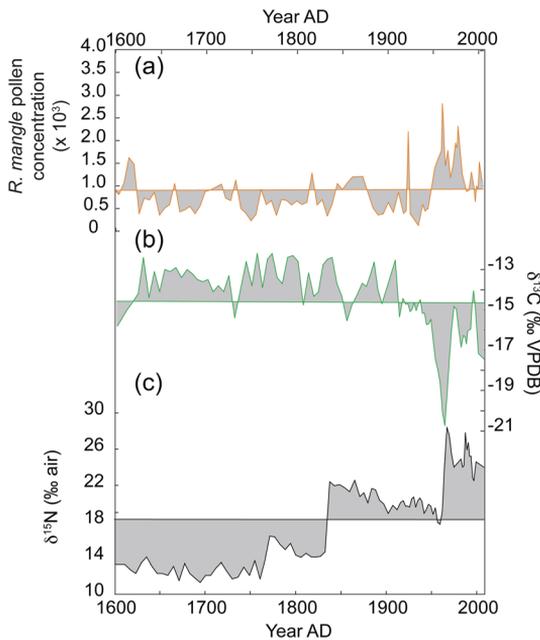


Figure 5 (a) Genovesa $\delta^{13}\text{C}$ (‰ VPDB), (b) *Rhizophora mangle* pollen concentration (grains per cc), (c) Genovesa $\delta^{15}\text{N}$ (‰ air). Isotope values are average of cores Gen-6 and GU-1 between 1800 and 1900 AD (see Figure S2 for individual time series)

Goodman (1972) originally hypothesised that geochemical variability in the Genovesa Crater Lake sediment record could archive a history of seabird presence through time. More recently, in other seabird-influenced lake systems, sediment $\delta^{15}\text{N}$ values have served as an indicator of past seabird abundance, due to the high $\delta^{15}\text{N}$ values of both local guano deposits and guano-influenced lake sediment (Michelutti *et al.* 2009). $\delta^{15}\text{N}$ values, which scale with trophic level, are relatively high in seabirds, which are positioned near the top of the marine food web (Hobson *et al.* 1994). We hypothesise that the high $\delta^{15}\text{N}$ values in the Genovesa sediment record are driven primarily by guano deposition and guano-related nitrogen runoff into the lake. Based on the huge numerical preponderance of RFBOs among the island

seabird species (Harris 1974), it is likely that RFBOs contribute most of the watershed guano, relative to other seabird species. However, the presence of great frigatebirds, which occupy a similar trophic level and kleptoparasitise the food of RFBOs (Nelson 1978), probably also contributes to guano flux and high $\delta^{15}\text{N}$ values in this watershed.

Given the trophic level of RFBOs (4.37 ± 0.79) (Karpouzi 2005; Palomares and Pauly 2014), $\delta^{15}\text{N}$ values of guano in Genovesa Crater Lake watershed should be high, but there are no published $\delta^{15}\text{N}$ values for Genovesa RFBOs. However, the $\delta^{15}\text{N}$ value of RFBO guano should reflect the $\delta^{15}\text{N}$ value of prey items (Mizutani and Wada 1988), which are primarily flying fish (Exocetidae) and squid (Teuthida) (Nelson 1978). The limited, available $\delta^{15}\text{N}$ data for regional flying fish ($13.3 \pm 0.1\text{‰}$; Cruz *et al.* 2012) overlaps the mean value of recent guano $\delta^{15}\text{N}$ ($13.4 \pm 3.8\text{‰}$) from Genovesa. Squid $\delta^{15}\text{N}$ values are more variable, but have a similar range ($\sim 8\text{--}14\text{‰}$) in this region (Ruiz-Cooley and Gerrodette 2012). In turn, Genovesa guano $\delta^{15}\text{N}$ values overlap the $\delta^{15}\text{N}$ values of Genovesa lake sediment. Thus, although the available $\delta^{15}\text{N}$ data for species in the RFBO food web are limited, RFBO prey, guano and sediment $\delta^{15}\text{N}$ values suggest that the high $\delta^{15}\text{N}$ values in the Genovesa sediment record are the result of abundant seabird guano in the watershed, similar to other seabird colonised lakes and ponds (Kienel *et al.* 2013; Michelutti *et al.* 2009; Mizutani and Wada 1988). While $\delta^{15}\text{N}$ data are not available for other hypersaline Galápagos lakes, Genovesa sediment $\delta^{15}\text{N}$ values are far higher than sediment $\delta^{15}\text{N}$ values from El Junco, a Galápagos lake watershed without a substantial seabird population or guano deposits [Figure 3(a)].

Secondary influences on Genovesa $\delta^{15}\text{N}$

Despite the overlap in the $\delta^{15}\text{N}$ of RFBO prey and Genovesa guano $\delta^{15}\text{N}$ values, median sediment $\delta^{15}\text{N}$ values from 1950 to 2005 are 10‰ higher than median $\delta^{15}\text{N}$ values measured in guano samples taken from the lake watershed in 2004 and 2009. Temporal variability in diet and guano $\delta^{15}\text{N}$ values may influence sedimentary $\delta^{15}\text{N}$ in Genovesa Crater Lake, but unfortunately, no long-term measurements of guano $\delta^{15}\text{N}$ values exist with which we can assess such changes.

Denitrification, the anaerobic bacterial reduction of NO_3^- to N_2 , may drive additional fractionation in NO_3^- , increasing $\delta^{15}\text{N}$ of NO_3^- , at least in the anoxic portion ($>7\text{--}10$ m) of the water column (Howmillier 1969). Subsequent mixing of the water column in cool periods (Conroy *et al.* 2014) would then provide primary producers with a more ^{15}N -enriched source of nitrogen. However, low NO_3^- concentrations at depth suggest that upwelled NO_3^- is not an abundant source of N for primary producers in the epilimnion (Howmillier 1969).

Ammonia volatilisation most likely plays a more important role in elevating sedimentary $\delta^{15}\text{N}$ values relative to fresh guano. This process increases $\delta^{15}\text{N}$ values of guano deposits as they mature on land; more mature guano deposits have higher $\delta^{15}\text{N}$ values than fresh deposits (Kienel *et al.* 2013). The $\delta^{15}\text{N}$ value of penguin rookery pond sediment was also found to be elevated relative to penguin guano $\delta^{15}\text{N}$ values (Mizutani and Wada 1988) for this reason. Thus, the lag time between guano deposition in the Genovesa watershed (as opposed to direct deposition on the lake), and its influx into the lake via runoff, likely elevates sedimentary $\delta^{15}\text{N}$ values relative to fresh guano $\delta^{15}\text{N}$ values via ammonia volatilisation.

Causes of temporal variability in sediment $\delta^{15}\text{N}$

Given the influence of guano on $\delta^{15}\text{N}$ values in Genovesa, temporal variability in sedimentary $\delta^{15}\text{N}$ values could be interpreted as changes in the relative flux of guano into the lake, scaling with the number of birds in the watershed (Liu *et al.* 2006a; Michelutti *et al.* 2009). In this sense, periods of relatively high $\delta^{15}\text{N}$ values would indicate periods of greater guano flux and a greater number of seabirds. Although an RFBO census has not been conducted for Genovesa, the 140 000 pairs estimated in 1964 AD did occur at the apex of $\delta^{15}\text{N}$ values (28.4‰) in the sediment record; far fewer birds have been observed in recent visits to the lake in the last three decades. However, other factors apart from population could also increase the amount of guano deposited in the watershed, including increased migration into the watershed (in the case of more migratory great frigatebirds), increased nesting, nestling mortality (Nelson, 1969), and seabirds spending more time on land versus at sea. Thus, guano influx likely scales with seabird activity in the watershed, but population is likely only one factor in this relationship.

However, key N-cycle processes could also influence temporal variability in sedimentary $\delta^{15}\text{N}$. Changes in the lag time between guano deposition and influx into the lake may influence the observed temporal variability in $\delta^{15}\text{N}$ by increasing ammonia volatilisation during dry periods (Kienel *et al.* 2013). In this case, we would expect higher $\delta^{15}\text{N}$ values to occur during drier, and by nature of climate variability in this region (i.e. La Niña events), cooler periods, which would increase the lag time between guano deposition on land and transport into the lake. In Genovesa Crater Lake, one downcore study of the late 20th century and one sediment trap study spanning 2009–2012 AD indicate more calcium carbonate precipitated during cool, dry La Niña periods (Conroy *et al.*, 2014). However, in the nineteenth and twentieth centuries, when $\delta^{15}\text{N}$ values are high, there is less calcium carbonate in the sediment, suggesting that drier conditions are not driving increases in sediment $\delta^{15}\text{N}$ values (Figure S3). There is also not a significant

relationship between $\delta^{15}\text{N}$ and the NINO1+2 Index, an index of eastern Pacific sea surface temperature variability (Smith *et al.* 2008) ($r=0.27$, $N=27$, $p=0.17$, for 5-year averages). A significant, negative relationship would be expected if cooler and drier La Niña conditions were enhancing ammonia volatilisation.

Periods of enhanced stratification could also increase denitrification, elevating the $\delta^{15}\text{N}$ values of aqueous NO_3^- , which could subsequently be used by primary producers in the lake. However, Genovesa stratification is also tightly linked to climate – warm periods drive water column stability (Conroy *et al.* 2014) – and again we find no relationship between the regional NINO1+2 SST index and $\delta^{15}\text{N}$. In addition, NO_3^- concentration in the hypolimnion is low, and regionally, the influence of denitrification translates into small (<3‰) changes in sedimentary $\delta^{15}\text{N}$ values (Gutierrez *et al.* 2009), so it is unlikely denitrification can explain the larger temporal changes (~10‰) we observe in Genovesa.

The observed increase in C and N abundance coincident with higher $\delta^{15}\text{N}$ values (Figure 5) indicates that $\delta^{15}\text{N}$ variability is more likely linked to changes in nutrient influx rather than solely ammonia volatilisation or denitrification. These processes alone would not be expected to increase C and N concentration. However, an increase in guano would be expected to drive this type of increase in nutrient concentrations as well as $\delta^{15}\text{N}$. Thus, given the available data, we conclude that high $\delta^{15}\text{N}$ in Genovesa lake sediment is primarily due to seabird activity and guano influx. Secondary N-cycle processes, especially ammonia volatilisation, likely elevate sediment $\delta^{15}\text{N}$ relative to fresh guano values, but they do not appear to be the main driver of temporal variability, which is most likely related to changes in the amount of seabird activity and guano deposition in the watershed. In the following section, we show more support for this hypothesis, revealing a clear relationship between Genovesa $\delta^{15}\text{N}$, and external, biologic influences on seabird activity.

Genovesa $\delta^{15}\text{N}$ and marine productivity

Comparison of the Genovesa $\delta^{15}\text{N}$ record and independent records of eastern tropical Pacific productivity over the last four centuries point to a large-scale ecological signal preserved in the Genovesa $\delta^{15}\text{N}$ record (Figure 6). The first large, abrupt increase in Genovesa $\delta^{15}\text{N}$ values at 1835 AD is also observed in multiple marine sediment $\delta^{15}\text{N}$ time series from coastal Perú and Chile (Guiñez *et al.* 2014; Gutierrez *et al.* 2009; Salvatelli *et al.* 2014), as well as other variables related to productivity, including diatom flux, total organic carbon, and the abundance of both anchovy and warm-water fish remains (Gutierrez *et al.* 2009). The increase in marine productivity inferred from higher marine $\delta^{15}\text{N}$, diatom fluxes, and fish remains is hypothesised to be due to a northward shift of the Intertropical Convergence Zone following the end of the Little Ice Age

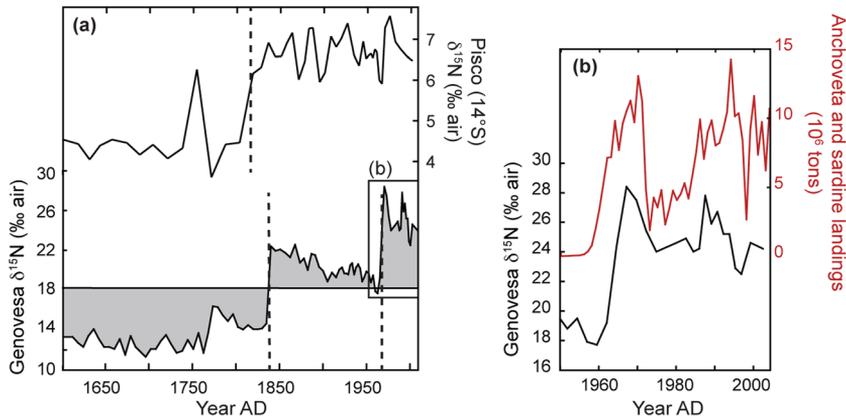


Figure 6 Genovaesa $\delta^{15}\text{N}$ and indicators of marine productivity: (a) $\delta^{15}\text{N}$ from marine sediment core near Pisco, Perú (Gutierrez *et al.* 2009), and Genovaesa $\delta^{15}\text{N}$ (‰ air). Dashed lines denote the timing of the regime shifts. (b) Genovaesa $\delta^{15}\text{N}$ record versus sum of anchoveta and sardine landings (FAO 2014)

period, leading to more upwelling and nutrient availability (Gutierrez *et al.* 2009). The abrupt shift in the marine record plotted in Figure 6(a) is reported at 1820 AD (Gutierrez *et al.* 2009), and is calculated at 1815 AD ($p < 0.001$) following the methods used in regime detection for Genovaesa $\delta^{15}\text{N}$ (Rodionov 2004 2006). In another sediment core from the coast of northern Chile, this transition is dated to 1840 AD (Guíñez *et al.* 2014). The abrupt increase in lake (at 1835 AD) and marine $\delta^{15}\text{N}$ records (at 1815–1840 AD) is well within the age model error of Genovaesa, and suggests that the abrupt increase in Genovaesa $\delta^{15}\text{N}$ is tied to a bottom-up trophic cascade in the eastern tropical Pacific, rather than only local processes (diagenetic or otherwise) within the lake or watershed. Seabird activity on Genovaesa likely increased at this time, along with regional ocean productivity, due to greater prey availability. Greater local food availability would limit time spent foraging away from the colony and may have also promoted increased breeding efforts on land, resulting in increased guano production and deposition at nesting sites. The abrupt nature of the $\delta^{15}\text{N}$ regime shifts also suggests that the increase in inferred guano flux into the lake at these times may have also been a result of migration, especially in the case of great frigatebirds (Dearborn *et al.* 2003; Weimerskirch *et al.* 2006). In sum, the coincident abrupt shift observed in regional marine records and at Genovaesa suggests enhanced regional ocean productivity and greater seabird activity on Genovaesa ultimately led to more guano deposition and guano influx into the lake in the early nineteenth century, subsequently elevating sediment $\delta^{15}\text{N}$ values, and driving increased C and N abundance.

Long-term, modern time series of marine productivity indicators are limited for the eastern tropical Pacific (Chavez *et al.* 2011). However, we find that time series of anchoveta (*Engraulis ringens*) and sardine (*Sardinops*

sagax) landings off the western coast of South America (Chavez *et al.* 2003; Jordon and Fuentes 1966), considered here as a metric of marine productivity, covary with $\delta^{15}\text{N}$ values in the Genovaesa sediment record in the latter half of the twentieth century [Figure 6(b)]. Greater landings of both species correlate with higher Genovaesa $\delta^{15}\text{N}$ values [for 5-year averages, Pearson's $r = 0.81$, $N_{\text{eff}} = 8.4$ (Dawdy and Matalas 1964), $p = 0.01$]. Although RFBOs feed primarily on flying fish, this relationship implies that ocean conditions may have become more amenable for RFBOs during periods of higher anchoveta or sardines. During anchoveta periods, which are associated with greater productivity in the eastern tropical Pacific (Chavez *et al.* 2003), the cause of this relationship is likely similar to the 1835 AD shift, that is, a bottom-up increase in productivity benefitting these fish species as well as RFBO prey. For example, associated decadal variability in zooplankton abundance (Ayón *et al.* 2004) may have influenced both flying fish as well as anchovies and sardines (Alheit and Niquen 2004; Palomares and Pauly 2014). RFBOs may have been more successful during sardine regimes due to increases in eastern tropical Pacific yellowfin tuna (*Thunnus albacares*) during these periods. RFBOs are part of the tuna–dolphin–seabird assemblage (Au and Pitman 1986; Ballance *et al.* 2006; Chavez *et al.* 2003; Vilchis *et al.* 2006) and hence more yellowfin tuna during sardine regimes may have improved RFBO prey detection. In addition, periods with more abundant sardines in the Galápagos may have reduced competition with blue-footed boobies (*Sula nebouxi*) and Nazca boobies (*Sula granti*) for flying fish (Anchundia *et al.* 2014), again benefitting RFBOs. In this sense, a biotic factor (competition) may have amplified the abiotic signal – ocean–atmosphere changes and their subsequent influence on marine productivity – archived in the Genovaesa sediment record.

Recent increase in $\delta^{15}\text{N}$ variance

Following the second shift to higher mean $\delta^{15}\text{N}$ values at 1965 AD, we observe an increase in $\delta^{15}\text{N}$ variance, calculated using 10-year interpolated $\delta^{15}\text{N}$ anomalies (using means for each regime) in discrete, 40-year bins (Figure 7) to account for changing temporal resolution and variance independent of the regime shifts. The enhanced variance observed in $\delta^{15}\text{N}$ in the latter half of the twentieth century is similar to results of other analyses of oceanic, biological archives that show anomalous variance or mean values in modern times relative to the deeper past, features attributed to anthropogenic influences and greater sensitivity to ocean–atmosphere forcing (Emslie and Patterson 2007; McKechnie *et al.* 2014; Wiley *et al.* 2013). For example, the effect of natural variability, such as the PDO, on population size can be enhanced in exploited populations (Pauly *et al.* 2002). During the recent period of higher variance in Genovaesa, we observe a positive correlation between $\delta^{15}\text{N}$ and total number of anchoveta and sardine landings [Figure 6(b)]. However, despite the hypothesised climatic control, namely, the PDO, on regime shifts between anchoveta and sardine-dominated systems (Chavez *et al.* 2003), we find no correlation between Genovaesa $\delta^{15}\text{N}$ and the PDO [Pearson's $r=0.13$, $N_{\text{eff}}=8.6$ (Dawdy and Matalas 1964), $p=0.76$ for 5-year averages]. The lack of a clear relationship between $\delta^{15}\text{N}$ and the PDO suggests that the response of Genovaesa seabirds to decadal-scale climate variability is complex

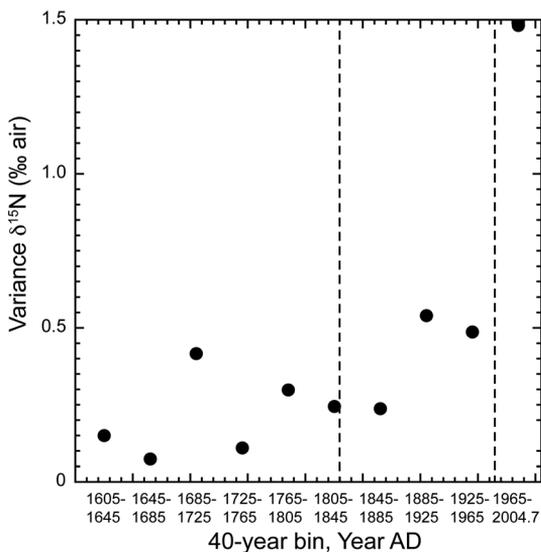


Figure 7 Genovaesa $\delta^{15}\text{N}$ variance, calculated from discrete, 10-year interpolated $\delta^{15}\text{N}$ anomalies in 40-year bins. To calculate variance in 40-year bins independent of the regime shifts, we use $\delta^{15}\text{N}$ anomalies, subtracting the long-term mean $\delta^{15}\text{N}$ value for each regime from each individual $\delta^{15}\text{N}$ value within the given regime. Dashed lines denote the timing of the regime shifts (Rodionov 2004)

(McClatchie 2012), and that the decadal-scale regime shifts that are so prominently manifested in the eastern tropical Pacific fish landings since the mid-twentieth century may be a feature unique to the latter half of the twentieth century.

Genovesa $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and *R. mangle*

Along with its influence on lake trophic status, seabird guano exerts a well known influence on vegetation (Anderson and Polis 1999; Stapp *et al.* 1999). Here we compare the dominant component of the pollen record from Genovaesa, *R. mangle*, with $\delta^{15}\text{N}$ variability to investigate the potential influence of seabird guano on mangroves in the lake watershed. *R. mangle* is the most abundant pollen species identified in the lake sediment record given its abundance within the Genovaesa watershed relative to other species. We observe that *R. mangle* pollen concentration abruptly increases coincident with the mid-twentieth century shift to higher $\delta^{15}\text{N}$ values. Sediment $\delta^{13}\text{C}$ values also decrease and C and N abundance increase at this time (Figures 4 and 5). As modern mangrove $\delta^{13}\text{C}$ values are much lower than measured sediment, algal and guano-derived $\delta^{13}\text{C}$ values (Figure 3), this decrease in sediment $\delta^{13}\text{C}$ values coincident with *R. mangle* pollen concentration suggests that *R. mangle* strongly influences sedimentary $\delta^{13}\text{C}$ values, or at least, that lake productivity and mangrove pollen production are tightly coupled.

However, we do not observe an increase in *R. mangle* pollen concentration following the 1835 AD shift in $\delta^{15}\text{N}$. Apart from nutrient availability, salinity is an additional key limiting factor for *R. mangle* (Lin and Sternberg 1992). Reduced salinity during the late nineteenth–twentieth centuries, as interpreted from the Genovaesa Ca record, coupled with the inferred increase in guano influx to the lake in the latter half of the twentieth century (Figure 6(b)), may have also contributed to enhanced mangrove productivity in the mid to late twentieth century. The smaller increase in *R. mangle* pollen concentration following the 1835 AD $\delta^{15}\text{N}$ shift may thus be due to more saline lake water at this time, as inferred from higher abundance of calcium carbonate in the sediment record (Figure S3). Although the coincident temporal variability in *R. mangle* pollen concentration, lake productivity indicators, and $\delta^{15}\text{N}$ are compelling, further investigation of $\delta^{15}\text{N}$ across a range of vegetation in the Genovaesa watershed is required to clarify the influence of guano on terrestrial productivity.

Conclusions

The seabird-influenced $\delta^{15}\text{N}$ record from Genovaesa is a rich source of information on the influence of large-scale shifts in eastern tropical Pacific productivity on a coastal environment over the last four centuries. We

have demonstrated that variability in marine productivity over the last 400 years transferred across the land–ocean boundary via seabird activity, and influenced Genovesa Crater Lake. These results document a high degree of natural ecological and biogeochemical variability in seabird-influenced coastal areas, which should be considered when assessing conservation strategies, long-term productivity, carbon storage, and greenhouse gas emissions in such regions. This study also supports the conclusion that non-stationarity and variance (Sydeman *et al.* 2013) are key metrics when assessing long-term marine–terrestrial interactions. In the last 40 years, an unprecedented degree of variability in seabird activity highlights the need to better understand the complex interplay among climate, productivity, and ecosystems at the land–sea interface.

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Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1. Age model for the top 54 cm of the Genovesa sediment record, created with Bacon 2.2 (Conroy *et al.*, 2014). Red line indicates the best-fit (median) age model through ^{210}Pb (teal) and radiocarbon (purple) age probabilities. Shaded area encompasses maximum and minimum age estimates.

Figure S2. Time series of (a) $\delta^{13}\text{C}$ (‰ VPDB), (b) %C, (c) %N and (d) $\delta^{15}\text{N}$ (‰ air) from three Genovesa sediment cores (indicated by black, red, and blue colors). Shaded bars highlight the two largest, abrupt shifts in $\delta^{15}\text{N}$ values.

Figure S2. (a) $\delta^{15}\text{N}$ from marine sediment core near Pisco, Perú (Gutierrez *et al.*, 2009), (b) Genovesa $\delta^{15}\text{N}$ (‰ air), (c) Genovesa calcium abundance record (Conroy *et al.*, 2014).