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Seabird guano influences on desert islands: soil chemistry and herbaceous species richness and productivity

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Abstract

An understanding of the effects of guano deposition on arid soil chemistry and the consequences for plant communities is lacking. This study examined patterns of herbaceous species richness and productivity, soil chemistry, soil moisture and soil respiration on 11 islands in the Gulf of California, six of which receive seabird guano deposition. Species richness was significantly lower on islands with guano ("Bird" islands) than islands without guano ("Non-bird" islands), with very little overlap in species composition; however, productivity was significantly greater on Bird than on Non-bird islands. As expected, Bird island soils had higher concentrations of NO_3^-, NH_4^+ and total nitrogen (N) than Non-bird island soils; and, measurements of $\delta^{15}N$ indicate that the higher concentrations of N were derived from guano. We also found that soil moisture and respiration were significantly higher, but pH was significantly lower, on Bird than Non-bird islands. These results suggest that guano deposition in deserts stimulates productivity—even in dry years—due to elevated N and, indirectly, soil moisture. Guano deposition also results in a decrease in species richness and a change in species composition probably due to elevated N, N toxicity, or low pH. However, we also found that pH varied more on Bird than on Non-bird islands; and that salinity—while not different between island types—was significantly patchier on Bird than on Non-Bird islands. These results suggest that guano deposition affects not only the general chemical composition of soils, but also results in greater spatial variation in soil chemical

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composition, which may ultimately affect species richness and composition. Therefore, understanding spatial patterning in soil chemistry as a result of guano deposition is critical for understanding guano effects on plant richness and productivity.

Keywords: Gulf of California; Soil salinity; Soil pH; Soil nutrients; Orthinogenic soils; Spatial variability; Soil respiration; Geostatistics

1. Introduction

Seabird colonies commonly roost and nest on small oceanic islands, and can significantly alter soil chemistry and plant communities (McColl and Burger, 1976; Nelson, 1979). However, there is not a strong understanding of guano deposition effects on soil chemistry and plant community dynamics. Therefore, studies establishing patterns between guano deposition, soil chemistry and plant community dynamics are needed. In addition, the general role of organisms in creating spatial pattern in soil properties, and the implications for plant community structure are just beginning to be understood (see Augustine and Frank, 2001 and refs within), while very little is known about these patterns and processes in arid environments.

Ornithogenic soils are extremely high in phosphate, nitrate, and ammonium (Hutchinson, 1950; Wainright et al., 1998; Anderson and Polis, 1999), which may facilitate growth of some plant species, but inhibit growth of others (Smith, 1978; Ryan and Watkins, 1989; Wainright et al., 1998). Inhibition may be a result of ammonium toxicity, or indirectly via low pH, which inhibits uptake of certain nutrients (Odasz, 1994). On the other hand, species that can tolerate guano deposition probably take advantage of the elevated nutrients via fast-growing life history strategies (*sensu* Grime, 1977; also see Vidal et al., 2000); however, these species may be absent from areas without guano deposition because they are not able to tolerate the low level of nutrients on "Non-bird" islands. Alternatively, competitive exclusion of slow-growing species induced by seabird presence may be a strong determinant of plant community structure on oceanic islands, as was illustrated on some Mediterranean islands (Vidal et al., 2000). Although the above illustrate some understanding of seabird–soil–plant community interactions, it not understood how seabird guano deposition in arid regions affects patterns in soil chemistry and what the consequences to plant communities are. Furthermore, studies of spatial patterns in soil chemistry in arid regions (e.g. Schlesinger et al., 1996) have never considered the influence of bird guano.

Soil salinity is a major edaphic factor influencing plant physiology and species distributions in desert, coastal and island areas (e.g. Dodd and Donovan, 1999 and references within). There is contrasting evidence as to whether differential germination and early growth responses to salinity contribute to species distributions and zonations in these habitats (see Dodd and Donovan, 1999). Desert soils are often highly saline because of the high rate of evaporation, and the additional influence of salt-laden sea spray may elevate island soil salinity to a level intolerable by many species. Few studies of seabird guano effects on soil chemistry have examined salinity and pH, and those that have reported increases (salinity), no effects (pH), and decreases (pH) (McColl and Burger, 1976; Sobey and Kenworthy, 1979; Hogg and Morton, 1983). This study attempts to establish a greater understanding of patterns in soil pH and salinity as a result of seabird guano deposition on desert islands, and how those patterns may relate to plant species richness and production.

This study was performed on 11 desert islands in the Gulf of California (see Methods for detailed description of study site). We examined general (non-spatial) patterns in plant species richness, productivity, soil ion content, nitrogen isotopic ratios, soil moisture, and soil respiration on these islands. To start to investigate spatial patterns in soil chemistry, we examined pH and salinity in a spatially explicit fashion over distances from 0.1 to 150 m on these islands. Six of these islands receive guano deposition, while five of the islands do not. Other seabird influences such as trampling, using live plants for nest building materials, and seed dispersal that are important in several other systems (e.g. Sobey and Kenworthy, 1979; Hogg and Morton, 1983) are apparently not as important in this system; e.g. most annual plants have nearly completed their life cycles prior to the seasons of highest bird occupancy of islands. Thus, the system is ideal for looking at guano deposition without the complications of other bird activities influencing soil chemistry and herbaceous plant community dynamics. The primary contribution to the general understanding of seabird–soil–plant interactions of this study is on patterns of herbaceous species richness and productivity associated with guano deposition on desert islands; the influence of guano on soil nutrients, moisture, pH and salinity; guano deposition effects on spatial heterogeneity in soil pH and salinity; and how patterns in soil chemistry are associated with herbaceous species richness and productivity.

2. Study site and methods

2.1. Study site

This study was conducted on 11 midriff islands in the Gulf of California near Bahia de los Angeles (28°55′ N latitude, 113°30′ W longitude), Baja California, Mexico. Seventeen species of seabirds (including Hermann and California gulls, Brown Pelicans, Blue-footed and Brown Boobies, and Common Cormorants) nest or roost regularly on six of the 11 islands, possibly due to predator avoidance or proximity to good foraging areas (Anderson, 1983; Sanchez-Piñero and Polis, 2000). Physical disturbance by birds is localized only around nesting areas on cliffs, which are areas that are not examined in this study (and are avoided to lessen disturbance to birds), and have such high guano levels that no plants occur. Most of the islands used by birds (“Bird” islands) (0.02–0.13 km^2) are smaller than the islands not used by birds (“Non-bird” islands) (0.09–1.27 km^2); however, species area relationships do not explain species richness patterns (see "Discussion" and Anderson and Wait, 2001).

These islands are located in a geologically active and complex region, and represent at least eight different geologic histories (Gastil et al., 1973). We have found no obvious correlations between bird usage and island geologic history; or, between soil chemistry, plant composition and geologic history (W.B. Anderson and D.A. Wait, unpublished data). For instance, the three southern-most islands in the bay are all part of a basaltic, Post-Batholithic volcanic flow that was historically continuous with the peninsula (Gastil et al., 1973). Only two of these islands are inhabited by birds, and plant species compositions of these three islands reflect guano presence or absence rather than the parent material or proximity to the peninsula (W.B. Anderson and G.A. Polis, unpublished data). The remaining eight islands are predominantly either or both Pre-Batholithic metasedimentary and Batholithic tonolite (Gastil et al., 1973), and there is no apparent association between geology and either bird presence or plant species composition.

The mean ($\pm$standard deviation) annual precipitation in this region between 1991 and 2002 was 52.6 ± 71.6 mm. Precipitation data was collected at Bahia de los Angeles and provided by the Comision Nacional del Agua, Mexicali, Mexico.

Note that the sampling of islands was constrained by traveling to the islands by boat from the village of Bahia de los Angeles (camping on all but one of the islands is prohibited). Windy conditions often limit the number of islands that could be visited, or the time spent on a given island. Therefore, sampling units (i.e. islands) are often less than ideal, with a maximum sampling unit size of 11 (i.e. 11 islands for each variable). In addition, sampling is done in areas where herbaceous plants are found. Much of an islands area is coastal (where salt concentrations limit herbaceous species) or rock or has high bird usage, all of which limit the area available for herbaceous species. Sampling is on a scale that we believe captures the properties of soils where herbaceous plants are found.

2.1.1. Plant production and species richness

Plant production and species richness were determined in a statistically rigorous fashion in March 1998 on five Non-bird islands and six Bird islands—the same islands used for spatial analysis of EC and pH. Species richness was determined by counting the total number of species found across 15 randomly placed 1 m^2 plots on each island and expressed as species m^{-2}. For production, 15 randomly chosen 0.25 m^2 plots on each island were cleared of all live herbaceous plants. In 2001 a walking survey of the entire area of every island for species richness did not qualitatively change the results from the 1998 survey. Likewise, periodic harvesting of productivity plots in 2001 and 2002 (very dry years) did not qualitatively change the patterns of productivity determined in 1998.

2.1.2. Soil moisture and respiration

Soil moisture was determined gravimetrically on four Bird and four Non-bird islands in May 2001 and 2002. Five–seven samples per island per year were obtained at a depth of 10 cm. Samples were taken at distances of 0.25 m along a transect in

2001 and at distances of 20–50 m in 2002 (i.e. samples in 2002 corresponded to pH and EC plots; see *Spatial variation in pH and salinity*)—with the transect being placed approximately 80 m from the nearest coast. Hundred grams of samples were immediately weighed in the field to the nearest 0.001 g, dried at 80 °C to a constant weight, and reweighed. Soil respiration was determined on two Bird and two Non-bird islands using a Li-Cor 6400 gas analyser attached to Li-Cor soil respiration chamber (Li-Cor, Lincoln, NE, USA) in May 2002. Soil respiration was measured to indicate if higher soil moisture on Bird islands (see Results) would potentially result in a stimulation of respiration rates. Seven soil collars per island were placed at distances of 0.25 m along a transect—with the transect being placed approximately 80 m from the nearest coast. One hour after placing collars in the soil, measurements were taken over a 90 s interval—with measurements logged every 30 s. The mean of the three measurements was used as the respiration value per sample collar.

2.1.3. Soil chemistry

Soil chemical variables from a subset of islands were analysed in soil labs. Soil for $\delta^{15}N$, and carbon and nitrogen content were collected from inland areas (80 m from the nearest coast) on two Non-bird and two Bird islands in 2001. Six samples per island were collected along a 6 m transect at randomly chosen points. 20 g samples were collected at a depth of 10 cm, dried at 80 °C, ground and sent to the University of Arkansas Stable Isotope Laboratory (UASIL) for analysis. UASIL analysed the stable isotope content of the samples using a CE Instruments NC2500 elemental analyser connected to a Finnigan Delta Plus stable isotope mass spectrometer. They combusted samples in an oxygen stream at 1100 °C then passed them through oxidation and reduction tubes to form N_2 gas. The precision was greater than 0.4‰ for $\delta^{15}N$.

Soil ion concentrations were obtained on four Non-bird islands and four Bird islands in 2001. Ten (approx. 100 g) samples from inland areas (80 m from the nearest coast) per island were taken at a depth of 10 cm from areas with *Atriplex* (interplant spaces; Sharma and Tongway, 1973) and combined. Soils were analysed at the University of Arizona Soil Lab. pH, EC, Ca, Mg, Na, K and NO_3^- were analysed from filtered extracts (1:1 soil:water ratio; ICP). Plant available PO_4^- was analysed colorimeterically from Olsen biocorbonate extractant (1:100 soil:biocarbonate reagent). Exchangeable NH_4^+ was analysed colorimetrically from 1:10 soil:KCl extracts.

2.1.4. Spatial variation in pH and salinity

Electrical conductivity and pH samples for geostatistical analysis were obtained from five Non-bird and six Bird influenced islands in 2002. Three–five 3 m × 3 m plots were sampled on each of these islands depending upon the size of each island. The first plot of each transect was chosen randomly within an area with herbaceous plant growth by throwing a Frisbee, the center of the plot being where the Frisbee landed. Each plot was oriented north to south and consisted of nine 1 m^2 subplots. Three of the nine 1 m^2 subplots were sampled within each plot; the north-western subplot, the center subplot, and south-eastern subplot. The center of each of these subplots was sampled, as well as points 10 cm to the east and 10 cm to the west of the center for a total of three samples per subplot. Therefore, three samples were taken from each of these three subplots for a total of nine samples per plot, yielding 27, 36, or 45 samples per island. Subsequent plots were selected randomly at a distance between 20 and 50 m from the previous plot measured with a transect tape from the center of one plot to the center of the next plot with a minimum distance of 20 m between plots and a maximum distance of 50 m between plots. In addition, GPS coordinates were obtained from the center of each plot and distances were verified by using a mapping program (ArcMap).

Soil was excavated from each sample point at a depth of 10 cm and sieved using a #35 mesh to remove all small rocks and debris. Approximately 150 g of soil were removed from each sample point for analysis. Distilled water was added to the soil until the point of saturation occurred following Rhoades protocol (Carter, 1993). These soil slurries then sat for two hours, allowing time for ions to enter the aqueous solution. After the slurries had set for the required time, the aqueous solution was extracted from the soil mixture using suction filtration. A Denver Instrument AP-50 pH/Ion/Conductivity meter (Denver Instrument Company, Arvada, CO, USA) was used for all soil extract analyses. Electrical conductivity and pH measurements were obtained using a Denver Instrument Conductivity/ATC cell electrode (Denver Instrument Company, Arvada, CO, USA) and a Denver Instrument pH/ATC Glass-body electrode (Denver Instrument Company, Arvada, CO, USA), respectively.

2.1.5. Data analysis

For species richness and plant production, a two-sample *t*-test was performed on mean richness and biomass from the 15 plots per island ($n = 5$ and 6 for Non-bird and Bird islands, respectively). For soil chemical characteristics, soil moisture, and soil respiration Nested ANOVA was used to compare differences between island types. Therefore, islands were the sampling unit, and individual measures within an island were subsampling units. The Nested ANOVA model was as follows: island type (Bird vs. Non-bird) was the main effect, and the error term used for calculating the F statistic for island-type effects was island nested within island type; island was treated as a random factor in the model. For all analyses the degrees of freedom for the F test is given. For example, a degrees of freedom of 1,6 would indicate that the between-island sum of squares (4 Non-bird vs. 4 Bird islands) was used to calculate the F statistic associated with island-type effects (i.e. Bird vs. Non-bird); a degree of freedom of 1, 2 would indicate that the sampling unit was 2 Bird islands and 2 Non-bird islands. For soil moisture year was also included in the Nested ANOVA model, but was not a statistically significant factor. All statistical analyses were performed using Minitab (12.23, Minitab, Inc.).

To characterize general variation in soil pH and EC between Non-bird and Bird islands we compared coefficients of variation, calculated from the data collected at spatial scales of 0.1–150 m within an island, using two-sample *t*-tests. To characterize patchiness in soil pH and EC we used semivariance analysis (Goovaerts, 1998), which examines changes in the amount of variation among sampling points separated by a given distance as that distance increases. We constructed semivariograms for each sampling grid on each island using GS+ (Gamma Design Software, 1998). The proportion of sample variance explained by patchiness was measured as 1−(Co/(C+Co)) where Co is the *y*-intercept or "nugget" of the best fit model and (C+Co) is the level of semivariance where the fitted model reaches an asymptote or "sill". The best-fit model was chosen by the software. We performed two-sample *t*-tests on the proportion of sample variance explained by patchiness (Augustine and Frank, 2001), where the greater the proportion of sample variance explained by patchiness, the higher the degree of spatial structure. A high degree of spatial structure indicates similar variance across the spatial scales measured (0.1–150 m), where a low degree of spatial structure indicates high variance at some spatial scales but not others, and therefore, a high degree of patchiness. Data exhibiting no patchiness across spatial scales will produce a semiovariogram that is essentially flat; data exhibiting only small-scale patchiness will produce a semiovariogram that first increases across spatial scales but then reaches an asymptote; if patchiness occurs at a higher scale than measured the data will produce a semiovariagram that increases linearly as distance increases.

3. Results

3.1. Plant production and species richness

Plant production and species richness were measured extensively in 1998 on the five islands with no obvious bird activity ("Non-bird" islands) and on the six islands with obvious bird activity ("Bird" islands). Plant production was significantly lower on Non-bird islands than on Bird islands ($t=3.95$; df = 9; $p=0.003$). Mean (±SE) biomass (g DW m^{-2}) on Non-bird islands was 60.2 (±15) and on Bird islands was 159.0 (±19). Herbaceous species richness was significantly higher on Non-bird islands than on Bird islands ($t=5.28$; df = 9; $p=0.003$). Mean (±SE) species richness on Non-bird islands was 10.2 (±1.10) and on Bird islands was 4.0 (±0.49). The dominant taxa by mass on Non-bird islands were *Cryptantha*, *Euphorbia*, *Lotus*, and *Plantago*; the dominant taxa by mass on Bird islands were *Amaranthus*, *Chenopodium*, and *Perityle* (names follow Wiggins, 1980). Sampling (clearing a subset of productivity plots, walking surveys) in the years soil chemistry was measured (2001–2002; data not shown) were quantitatively lower, but exhibited the same relative differences in productivity and richness as the data from 1998.

3.1.1. Soil moisture and respiration

Soil moisture content, determined 80 m from the nearest coast, of Bird island soils was significantly higher than the soil moisture content of Non-bird island soils (Table 1). Likewise, soil respiration on Bird islands was significantly higher than soil respiration on Non-bird islands (Nested ANOVA; $p=0.052$; df = 1, 2); where, mean (±SE) respiration ($u$mol CO_2 m^{-2} s^{-1}) for Non-bird islands was 0.45 (±0.18) and for Bird islands was 1.33 (±0.21).

Table 1
Mean (±S.E) soil moisture from the interior (80 m from nearest coast) of four islands not influenced by seabird guano (Non-bird) and four islands influenced by seabird guano (Bird) in the Gulf of California in two different years

Island type	Soil moisture 2001 (%)	Soil moisture 2002 (%)
Non-bird	0.24^{a}	1.28^{a}
	(0.08)	(0.21)
Bird	0.95^{b}	1.94^{b}
	(0.39)	(0.28)

Letters within a column that are different indicate significant differences in means ($p<0.05$; Nested ANOVA; df = 1, 6).

Table 2
Nitrogen isotopic composition, percent nitrogen and carbon, and the carbon/nitrogen ratio of soils from the interior (80 m from nearest coast) of two islands in the Gulf of California not influenced by seabird guano (Non-bird) and two islands influenced by seabird guano (Bird)

Island type	$\delta^{15}N$ (‰)	N (%)	C (%)	C/N
Non-bird	7.46^{a}	0.016^{a}	0.35^{a}	29.92^{a}
	(0.32)	(0.002)	(0.05)	(8.16)
Bird	35.64^{b}	0.35^{b}	0.91^{a}	3.77^{b}
	(2.61)	(0.21)	(0.63)	(1.09)

Values are means (±S.E). Letters within a column that are different indicate significant differences in means ($p<0.05$; Nested ANOVA; df = 1, 2).

3.1.2. Soil chemistry

Soils collected from the interior (80 m from nearest coast) of Bird islands were highly enriched in $\delta^{15}N$ compared to soils collected from the interior of Non-bird islands (Table 2). This enrichment in $\delta^{15}N$ is consistent with guano deposition (Mizutani and Wada, 1988; Anderson and Polis, 1999). Not surprisingly, Bird island soils also had a significantly higher total N content than Non-bird island soils (Table 2). Soils from Bird islands also had a significantly lower C/N ratio than soil from Non-bird islands, and this was driven more by the differences in the N content of the soil than the differences in the C content of the soil (Table 2).

The nitrate, phosphate, and potassium content of soils collected from the interior (80 m from nearest coast) of Bird islands were significantly higher than the content of those ions in Non-bird island soils (Table 3). The ammonium content of Bird island soils was 3.4 times higher than the ammonium content of Non-bird island soils, but due to a high variance (e.g. coefficient of variation for Bird = 266; coefficient of variation for Non-bird = 107) this difference was not statistically different (Table 3). Only the sodium content was significantly higher (7.8 times) in Non-bird island soils than in Bird island soils (Table 3).

The pH of the Bird island soils used for the soil chemical analysis reported above was significantly lower than the pH of the Non-bird island soils (Table 3). The

Table 3
Soil chemistry from the interior (80 m from nearest coast) of four islands not influenced by seabird guano (Non-bird) and four islands influenced by seabird guano (Bird) in the Gulf of California

Island type	NO_3^--N ($\mu g\,g^{-1}$)	NH_4^+-N ($\mu g\,g^{-1}$)	PO_4^--P ($\mu g\,g^{-1}$)	Na ($\mu g\,g^{-1}$)	K ($\mu g\,g^{-1}$)	Ca ($\mu g\,g^{-1}$)	Mg ($\mu g\,g^{-1}$)	pH	EC (mmhos cm^{-1})
Non-bird	15.3[a]	19.7[a]	24.0[a]	3311[a]	92.2[a]	624.1[a]	137.0[a]	7.36[a]	10.74[a]
	(3.5)	(7.5)	(11.6)	(1174)	(22.5)	(318.2)	(62.1)	(0.18)	(4.69)
Bird	311.6[b]	66.7[a]	437.0[b]	427[b]	240.0[b]	342.6[a]	182.5[a]	6.49[b]	4.12[a]
	(98.7)	(33.1)	(143.5)	(90)	(58.3)	(123.3)	(56.0)	(0.32)	(0.89)

Values are means ($\pm$S.E). Letters within a column that are different indicate significant differences in means ($p<0.05$; Nested ANOVA; df = 1, 6).

Table 4
Mean ($\pm$S.E) soil pH and electric conductivity (EC) measured in a spatially explicit fashion across five Non-bird ($n=122$) influenced and six Bird ($n=176$) influenced islands in the Gulf of California

Island type	pH	EC (mmhos cm^{-1})
Non-bird	7.79[a] (0.04)	13.89[a] (1.51)
Bird	6.42[b] (0.09)	16.19[a] (1.21)

Samples occurred at distances between 0.01 and 150 m. Letters within a column that are different indicate significant differences in means between island type ($p<0.05$; Nested ANOVA; df = 1, 9). Spatial analysis data are provided in Figs. 2 and 3.

electric conductivity (EC) of the Non-bird island soils used for the soil chemical analysis was 2.6 times higher than the EC of the Bird island soils; however, due to high variation, this difference was not statistically different (Table 3). A more expansive survey of pH and EC indicates the same trend in pH but an opposite trend in EC, where Bird island soils tend to have higher, albeit non-significant, EC (see Table 4).

3.1.3. Spatial variation in pH and salinity

Soil pH measured across scales from 0.1 to 150 m was significantly higher in Non-bird island soils than Bird island soils; while there was no significant difference in the EC of soils between island types (Table 4). These results are statistically consistent with the small-scale sampling from only the interior of islands reported in Table 3. However, the focus of this aspect of the study was spatial variation in soil pH and EC. Within all islands, variation in pH was relatively low, while variation in EC was very high (see Figs. 1 and 2). Across the 11 islands, Bird islands had a significantly greater amount of variation (coefficient of variation) in pH (see Fig. 1; $t=3.94$, $p=0.003$, df = 9) than Non-bird islands, but the total amount of variation in EC was not different between island types (see Fig. 2; $t=0.59$, $p=0.572$, df = 9). However, we found that the proportion of sample variance explained by patchiness ($1-C_0/(C+C_0)$) was not significantly different between island types for pH (Fig. 1;

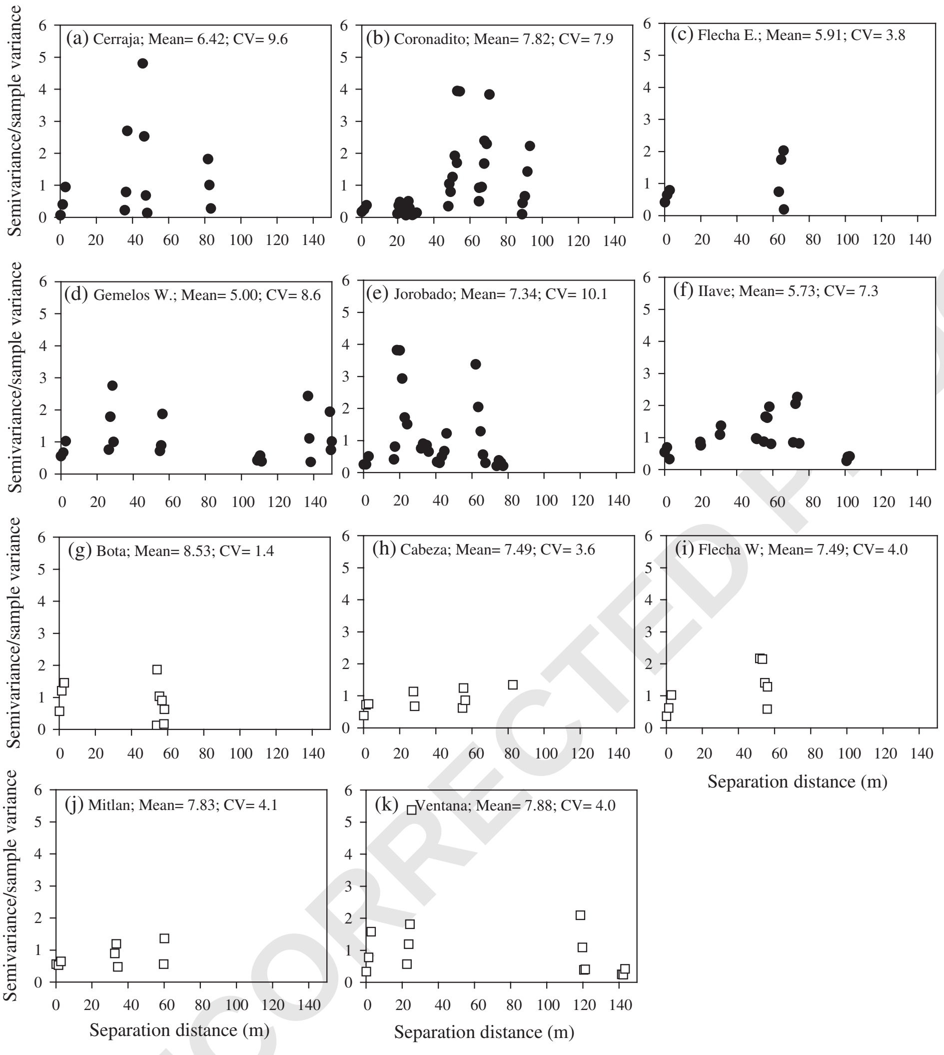

Fig. 1. Semiovariograms for soil pH on six islands influenced by seabirds (a–f: ●), and five islands not influenced by seabirds (g–k: □) in the Gulf of California. Island name, mean pH, and coefficient of variation are provided in the figure.

$t = 0.29$, $p = 0.77$, df $= 9$); but, the proportion of sample variance explained by patchiness for EC was significantly greater for Non-bird islands than for Bird islands (Fig. 2; $t = 2.93$, $p = 0.017$, df $= 9$). This indicates that there is a higher degree of spatial structure (i.e. less patchiness) in EC on Non-bird islands than Bird islands. Finally, EC appears to be related to distance from a coast on Bird islands but not Non-bird islands. Regression analysis indicated a significant negative relationship between EC and distance from nearest coast on Bird islands, but no relationship

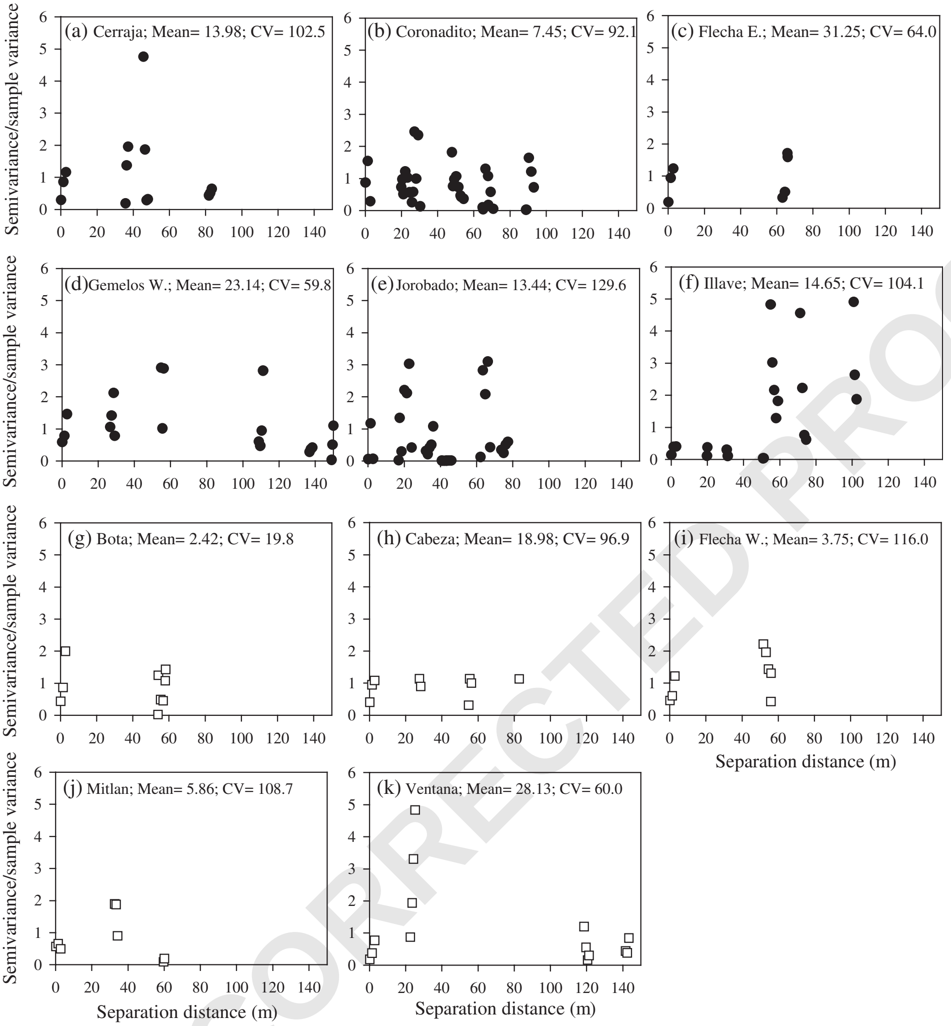

Fig. 2. Semiovariograms for soil EC (mmhos cm^{-1}) on six islands influenced by seabirds (a–f: ●), and five islands not influenced by seabirds (g–k: □) in the Gulf of California. Island name, mean EC, and coefficient of variation are provided in the figure.

between EC and distance from coast on Non-bird islands (Fig. 3). There were no significant relationships between pH and distance from coast (data not shown).

4. Discussion

Results from this study illustrate how long-term guano deposition in an arid region alters soil chemistry, soil moisture and respiration, plant production and

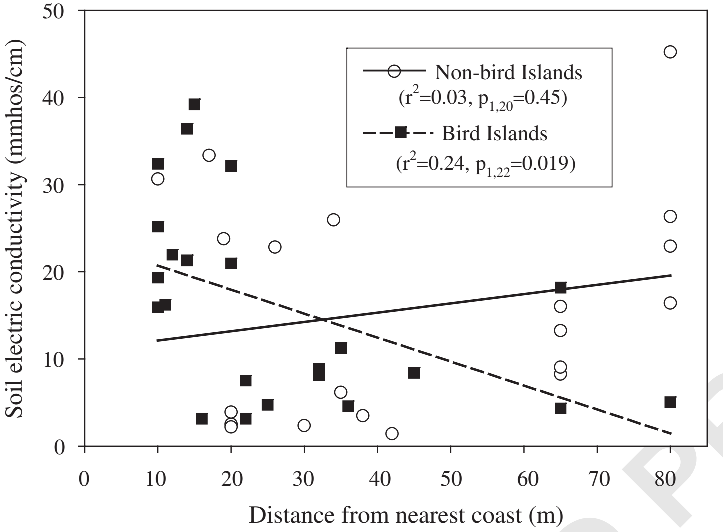

Fig. 3. Regressions of salinity against distance from nearest coast for five islands not influenced by seabird guano (Non-bird) and six islands influenced by seabird guano (Bird) in the Gulf of California. Each point is the mean of nine samples obtained within a 1 m^2 plot, with the distance to nearest coast measured from the center of the plot. Summary statistics from linear regression analysis are provided in the figure.

herbaceous plant species richness. Long-term guano deposition is associated with increased soil nitrogen, phosphorous, moisture, and respiration; decreased pH; but not with broad patterns of salinity. Long-term guano deposition increases variation in pH and patchiness in salinity. Finally, long-term guano deposition increases plant production, but decreases herbaceous species richness.

Increases in plant production are easily attributed to the elevated soil nitrogen and phosphorous (Tables 2 and 3) as a result of guano deposition (Anderson and Polis, 1999). However, one would predict that increased production would only occur in wet years (Romney et al., 1978). But we found that guano deposition increased soil moisture (Table 1) even in very dry years. This was probably due to the increased organic matter of soils (see Table 2), which was probably due to the build up of detritus from wet years associated with El Niño. Therefore, our results suggest that guano deposition will increase primary productivity even in dry years. Preliminary data suggests that productivity in a dry year—while 95% lower than the wet year productivity reported in this study—is up to 6 times greater on islands with bird guano than islands without bird guano (Anderson and Wait, unpublished data).

Species richness patterns in this study indicate that increased resources and productivity in an arid region will lead to decreased species richness, suggesting that desert islands receiving guano deposition will be on the descending portion of the hypothesized unimodal curve that Rosenzweig (1995) and others have used to describe the productivity diversity relationship (see Anderson and Wait, 2001; Mittelbach et al., 2001). Species area relationships do not explain plant species richness patterns on these 11 islands (see Anderson and Wait, 2001); e.g. the smallest Non-bird island has 2 times as many species as the largest Bird island. However, competitive exclusion could also explain lower species richness on islands with guano deposition (Vidal et al., 2000). Species richness patterns may also be related to soil pH (Pärtel, 2002). In general, arid soils have relatively high pH; however, guano deposition in our study significantly lowered the soil pH (Tables 3 and 4). It would be expected that in an evolutionary sense the herbaceous species pool in this region adapted for low-pH soils would be lower than the species pool adapted high-pH soils—leading to decreased species richness (Pärtel, 2002). Finally, spatial patterns in soil chemistry associated with guano deposition may be related to species richness (see Augustine and Frank, 2001), with increased spatial heterogeneity leading to lower species richness, which is contrary to general patterns of species richness associated with spatial heterogeneity at both large and small scales (Krebs, 2001).

The role of biotic factors in creating spatial patterns in soil chemistry and the implications for community dynamics are not clear (Augustine and Frank, 2001). Our study is the first to address how guano deposition affects spatial patterns in soil chemistry, although it is limited to just two soil characteristics (pH and salinity). Analyses of coefficients of variation suggest that guano deposition increased variability in pH but not EC, but semivariance analyses suggested that guano deposition increased the patchiness of EC but not pH. Therefore, birds significantly altered the spatial heterogeneity of these two soil characteristics. For example, besides the greater coefficient of variation in pH on "Bird" than "Non-bird" islands, semiovariograms indicated some small-scale patchiness in pH on Bird islands because the semivariance was low at distances between 0.1 and 1.00 m, but then increased before leveling off at distances between 20 and 40 m (Fig. 1). On Non-bird islands there appeared to be no patchiness at any spatial scale because the semiovariograms were all relatively flat (Fig. 2). These patterns in pH, higher coefficients of variation and small-scale patchiness, indicate "hot spots" of guano deposition arranged randomly across relatively small areas, which is analogous to spatial patterns of N associated with islands of fertility in desert ecosystems (Schlesinger et al., 1996). Why guano deposition resulted in significantly greater patchiness in soil EC on Bird than Non-bird islands is hard to explain. The semiovariograms for Bird islands illustrate all possible patterns—from flat to increasing to asymptotic to higher-order polynomial, while Non-bird island semiovariograms, in general, are relatively flat (Fig. 2). In part, patchiness may be related to EC being generally high near the coast on both island types, but generally lower in the interior of Bird islands than Non-bird islands. This pattern can be potentially explained by higher soil moisture in the interior of Bird islands (see Table 1), which is probably due to the greater organic matter and soil respiration on Bird islands. Future research will examine spatial relationships between plants and soil chemistry (including NO_3^- and NH_4^+). Based on the data reported here we hypothesize that spatial patterns in salinity as a result of guano deposition contribute to species distributions on these islands.

This study illustrates the effects long-term guano deposition can have on soil chemistry and herbaceous plant communities in arid regions. Given the large number of desert islands, increasing desertification, and increasing nitrogen deposition across the globe, this study provides important data for understanding both the roles of birds and nitrogen in structuring plant communities in arid regions.

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References

Anderson, D.W., 1983. The seabirds. In: Case, T.J., Cody, M.L. (Eds), Island Biogeography in the Sea of Cortez, pp. 246–264. University of California Press, Berkeley, 508pp.

Anderson, W.B., Polis, G.A., 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118, 324–332.

Anderson, W.B., Wait, D.A., 2001. Subsidized island biogeography hypothesis: another new twist on an old theory. Ecology Letters 4, 289–291.

Augustine, D.J., Frank, D.A., 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology 82, 3149–3162.

Carter, M.R., 1993. Soil Sampling Methods of Analysis. Canadian Society of Soil Science, Lewis Publishers, Baco Raton, 823pp.

Dodd, G.L., Donovan, L.A., 1999. Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. American Journal of Botany 86, 1146–1153.

Gamma Design Software, 1998. GS+: geostatistics for the environmental sciences. Version 3.07, Gamma Design Software, Michigan.

Gastil, R.G., Phillips, R.P., Allison, E.C., 1973. Geological maps of the State of Baja California. Geological Society of America.

Goovaerts, P., 1998. Geostatistical tools for characterizing the spatial variability of microbiological and physico-chemical soil properties. Biology and Fertility of Soils 27, 315–334.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111, 1169–1194.

Hogg, E.H., Morton, J.K., 1983. The effects of nesting gulls on the vegetation and soil of islands in the Great Lakes. Canadian Journal of Botany 61, 3240–3254.

Hutchinson, G.E., 1950. Survey of existing knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion. Bulletin of the American Museum of Natural History 96, 483–519.

Krebs, C.J., 2001. Ecology: The Experimental Analysis of Distribution and Abundance, fifth ed. Benjamin Cummings, New York, 695pp.

McColl, J.G., Burger, J., 1976. Chemical inputs by a colony of Franklin's Gulls nesting cattails. American Midland Naturalist 96, 270–280.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82, 2381–2396.

Mizutani, H., Wada, E., 1988. Nitrogen and carbon isotope ratio in seabird rookeries and their ecological implications. Ecology 69, 340–349.

Nelson, B., 1979. Seabirds: their biology and ecology. A&W Publishers, New York, 219pp.

Odasz, A.M., 1994. Nitrate reductase activity in vegetation below an arctic bird cliff, Svalbard, Norway. Journal of Vegetation Science 5, 913–920.

Pärtel, M., 2002. Local plant diversity patterns and evolutionary history at the regional scale. Ecology 83, 2361–2366.

Romney, E.M., Wallace, A., Hunter, R.B., 1978. Plant responses to nitrogen fertilization in the northern Mohave desert and its relationship to water manipulation. In: West, N., Skujins, J.J. (Eds), Nitrogen in Desert Ecosystems, pp. 232–243. Dowden, Hutchinso & Ross, Inc., Pennsylvania, 297pp.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK, 436pp.

Ryan, P.G., Watkins, B.P., 1989. The influence of physical factors and ornithogenic products on plant and arthropod abundance at an inland Nunatak Group in Antarctica. Polar Biology 10, 151–160.

Sanchez-Piñero, F., Polis, G.A., 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology 81, 3132–3317.

Schlesinger, W.J., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Sharma, M.L., Tongway, D.J., 1973. Plant induced soil salinity patterns in two saltbrush (*Atriplex* spp.) communities. Journal of Range Management 26, 121–125.

Smith, V.R., 1978. Animal–plant–soil nutrient relationships on Marion Island (Subantarctic). Oecologia 32, 239–253.

Sobey, D.G., Kenworthy, J.B., 1979. The relationship between herring gulls and the vegetation of their breeding colonies. Journal of Ecology 16, 193–268.

Vidal, E., Medail, F., Tatoni, T., Bonnet, V., 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. Oecologia 122, 427–434.

Wainright, S.C., Haney, J.C., Kerr, C., Golovkin, A.N., Flint, M.V., 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. Marine Biology 131, 63–71.

Wiggins, I.L., 1980. Flora of Baja California. Stanford University Press, Stanford, 1025pp.