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Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands

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Abstract Energy and nutrient fluxes across habitat boundaries can exert profound direct and indirect effects on the dynamics of recipient systems. Transport from land to water is common and well studied; here, we document a less recognized process, substantial flows from water to land. On hyperarid, naturally nutrient poor islands in the Gulf of California, nutrient input via seabird guano directly increases N and P concentrations up to 6-fold in soils; these nutrients enrich plants. Nutrients in a long-lived cactus, a short-lived shrub, and annuals were 1.6- to 2.4-fold greater on bird versus nonbird islands. Because plant quality affects consumer growth and reproduction, we suggest that nutrient enrichment via guano ramifies to affect the entire food web on these islands.

Key words *Atriplex* · Desert nutrients *Opuntia* · Seabird guano · Spatial subsidies

Introduction

> "Wherever a large bird colony exists, the birds may be regarded as dominants in the sense that ... they determine the nature of the community of the area occupied by the colony." (Hutchinson 1950, p. 369)

Ecologists now recognize that different habitats affect one another in many ways, ranging from metapopulation to food web dynamics (Polis et al. 1996; Wiens 1997). In particular, habitats are frequently linked trophically, such that energy and nutrients originating in one place are transported elsewhere (Polis et al. 1997a). This is well established for land-to-water transfers such as watershed effects on streams and lakes (e.g., Borman and Likens 1967; Ward 1989; Wetzel 1990) and terriginous input to coastal marine systems (Barnes and Hughes 1988; Mann and Lazier 1991; Smith 1991). Here we focus on a much less recognized process (Polis and Hurd 1996a; Willson et al., in press): transport from water to land. We explore how spatial subsidies of marine nutrients affect plants that live on desert islands in the Gulf of California.

Desert systems are characterized by very low, highly variable precipitation; consequent rates of primary productivity are one to three orders of magnitude below those of other habitats (Louw and Seely 1982; Ludwig 1986, 1987; Polis 1991). However, primary productivity may be limited by nutrients as well as water since most desert soils are depauperate in available nutrients relative to most other habitats (Charley and Cowling 1968; Ettershank et al. 1978; West and Skujins 1978; Hadley and Szarek 1981; Smith 1981; Louw and Seely 1982).

Islands in the Bahia de los Angeles region of the Gulf of California receive an average of 59 mm of rain annually (Reyes-Coca et al. 1990); in most years, < 100 g C/m^2 per year is produced by plants (Polis and Hurd 1996a). These islands are surrounded by an extremely productive marine system, and organic carbon orginally fixed in the ocean regularly crosses the water-land interface via two conduits: shore drift and marine birds. Marine carbon arrives via algal detritus, marine carrion, and seabird carcasses and by-products (i.e., guano, feathers, fish scraps). These materials act as major "top-down" factors that directly and indirectly subsidize consumer communities on these islands (Polis and Hurd 1995, 1996a,b; Rose and Polis 1998; F. Sanchez-Piñero and G.A Polis, unpublished data). Because of perimeter-to-area relationships, marine drift disproportionately enriches smaller islands (Polis and Hurd 1995, 1996 a,b).

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Here we address another, largely independent, conduit by which marine materials affect terrestrial systems on these islands: the transport of marine-derived nutrients (nitrogen and phosphorus) that act as a major "bottom-up" factor stimulating primary productivity. Specifically, we assess how seabird guano affects soil and plant nutrient concentrations, nutrient pools, and plant biomass. Unlike shore drift, the importance of seabird nutrients is somewhat decoupled from island size; although seabirds occupy many small islands, many other small islands are not influenced, and several large islands support seabird colonies.

Because seabird diets consist primarily of fish and squid, they excrete nutrient-rich guano, high in N and P (Hutchinson 1950). For example, guano deposited on islands in the Gulf of California averages approximately 9% N and 11% P_2O_5, depending on which seabirds are present (Hutchinson 1950). Our observations suggested that guano greatly enhances plant growth on Gulf islands, but only during wet years.

On Gulf of California islands, there is high temporal and spatial variability in primary and secondary productivity. In years of high precipitation, such as during El Niño-Southern Oscillation (ENSO) events, water becomes less limiting and primary productivity increases (Polis et al. 1997b). However, the magnitude of increased productivity varies greatly among islands, despite the fact that all lie within 20 km of each other and receive equal rainfall. In 1992 and 1993 (wet years), islands where seabirds nest or roost supported 1.1- to 1.7-fold more plant (annuals and perennials) cover and 9.6- to 12.0-fold more plant (annuals) biomass than other islands (Polis et al. 1997b).

The diversity of plants on our study islands ranged from 3 to 55 species per island (unpublished data). These species and desert plant communities in general include life history strategies ranging from slow-growing, long-lived perennials (> 50 years) to short-lived perennials (2– < 10 years) and fast-growing annuals that die in a few months. Plants with low relative growth rates have a high capacity to store sporadically available nutrients, rather than immediately channeling nutrients into new biomass. Fast-growing plants typically respond to pulses of water and nutrient availability with increases in biomass rather than by nutrient storage (Grime 1977; Chapin 1980). In our system, we expect the two categories of perennial plants to respond to elevated nutrient levels with increased nutrient storage; in contrast, annuals should respond with growth but not store nutrients.

We compare the nutrient concentrations of long-lived perennial cacti, a short-lived perennial subshrub, and various annuals from well-fertilized bird islands and nutrient-poor islands without seabirds. We also compare the biomass and nutrient pools of annuals in 1995, a wet year, between bird and nonbird islands. *Opuntia acanthocarpa* (Buckhorn cholla; Cactaceae) and *O. bigelovii* (Teddy bear cholla) are slow-growing, drought-resistant succulents. *Atriplex barclayana* (saltbush; Chenopodiaceae) is a fast-growing, partially drought resistant subshrub. We selected *Opuntia* and *Atriplex* for analyses because they are the only two perennial species present on all our major study islands. The composition of fast-growing annuals varies among islands.

We also present δ^{15}N stable isotope data to show that ^{15}N signatures in *Atriplex* from bird and nonbird islands reflect the signatures in soils with and without guano input. Guano is very enriched in ^{15}N, probably due in part to the high trophic position of seabirds in the marine food web. If seabird guano is the primary source of N on bird islands, these plants should exhibit an ^{15}N signature similar to that of guano.

Materials and methods

This research was conducted on the midriff islands of the Gulf of California near Bahia de los Angeles (28°55′N latitude, 113°30′W longitude), Baja California Norte, Mexico. The 14 study islands in this archipelago range in size from 0.020 to 8.684 km^2 (Table 1). Seventeen species of seabirds (see Table 1 for identity) nest or roost regularly on 7 islands, possibly due to predator avoidance or proximity to good foraging areas (Hutchinson 1950; Anderson 1983; F. Sanchez-Piñero and G.A. Polis, unpublished data). Although most of the bird islands are relatively small, not all small islands are used by birds (e.g., Cerraja and Pata; Table 1) and birds use some large islands (e.g., Piojo; Table 1). Density and species composition of seabirds vary substantially among years (Anderson 1983; F. Sanchez-Piñero and G.A. Polis, unpublished data). Winter precipitation in this region prior to summer sample collection was 109 mm in 1995, 0 mm in 1996, and 2 mm in 1997.

Guano cover estimates

We used guano cover as an index of seabird nutrient input. On each island, guano cover was estimated in July 1996 using the point quarter method (Cottam and Curtis 1956): the percentage of ground covered with guano was visually estimated along two perpendicular 100- to 250-m transects on each island. At every fifth or

Table 1 Island location, size, and seabird usage category. Birds that import marine guano to these islands include gulls (three species), commorants (two species.), boobies (two species), terns (three species), herons (three species), and one species of each pelican, frigate, oystercatcher, and osprey. Seabird densities for these islands are available from in F. Sanchez-Piñero and G.A. Polis (unpublished data; also see Anderson 1983)

Island	°N/°W	Area (km^2)	Category
Gemelos W	28 57′/113 28′	0.020	Bird
Llave	29 00′/113 31′	0.022	Bird
Cerraja	29 00′/113 31′	0.037	Nonbird
Jorobado	29 01′/113 31′	0.039	Bird
Gemelos E	28 57′/113 29′	0.047	Bird
Coronadito	29 10′/113 36′	0.072	Bird
Bota	29 01′/113 31′	0.093	Nonbird
Flecha	29 00′/113 31′	0.129	Bird
Pata	29 01′/113 31′	0.136	Nonbird
Mitlan	29 06′/113 31′	0.156	Nonbird
Piojo	29 01′/113 31′	0.533	Bird
Cabeza	28 58′/113 29′	0.704	Nonbird
Ventana	29 00′/113 31′	1.275	Nonbird
Smith	29 04′/113 31′	8.684	Nonbird

tenth step, cover was assessed in the four 1-m^2 plots surrounding the point defined by that step. Transects were laid to avoid cliffs and to sample microhabitats (e.g., alluvial plains, talus slopes) in their approximate proportions of total island area. In total, we estimated guano for 120–160 m^2 points per island. Guano on bird islands often forms thick (5–>50 cm), well-baked deposits whose area is not affected by rainfall. It is possible that a small percentage of the low guano cover on nonbird islands was washed away by heavy rains in 1995.

Soil and plant nutrient concentrations, pools, and biomass

In 1995, we collected soil and *Atriplex* samples from five points on 14 islands. In 1997, we collected five samples of *Opuntia* from 9 (5 bird and 4 nonbird) islands. In 1995 and 1996, plant tissue (leaves and stems) from all plants in 10- to 15 1-m^2 plots was harvested on two bird (Gemelos West, 0.02 km^2, and Coronadito, 0.07 km^2) and two nonbird islands (Ventana, 1.28 km^2, and Smith, 8.68 km^2) to assess biomass and productivity. Live biomass (in 1995) and detritus (in 1996) of all species of annuals in each plot were also analyzed for nutrient concentration. Nutrient pools in live annuals from 1995 were calculated as biomass×nutrient concentration.

To determine N and P concentrations, each plant sample was oven-dried then homogenized in a blender. Microkejldahl digestions were performed on 0.1-g samples, using a sulfuric acid-hydrogen peroxide mixed acid reagent (Allen 1989). Digests were analyzed with a Varian Techtron (model 635) spectrophotometer using a salicylate-cyanurate reagent for total N concentration (Havilah et al. 1977), and a molybdenum-ascorbate reagent for total phosphate P (Taras et al. 1976). Data are expressed as percent dry mass. In total, we analyzed 65 soil and 186 plant samples.

Stable isotope analyses

Analyses of δ^{15}N ratios were performed on soil and *Atriplex* samples from two islands, representing extremes of seabird influence. The bird island, Gemelos West, is almost entirely covered by guano (76.6% cover); the nonbird island, Ventana, has 0% guano cover. Six soil and three plant samples from each island were analyzed by facilities at the Environmental Science and Policy Management Department, University of California, Berkeley, Calif.

Statistics

For some analyses, we grouped islands into two categories of seabird use. However, in reality, a continuum of bird influence exists. Therefore we analyzed data both categorically and continuously. After testing the data for normality and heteroscedasticity (and sometimes transforming), Student's *t*-tests compared sample means from bird versus nonbird islands. Simple linear regressions tested the relationships between soil nutrient availability (guano cover or soil N and P) and plant nutrient concentrations. Biomass and detrital N pools were log-transformed prior to analysis to normalize the data. However, we present untransformed means in Table 2 for clarity. We accepted *P*-values of <0.05 as statistically significant. We denote *P*-values >0.05, but ≤0.07 as marginally significant.

Results

Guano and soil nutrients

Seabird activities significantly influence guano cover. On average, guano covered 34.5% of islands on which seabirds nest or roost (range: 13.3–76.0%). In contrast, guano cover averaged <1% on islands without nesting or roosting sites (range: 0–5.5%; Table 2). Although a continuum of seabird influence exists among islands, islands can be divided into distinct bird and nonbird categories.

Table 2 Differences in soil and plant nutrient concentrations (%), biomass and N pools (g/m^2) between bird and nonbird islands. Values are the mean ± 1 SE

	Bird islands	Nonbird islands	*t*-test (*P*)
Guano cover	34.47 ± 8.30	0.79 ± 0.78	3.54 (0.003; 12 *df*)
Soil %N	0.22 ± 0.03	0.03 ± 0.01	2.24 (0.045; 12 *df*)
Soil %P	1.30 ± 0.24	0.35 ± 0.17	2.73 (0.018; 12 *df*)
Opuntia %N	1.20 ± 0.11	0.49 ± 0.12	4.28 (0.004; 7 *df*)
Opuntia %P	0.28 ± 0.03	0.14 ± 0.03	3.10 (0.017; 7 *df*)
Atriplex %N	1.68 ± 0.17	0.71 ± 0.12	5.21 (<0.001; 12 *df*)
Atriplex %P	0.35 ± 0.03	0.19 ± 0.02	4.58 (<0.001; 12 *df*)
Annuals %N	1.83 ± 0.11	0.71 ± 0.16	1.87 (0.20; 2 *df*)
Annuals %P	0.59 ± 0.81	0.15 ± 0.01	1.49 (0.27; 2 *df*)
Detritus %N	1.38 ± 0.08	0.89 ± 0.07	22.59 (<0.001; 2 *df*)
1995 biomass	191.61 ± 77.72	16.14 ± 7.02	3.93 (0.05; 2 *df*)
Annual N pools	3.97 ± 2.57	0.11 ± 0.04	3.92 (0.05; 2 *df*)
Annual P pools	1.36 ± 1.01	0.03 ± 0.02	2.99 (0.09; 2 *df*)
Detrital N pools	2.55 ± 1.35	0.15 ± 0.07	3.61 (0.06; 2 *df*)

Seabird guano on bird islands was incorporated into the soil as nutrients. Soil on bird islands averaged 7.0-fold more N and 4.9-fold more P than nonbird islands (Table 2). Concentrations of N and P in soils were positively associated with guano cover across islands (Fig. 1).

We used guano cover in our figures to illustrate plant-nutrient relationships. In all cases and for several reasons (see Discussion), guano cover had a stronger statistical relationship with plant nutrient concentrations than did soil nutrient concentration. Nevertheless, we also present data for soil nutrients because of their direct, mechanistic importance.

Plant quality for each life history strategy

Tissue nutrient concentrations of plants from all three life history strategies were positively correlated with guano cover and soil nutrients. Slow-growing, long-lived *Opuntia* had 2.4-fold higher N concentrations and 2.1-fold higher P concentrations on bird versus nonbird islands (Table 2). Moreover, a positive relationship existed between guano cover and both N and P in *Opuntia* (Fig. 2). However, the linear relationship between soil P and *Opuntia* P was only marginally significant ($R^2=0.60$, $P=0.07$) and that between soil N and *Opuntia* N was not significant ($R^2=0.19$, $P=0.33$).

Short-lived *A. barclayana* had 2.4-fold higher N concentrations and 1.8-fold higher P concentrations on bird versus nonbird islands (Table 2). Nutrient concentrations in *Atriplex* were likewise related to guano cover (Fig. 3). Significantly positive linear relationships existed between soil N and P and *Atriplex* N and P, respectively (N: $R^2=0.36$, $P=0.03$; P: $R^2=0.41$, $P=0.02$).

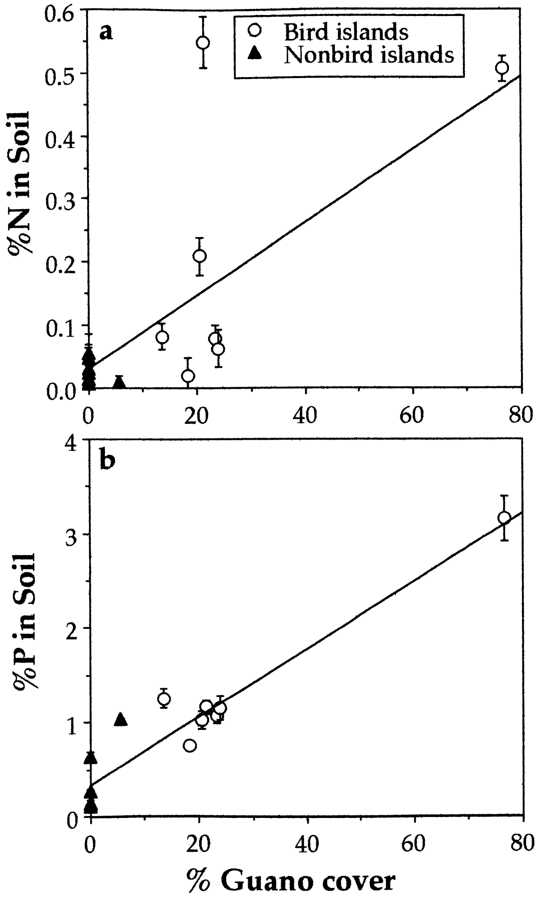

Fig. 1 Linear relationships on seven bird and seven nonbird islands between guano cover and %N in soil ($R^2=0.56$, $P=0.002$) (**a**) and %P in soil ($R^2=0.89$, $P<0.001$) (**b**). Each point represents the mean ± 1 SE from one island

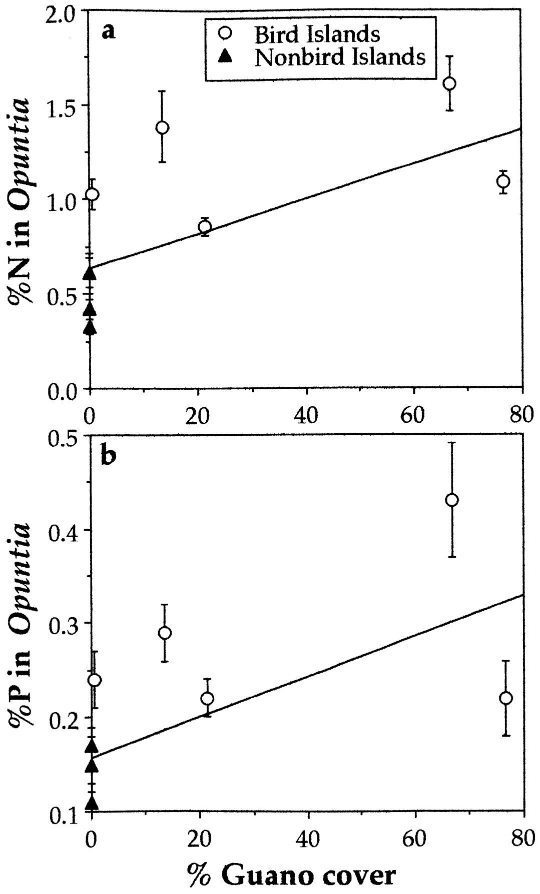

Fig. 2 Linear relationships on five bird and four nonbird islands between guano cover and %N in *Opuntia* ($R^2=0.52$, $P=0.03$) (**a**) %P in *Opuntia* ($R^2=0.46$, $P=0.04$) (**b**). Each point represents the mean ± 1 SE from one island

Annual plants on bird islands were dominated by *Amaranthus* spp. and *Chenopodium* spp. Nonbird islands included a higher diversity of plants including several genera in each of the Poaceae, Fagaceae, Euphorbiaceae, and Asteraceae. In 1995, annuals had 2.6-fold higher N and 3.9-fold higher P concentrations on bird islands than on nonbird islands (Table 2). However, the differences between bird and nonbird islands were not significant, probably due to low sample size (two islands) in each category. Both %N and %P of live annuals were significantly correlated with guano cover on the four islands (Fig. 4a,b). Detritus of annual plants in 1996 on bird islands had 1.6-fold higher N concentrations than that on nonbird islands (Table 2). Phosphorus was nearly undetectable in all our detritus samples. A strong, positive, linear relationship existed between detritus N and guano cover (Fig. 4c) and soil N ($R^2=0.96$, $P=0.02$).

Biomass and N pools of annuals

Biomass of annuals in 1995, a wet year, was 11.8-fold greater on bird islands than on nonbird islands (Table 2). Further, a strong, positive, linear relationship existed between plant biomass and guano cover (Fig. 5a). When biomass and nutrient concentrations were combined to calculate nutrient pools, bird islands had 36.1-fold more mass·area^{-1} of N and 45.3-fold more mass·area^{-1} of P in annual plants than nonbird islands, although the P pools were not significantly different due to large variation and small sample sizes. Nutrient pools were also highly correlated with guano cover on these islands (Fig. 5b,c).

Stable isotopes of soil and *Atriplex*

On Gemelos West, a bird island with 76.6% guano cover, the $\delta^{15}N$ ratio in the soil, which is largely guano, averaged 33.61 ± 1.96. In *A. barclayana*, this ratio was 36.36 ± 2.72. In contrast, soil on Ventana, the nonbird island, had a $\delta^{15}N$ signature of 7.16 ± 1.15. The Ventana *Atriplex* $\delta^{15}N$ ratio was 5.26 ± 0.85.

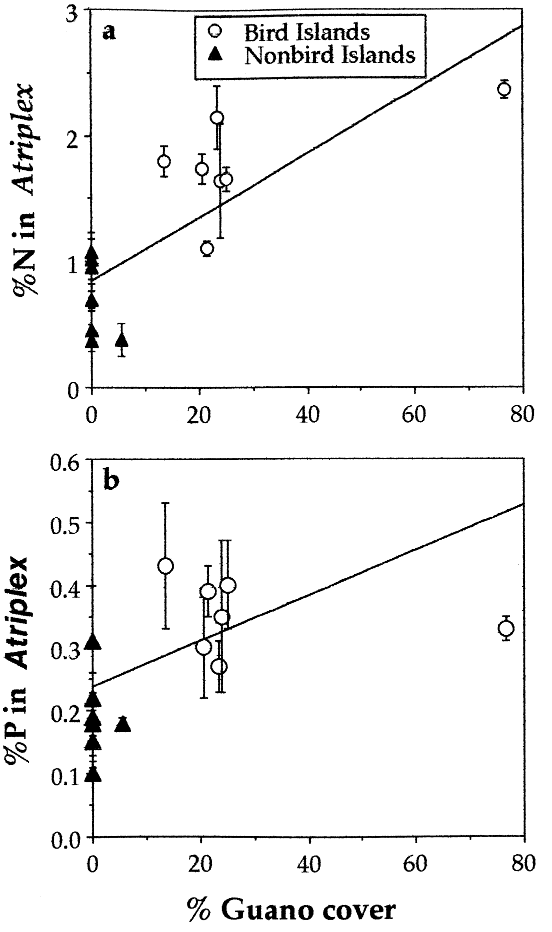

Fig. 3 Linear relationships on seven bird and seven nonbird islands between guano cover and %N in *Atriplex* ($R^2=0.58$, $P=0.003$) (**a**) and %P in *Atriplex* ($R^2=0.50$, $P=0.007$) (**b**). Each point represents the mean ± 1 SE from one island

Discussion

Seabirds use > 50 desert islands in the Gulf of California to nest or roost (Hutchinson 1950; Anderson 1983; G.A. Polis and F. Sanchez Piñero, unpublished data). These islands receive large quantities of guano, which substantially increase soil concentrations of N and P. Enriched soils then provide nutrients to the local flora, thus altering the nutrient concentrations, pools, and biomass of live plants and detritus. Such enrichment likewise occurs on islands in other archipelagoes: guano increases N and P in soils (Hutchinson 1950; Smith 1976, 1978a,b; Burger et al. 1978; Siegfried 1981; Ryan and Watkins 1989; Okazaki et al. 1993) and enhances plant growth and primary productivity (Gilham 1977; Burger et al. 1978; Smith 1978a; Siegfried 1981; Lindeboom 1984; Ryan and Watkins 1989; Daugherty et al. 1990; Myrcha and Tatur 1991; Odasz 1994). Guano also stimulates primary productivity in aquatic systems (e.g., the intertidal: Bosman et al. 1986; Bosman and Hockey 1988; Wootton 1991; Beckley and Branch 1992; Loder et al. 1996; mangroves: Onuf et al. 1977; lotic freshwater systems: Brinkhurst and Walsh 1967; Leentvaar 1967; Manny et al. 1994; Kitchell et al., in press). Often, widespread bottom-up effects propagate throughout the food web of communities enriched by allochthonous input (Polis et al. 1997b; see below).

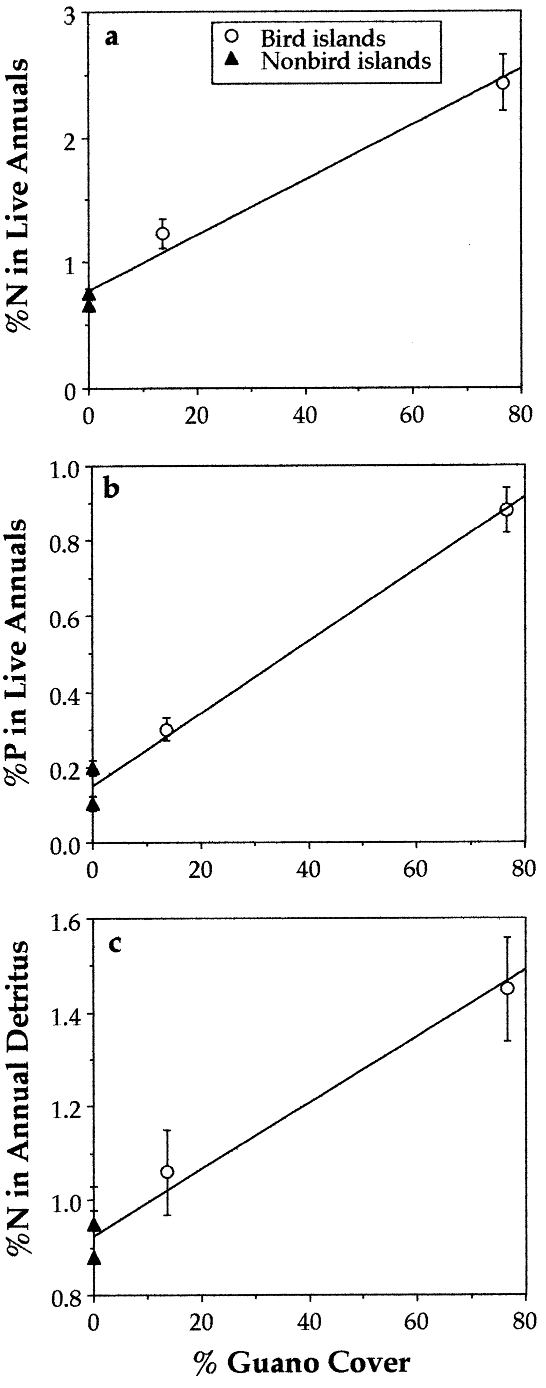

Fig. 4 Linear relationships on two bird and two nonbird islands between guano cover and %N in live annuals ($R^2=0.98$, $P=0.009$) (**a**), %P in live annuals ($R^2=0.99$, $P=0.006$) (**b**) and %N in annual detritus ($R^2=0.98$, $P=0.01$) (**c**). Each point represents the mean ± 1 SE from one island

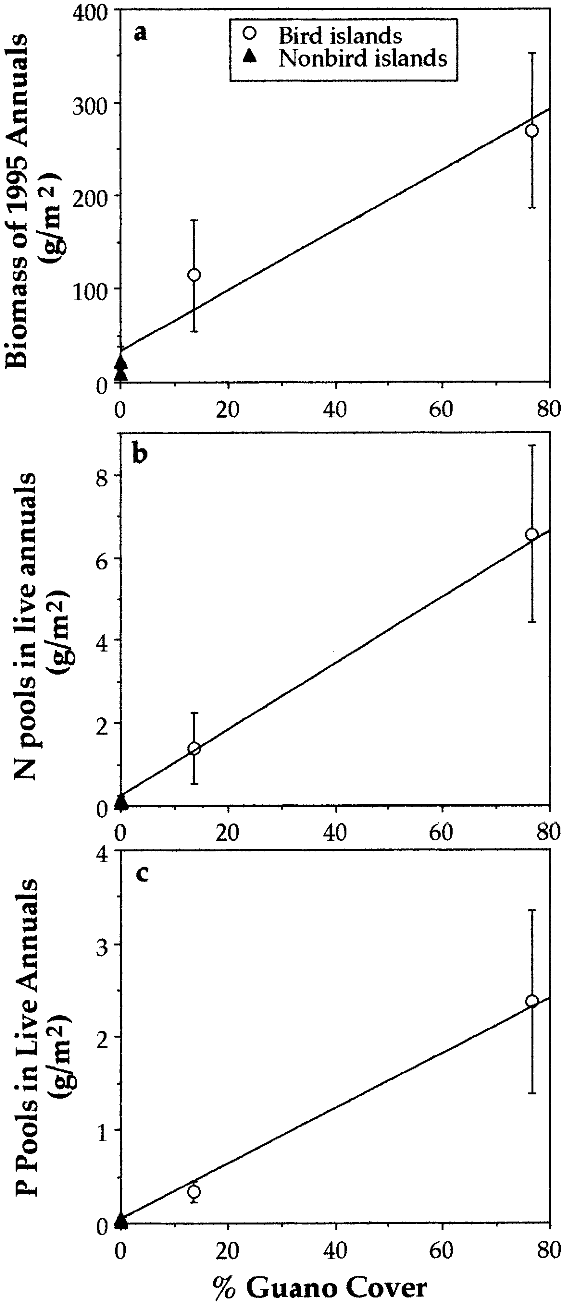

Fig. 5 Linear relationships on two bird and two nonbird islands between guano cover and 1995 annual biomass ($R^2=0.95$, $P=0.03$) (**a**), N pools in annuals ($R^2=0.99$, $P=0.003$) (**b**), and P pools in annuals ($R^2=0.99$, $P=0.002$) (**c**). Each point represents the mean ±1 SE from one island

Guano and soil nutrients

Soils on bird islands in the Gulf of California are covered by significantly more guano and contain significantly more N and P than on nonbird islands. The relationship between guano cover and soil P is stronger than that for N. We surmise this occurs because much N in avian uric acid decomposes over time into gaseous ammonia, whereas phosphate P is quite stable (Hutchinson 1950; Smith and Johnson 1995; Loder et al. 1996). Indeed, guano-derived P remains in soils for hundreds to thousands of years after seabirds have departed (Hutchinson 1950; Burger et al. 1978; Myrcha and Tatur 1991). Nevertheless, in our system, differences in soil between bird and nonbird islands are still significant for both P and N.

We suggest that guano cover is a reasonable, practical and particularly useful alternative to soil nutrient analyses, particularly in arid systems. First, a strong relationship exists between guano cover and soil nutrients. Second, very similar relationships existed between these two measures and plant nutrient quality. In all cases, guano cover exhibited a stronger statistical relationship with plant nutrient concentration than did soil nutrient concentration. Third, guano cover, readily estimated in the field, is more accessible than soil nutrient availability. Thus, using guano cover instead of laboratory analyses of soil nutrients would facilitate nutrient assessment in other archipelagoes.

Guano and plant quality

During infrequent rainy periods, soil nutrients become available to plants. This stimulates both greater nutrient uptake and productivity by plants on bird versus nonbird islands (Polis et al. 1997b). Grime (1977) and Chapin (1980) suggest that slow-growing plants in infertile or pulsed environments do not respond to pulses of resource availability with immediate growth, but rather exhibit "luxury consumption" and store excess nutrients. In contrast, fast-growing, ruderal species should respond quickly to sudden increases in resource availability, primarily via growth rather than nutrient storage.

However, plants from each life history strategy showed higher nutrient concentrations in response to greater nutrient supply. *Opuntia* sp. (a long-lived cactus), *A. barclayana* (a short-lived subshrub), and ephemeral annuals all stored or assimilated N and P as a function of soil nutrient availability. Thus, all plant species we analyzed, regardless of the specifics of their life history, responded similarly in their nutrient concentrations.

Although nutrient uptake probably occurs primarily during wet periods, differences in quality remain during dry periods. For example, our *Opuntia* samples were collected in 1997 after 18 months of severe drought (3 mm rain) and very little growth. Storage is expected in such slow-growing, long-lived plants adapted to infertile desert conditions (Grime 1977). Annual species likewise accumulated nutrients from growth during wet periods: tissue from bird islands had more N and P than that from nonbird islands. This difference existed in live plants in 1995 and in the detritus collected in 1996. Note that this result may reflect variation in species composition among islands. Assemblages of annual plants on bird islands have a higher proportion of nitrophilous species (*Amaranthus*, *Chenopodium*); in general, such species show lower nutrient use efficiencies (Chapin 1980; Vitousek 1982). This means that annual plants on bird islands do not necessarily store excess nutrients but simply require more nutrients per gram of tissue produced.

Stable isotope ratios of ^{15}N support our conclusion that N from bird guano is used by plants. Plants from bird islands are enriched in ^{15}N, reflecting the high ratios of ^{15}N in these guano-based soils. Plants from nonbird islands show relatively low ^{15}N signatures which reflect the soils on those islands.

Comparison with other systems

How do our plant responses compare to other island systems with seabirds? On high-latitude Marion Island, plants influenced by seabirds were 55% more enriched in N (1.59% vs 2.46% N) and 88% in P (0.17% vs 0.32% P) than plants away from guano areas (Smith 1978b). Plants from bird islands in our system were 55–145% more enriched in N (mean: 0.70% vs 1.42% N) and 84–100% in P (mean: 0.17% vs 0.32%P) than plants from nonbird islands. Although the absolute concentrations for our plants from a hyperarid region are somewhat lower than those from mesic Marion Island, they show a similar relative enrichment.

How do our nutrient values compare to other desert sites? Killingbeck and Whitford (1996) reviewed foliar and litter N concentrations of shrubs from many biomes. They reported a mean foliar N in desert shrubs of 2.2%, ranging from 1.0 to 4.4%. Our mean of 1.68% in *Atriplex* from bird islands was at the low end of this range; the mean (0.7%) from nonbird islands was lower than any study reviewed. Our *Opuntia* stems were even lower, with means of 1.20% and 0.49% N from bird and nonbird islands, respectively. The %N of living annuals on bird islands (1.83%) approached the mean for all studies; %N on nonbird islands (0.71%) is slightly lower than Killingbeck and Whitford's range. The %N of annual detritus on both bird (1.38%) and nonbird (0.89%) islands was within reported values for leaf litter (mean 1.1%, range 0.4–2.6%) (note that Killingbeck and Whitford summarized data from leaf detritus of shrubs; we analyzed detritus from annuals).

Overall, then, plants from all three categories were at the low end of the range of %N from other deserts. We can offer several reasonable explanations. Our *Atriplex* tissue included N-poor stems; values in Killingbeck and Whitford (1996) are just for leaf tissue. Analogously, *Opuntia* stems have photosynthetic tissue only superficially and are, by dry weight, primarily lignin, a material low in N. Nevertheless, we were surprised that %N of plants from apparently well-fertilized bird islands was low relative to other desert areas. We speculate that the very low precipitation in our study area may contribute to our findings; this area is one of the driest in North America (Polis et al. 1997b).

Dynamics of open versus closed island ecosystems

We can view islands as either "open" and receiving substantial input of guano, or "closed," receiving relatively little allochthonous input. In closed systems, nutrient availability and subsequent productivity are a function of nutrient recycling rates; rates are a function of herbivory, detritivory, excretion, and decomposition (Carpenter et al. 1992). In open systems, both in situ recycling and external inputs provide nutrients to plants. Thus, on open islands with guano inputs, plants are not as sensitive to in situ nutrient recycling rates or to losses of nutrients via physical (e.g., wind, runoff, mineralization) or biotic (e.g., herbivory) factors as are plants on nonbird islands. (not that recycling rates may actually be faster on bird islands – detritus on bird islands is of higher quality and thus may be decomposed by soil microbes or detritivores more rapidly; Melillo et al. 1982).

On islands with open systems, effects of seabird guano and other marine input ramify directly and indirectly throughout the food web to affect processes at the community and ecosystem levels. Populations of detritivores (e.g., tenebrionid beetles), herbivores (e.g., Hemiptera), and predators (e.g., spiders and lizards) are 3- to 24-fold larger on bird versus nonbird islands (Polis et al. 1996, 1997b; F. Sanchez-Piñero and G.A. Polis, unpublished data). Plants on bird islands are both higher in nutrient content and more productive. Although plant productivity clearly exerts strong effects on consumer abundance, plant nutrient quality also can be significant. Consumer reproduction, and thus abundance, is a direct function of N availability (White 1993). In particular, arthropod growth and egg production is often more limited by N than by carbon (Mattson 1980; Slansky and Rodriguez 1987; White 1993). Thus, on bird islands, consumption of plants or detritus high in N can lead to larger body size and greater fecundity, and thus contribute substantially to abundant populations of both herbivores and detritivores (F. Sanchez-Piñero and G.A. Polis, unpublished data). Such responses to increased nutrients likely propagate to higher-level consumers (Polis et al. 1997b).

Spatial subsidies of nutrients from water to land

A general notion widely held by ecologists is that the flow of energy and nutrients occurs commonly from land to water but that reverse exchange, from water to land is neither frequent nor significant (Polis et al. 1997a; Willson et al., in press). Thus watersheds affect processes in streams, rivers, lakes, and estuaries (Bormann and Likens 1967; Ward 1989; Wetzel 1990), and terrestrial materials entering the sea via rivers and wind enhance coastal productivity (Barnes and Hughes 1988; Mann and Lazier 1991; Smith 1991). Our previous research quantified the biomass flow from the sea to land and how such input of organic carbon affected the dynamics of land communities on islands and coasts (Polis and Hurd 1995, 1996a,b; Anderson and Polis 1998; Polis et al. 1998; Rose and Polis 1998). This study focused on the flow of nutrients from sea to land. A review of other systems (Polis et al. 1997a) suggested that water-to-land transport is ubiquitous, affecting the dynamics of island, coastal, and riparian communities along the land interface with both marine and freshwater systems.

Our review (Polis et al. 1997a) also suggested that the flow of nutrients across habitat boundaries is, on many occasions and in many communities, equally or more important than the flow of energy. Input of organic carbon targets consumers, thus bypassing and reducing the importance of primary producers; nutrient input stimulates primary production and plant quality, with subsequent indirect effects on consumers. Allochthonous nutrients entering nutrient-poor systems can drive productivity and dynamics, in both model (DeAngelis 1992; Polis et al. 1997a) and real (Polis et al. 1997a) systems. Such input, as in our desert island system, is often more than a mere "subsidy" that slightly increases primary productivity. Allochthonous nutrient inputs can be a key component that contribute greatly to explain system-wide productivity and dynamics.

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