Marine Subsidies Produce Cactus Forests on Desert Islands

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Abstract

Marine nutrient subsidies can shape terrestrial plant biodiversity. In island systems, nitrogen-rich seabird guano is a large component of such marine subsidies. In zones of nutrient upwelling such as the Gulf of California, copious seabird guano is commonplace on bird islands. Several bird islands host regionally unique cactus forests, especially of the large columnar cactus, cardón (*Pachycereus pringlei*). We propose that a chain of interactions across the land-sea interface yields an allochthonous input of nitrogen in the form of seabird guano, fueling the production of some of the densest cactus populations in the world. Fish, seabird, guano, soil, and cactus samples were taken from Isla San Pedro Mártir for nitrogen stable isotope ratio measurements, which were compared to soil and cactus samples from other seabird and non-seabird Gulf islands and terrestrial ecosystems throughout the range of the cardón. Isla San Pedro Mártir δ^{15}N values of the food/nutrient cycle are distinctively high, ranging from fish +17.7, seabird +19.7, guano +14.8, soil +34.3 and cactus +30.3. These δ^{15}N values are among the highest ever reported for plants. Seabird island soil and cactus δ^{15}N values were consistently enriched relative to mainland and non-bird islands. Our findings demonstrate that seabird mediated marine nutrient deposits provide the source for solubilized N on desert islands, which stimulate terrestrial plant production in the cardón cactus significantly beyond that seen in either mainland ecosystems or non-seabird islands. These results elucidate the integral nature of nutrient movement across the land-sea interface.

Introduction

The land-sea interface is distinguished by near constant movement of materials between biomes. Allochthonous subsidies, originating in one location and transported to a disparate environment, often take the form of marine nutrients. Marine derived subsidies, when delivered to coastal regions or islands, can provide nutrient inputs that impact the functioning of terrestrial ecosystems (1–3). The iconic example of the decaying bodies of spawning salmon enhancing soil profiles and terrestrial plant biodiversity illustrates the importance of these multi-step trophic land-sea linkages (4, 5).

There are a number of examples of how trophic cascades alter ecosystem functioning. As noted, salmon species contribute to nutrient levels at their spawning sites, leaving a record of this marine-to-terrestrial transfer in the resulting nitrogen and carbon isotope ratios of the locality (6). Artic foxes have been shown to be ecosystem engineers by increasing soil nutrients and enhancing plant productivity and diversity at den sites (7, 8). Seabird species can be important vectors across the land-sea interface for nutrients from marine environments, increasing native tree abundance and soil nitrogen where they roost (9). Seabird guano, which is deposited on land in coastal regions or island systems, as well as seabird bodies themselves (dead adults, chicks, and eggs) are a prime example of land-sea connectivity. Commonly, nitrogen deposits of marine origin are delivered to terrestrial soil—potentially through decaying fish matter or seabird excrement—where changes in soil composition or plant production occurs (1, 4, 10). These inputs can greatly impact the nitrogen nutrients found in soils (11).

Globally, coastal areas represent only 8% of total land area but provide 20% of oceanic production (12). Seabirds are present in a wide range of high productivity marine systems around the world and are essential to nutrient cycling between land-sea systems. They facilitate the exchange of nitrogen and other chemical subsidies between the two biomes (11, 13–16) and alter physical and soil conditions directly affecting plant richness and distribution (17). In the San Juan archipelago, seabird derived guano in intertidal regions appears to increase the abundance of certain algal species while simultaneously decreasing intertidal plant biodiversity (18). In coastal areas where native plants create poor bird habitat, nutrient cycling is limited due to decreased seabird guano deposits (19). In Antarctica, penguin rookeries classically exhibit significant nitrogen deposition to the island ecosystem (11, 20, 21). Similarly, in the Gulf of California, areas of seabird influence possess increased nitrogen content and stable isotope ratios (16, 22).

Guano contains nitrogen in the form of NH_4^+, NO_3^-, and as a component of uric acid ($C_5H_4N_4O_3$). Each of these undergoes chemical alteration at different rates of decomposition (20). Previous research has demonstrated that the nitrogen isotope composition of bulk guano enriched soils is significantly elevated due to the volatilization of ammonia, leaving the remaining material with more positive $\delta^{15}N$ values (11). Guano enriched soils have much higher nitrogen isotope ratios than non-guano enriched areas (10) and create spatial variation in the chemical soil composition of island systems (15).

In years of higher precipitation such as El Niño years in the Southwest U.S. or when hurricanes reach this region, there is an elevated presence of decomposed guano due the mobilization of the nutrients from the increased moisture. During these pulse years, the soil exhibits increased nitrogen levels with increased plant productivity (10). It is suggested that guano deposition in terrestrial ecosystems could increase soil nitrogen content by up to 100 times its original amount (13). Plants growing in areas with higher guano concentrations take up nitrogen sourced in guano and as a result have significantly elevated $\delta^{15}N$ values (2, 15, 16, 23). These elevated $\delta^{15}N$ values therefore become a tracer for the impact of seabird guano in the plant community.

The arid islands in the Gulf of California, Mexico manifest the effects of marine nutrient cycling to terrestrial systems. Bird islands— typically small (<3 km^2), predator free, with low topography, that occur in high productivity waters — are utilized for habitat by a large quantity of seabirds. Due to high perimeter-to-area ratios, these small islands are disproportionally influenced by the surrounding marine environment (24). Guano excreta on bird islands is a significant component of both island appearance and island function, with bright white guano crusted over rock surfaces once as thick as 10 cm in some places (25). A variety of bird species are known to frequent bird islands; in the Gulf of California, species with the highest abundances include Heermann's Gulls, Elegant Terns, Blue-footed Boobies, and Western Gulls (26).

These bird islands have also been shown to have significantly reduced plant diversity, likely due to the higher N and P nutrient concentrations that act as a filter (27), which has also been seen in other bird island systems (28). However, cacti are seen to occur in both higher diversity and abundance on bird islands (29). What then is the role of the marine nutrients on the structure of these island communities? We focus on the land-sea connections of several bird islands in the Midriff region of the Gulf of California, including several of the most important seabird islands in Mexico. These islands, especially San Pedro Mártir and Cholludo are distinguished by a forest of the widespread Sonoran Desert columnar cactus *Pachycereus pringlei* (S. Watson) Britton & Rose (*cardón* or *sahueso*, Cactaceae), which cover the island and contributes a shocking amount of plant biomass in such an arid setting (29) (Figure 1).

We use nitrogen stable isotope ratios to (a) test if there is a trophic cascade that originates in the ocean, is linked to land by seabirds and their guano, deposited into the soil, and then utilized by the tissue of the cardón, and (b) assess if this nutrient transfer is a manifestation of sea to land connections on seabird islands that is not found in mainland habitats or islands without seabird colonies.

Results

Nitrogen stable isotope values show a trophic chain from the sea onto the land on the seabird islands of the Midriff region of the Gulf of California (Figure 2; Table 1). On Isla San Pedro Mártir, fish samples generally had a mean nitrogen stable isotope content of +17.7 ± 0.88, seabird feathers displayed $\delta^{15}N$ values with a mean value of +19.7 ± 0.67 (all nitrogen isotope values are reported in ‰ units relative to the $^{15}N/^{14}N$ ratio of atmospheric nitrogen, ATM). Fresh guano deposited by seabirds on the island had a mean $\delta^{15}N$ value of approximately +14.8 ± 2.12, which, through microbial degradation and then volatilization of ammonia, became greatly elevated in the soil, +32.4 ± 3.55. Mártir cardón specimens had an average $\delta^{15}N$ value of +30.3 ± 3.86. Other seabird islands in the Midriff region (Islas Alcatraz, Las Ánimas, Cardonosa, Cholludo, Partida, Rasa, and Salsipuedes) showed consistently high soil and cardón stable nitrogen isotope values, with an average of +34.3 for soil (range of +24.3 to +48.0) and +30.3 for cacti tissue (range of +21.1 to +38.7) (Table 1).

Table 1

Average $\delta^{15}N$ values for the five primary sample regions. [1] Bird island values include Isla San Pedro Mártir. [2] Non-bird island values exclude Isla San Diego

Isla San Pedro Mártir				
Sample	N	$\delta^{15}N$	S.D.	Range
Fish	11	+17.7	0.88	+16.6–19.3
Seabird Feather	16	+19.7	0.67	+18.2–20.5
Guano	15	+14.7	2.26	+11.4–20.3
Soil	20	+32.4	3.55	+25.9–37.9
Cardón Tissue	20	+30.3	3.86	+25–37.6
Bird islands [1]				
Sample	N	$\delta^{15}N$	S.D.	Range
Soil	85	+34.3	3.84	+24.3–48.0
Cardón Tissue	85	+30.3	3.44	+21.1–38.7
Non-bird islands [2]				
Sample	N	$\delta^{15}N$	S.D.	Range
Soil	74	+15.0	3.40	+9.0–25.1
Cardón Tissue	74	+11.7	2.26	+4.3–20.8
Mainland Sonora				
Sample	N	$\delta^{15}N$	S.D.	Range
Soil	30	+13.8	2.01	+10.3–21.1
Cardón Tissue	30	+11.2	1.88	+7.8–14.9
Baja California peninsula				
Sample	N	$\delta^{15}N$	S.D.	Range
Soil	109	+11.4	2.92	+5.5–18.9
Cardón Tissue	110	+8.1	3.12	+2.5–17.3

Comparative samples of soil and cardón cacti from the Baja California peninsula, non-bird islands of the Gulf of California, and mainland Mexico had lower and consistent stable nitrogen isotope values (Figures 3 and 4). Average nitrogen isotope values for peninsular populations of soil were +11.4 (range of +5.5 to

+18.9) and +8.13 for cacti tissue (range of +2.5 to +17.3). Likewise, the non-bird Gulf islands average values per population for soils was +15.0 (range of +7.0 to +25.1) and +11.7 for cardón cacti (range of +6.8 to +20.8). One non-bird island, Isla San Diego, had significantly higher values of +34.0 ±1.89 and +32.8 ± 2.67 for soil and cardón respectively and is reported separately from the other non-bird islands. Mainland Sonora populations had average values of +11.4 for soil (range of +12.4 to +15.4), and +11.2 for cacti (range of +9.4 to +12.3) (Table 1, Table S1).

Discussion

Nutrient subsidies are known to supply otherwise unavailable resources that create unique growing conditions in diverse habitats around the world. Seabirds are an important vector, which have large population densities at oceanic sites of high primary productivity, often associated with upwelling. Zones of upwelling often correspond with mediterranean or arid climates on the western side of continents (30). Accordingly, the effect of seabird transmitted marine nutrients in shaping vegetation patterns can be overlooked due to relatively modest and arid adapted floras. Yet, columnar cactus diversity is high in the Sonoran Desert of the Gulf of California (31) with one such species, *Pachycereus pringlei*, ubiquitous on the Gulf islands. Within this context, several islands in the Gulf of California stand apart, covered in a green forest of columnar cacti, unrivaled in density (Figure 1). As evidenced by the $\delta^{15}N$ values presented in this study, we now have a better understanding of the important role seabirds play in bridging the land-sea barrier and shaping terrestrial ecosystems.

Land-sea interface in the Gulf of California

Strong winter and spring winds from the northwest, year-round tidal fluctuations, and constriction points between the Midriff Islands cause coastal trapped waves that lead to mixing and upwelling that stimulate globally high values of primary productivity in the Gulf of California (rates can exceed 4 g C/m^2/day; 32, 33). The persistent cold-water upwelling in combination with the arid climate of the Sonoran Desert leads to a marked aridity on the islands. Upwelling of cold water with nitrogen rich nutrients provides food for coastal fish species, who are then consumed by resident and semi-resident island bird populations, as well as numerous marine mammal and fish species. These birds deposit guano onto island habitats, and as nutrients from guano leach into the soil, they are then able to be utilized by cacti and annual plant species on the island (Figure 2).

The flow of nutrients from marine to terrestrial environments has been well documented on small islands in the Gulf of California, both in the form of oscillating land driven (wet, El Niño years) or sea based (dry, La Niña and most years) trophic cascades (34), and by nesting seabirds (14, 15). We can now extend this chain of interactions to the regions anomalously dense cactus forests.

The cactus forest on Isla San Pedro Mártir has a density of ca. 2,700 plants/ha (35) and a neighboring bird island, Isla Cholludo, has an order of magnitude more cardón cacti with ca. 23,500 plants/ha (Wilder unpublished data). These densities are far greater than the rest of the species range (ca. 150 plants/ha in

Baja California, ca. 60 plants/ha in Sonora; 36) and are likely some of the densest, if not the densest, columnar cacti populations in the world (31). In addition to the role of nitrogen subsidies from guano, the increased abundance of cardón cacti on the islands are thought to be due to the absence of native rodents and other terrestrial herbivores that are known to prey on seedlings and young columnar cacti, as well as a favorable maritime climate (35, 37). As these cacti mature on the island, they tend to topple, potentially because of strong ocean winds and occasional tropical storms and their position in a loose, rocky substrate (35). Their decomposition propagates the nutrient cycle.

Nitrogen stable isotope ratios clearly set the bird islands apart from other locations around the Gulf of California due to the transfer of nitrogen from the marine to island setting. Our data shows a large difference in $\delta^{15}N$ values between bird islands, compared to non-bird island, mainland, and peninsular populations, with higher mean nitrogen isotope ratios present in bird islands compared to the other localities (Figure 4).

One other island sampled, San Diego, also exhibited higher $\delta^{15}N$ values (+34.0 for soil and +32.8 for cardón) on par with those of bird islands. San Diego does not demonstrate direct bird guano influence as Mártir does, but observations at the study site did find seabird bone remains at the base of several cardón cacti sampled. It is possible that seabirds maintain an influence on this island via nesting, death, and decomposition at the base of the cacti that permits elevated $\delta^{15}N$ values, uncharacteristic of non-bird guano island systems. Nutrient cycling on San Diego island, as well as other islands that indicate presence of seabirds though lack the characteristic guano white-wash, deserve further study.

Lessons from nitrogen

The patterns present on seabird islands in the Gulf of California are consistent with previous research; systems subsidized with external nitrogen deposits tend to include fewer species (18, 28, 38). Species richness and type can be impacted by spatial subsidies (39). It is possible that cacti and other organisms present on seabird islands necessitate the development of a physical tolerance to high, “toxic” levels of guano to be successful in such environments. It has been shown that plants on subsidized island systems possess different physiological mechanisms to manage increased resources (10). Increased guano deposition on the seabird islands of the Midriff region deliver nutrients that may be used uniquely by cardón cacti (and cholla cacti on some islands, e.g., Rasa) to increase their population density in a way that is not seen in other island plant species.

Increased nitrogen deposits have shown to have both beneficial and limiting impacts on plant species (29, 40). Cacti utilize nitrogen in a variety of ways, such as components of chlorophyll and nucleic acids, and as a factor in protein synthesis. When there is a greater store of available nitrogen during cacti development, cacti exhibit an increase in soil root growth and shoot growth (40). Plants with low relative growth rates are known to have a high capacity to store sporadically available nutrients (22).

The nitrogen isotope values obtained on Midriff seabird islands are some of the highest reported for any region globally and consistent with previous research in this region. Previously, the highest $\delta^{15}N$ value (that we have located) for a plant in a natural environment outside the seabird islands of the Gulf of California was +21.4 from a prairie wildflower (*Callirhoe involucrata*) in a tallgrass prairie (41, 42). Schoeninger & DeNiro (43) likewise did not find $\delta^{15}N$ values higher than +20.0 for plants, although they report $\delta^{15}N$ values for marine fish (+11.1 – +16.0) and seabirds (+9.4 – +17.9), the higher values of which compare well with our results. Studies in the Gulf of California islands by Stapp et al. (16) similarly compare well to the $\delta^{15}N$ levels we obtained for guano from Isla San Pedro Mártir of +14.77 ± 2.26 (their values, +14.2 ± 2.34) as well as our average bird island $\delta^{15}N$ soil values +34.3 ± 3.84 (their values, +28.3 ± 5.44). Enriched $\delta^{15}N$ values in plants correspond with high productivity or fertilized habitats (agricultural and ecologically), largely due to ammonia volatilization (44). These results further confirm that guano serves as excellent fertilizer, which was harvested from many of the bird islands of the Gulf of California in the late 1800s (45).

In all study populations, a significant increase in the mean $\delta^{15}N$ values occurs between seabird guano and soil. Other studies have also observed this dramatic increase in $\delta^{15}N$ soil values relative to the source guano and argue that the volatilization of ammonia during diagenesis of these nitrogen rich deposits (11, 23), leads to the high $\delta^{15}N$ soil values we documented on bird islands, + 24.3 to +48.0. Our data show the trophic level increases in marine-sourced nitrogen isotope values as well as the notable increase from guano to soil and cardón samples (Table 1). Our data also records a consistent decrease in $\delta^{15}N$ values from soil to cactus tissue of about 2.6 to 4.0‰. Although the causes of this decrease in $\delta^{15}N$ values are not well understood, this is in agreement with most plant tissues, which have slightly lower $\delta^{15}N$ values than the soil on which they grow (42). Nitrogen isotope ratios can show high variance in systems where isotopic fractionation involves significant losses of volatile nitrogen as ammonia (6, 16, 23, 46).

Other terrestrial systems at the land-sea interface, such as penguin rookeries, display a similar mechanism of marine to terrestrial nutrient transfer where large isotopic fractionation of nitrogen is evident (11, 20). Guano deposits onto soil substrate allow uric acid to leech into soil and decompose. A study by Mizutani et al. (21) incubated rookery soil with added uric acid. In 10 days, the decay of the uric acid and volatilization and loss of ammonia led to an 8.4‰ increase in $\delta^{15}N$ values of the remaining soil nitrogen.

Conclusion

The enriched $\delta^{15}N$ values exhibited in soil and cardón cacti on bird islands in the Gulf of California are established by marine nitrogen subsidies deposited via seabird guano and its subsequent decay. The ammonia rich guano accumulated on these desert islands, once the focus of extensive commercial harvesting, is a byproduct of regional marine productivity. Nitrogen cycling mediated by seabirds moves nutrients from marine to terrestrial biomes, significantly affecting terrestrial plant production – in this case producing the densest columnar cactus populations in the world, a nutrient relationship that transcends the land-sea boundary.

Methods

Study system

The Gulf of California, also known as the Sea of Cortés, is an ecologically and geologically diverse region (47). The Gulf separates the Baja California peninsula and mainland Mexico, housing numerous islands and an array of both endemic and migratory species of marine organisms, mammals, plants, insects, and birds (48). Gulf of California islands have diverse geological histories and run the spectrum of island biogeographic variables in scale, isolation, and age (27, 48) The 17 islands sampled in this study, including the eight bird islands, encompass land bridge and oceanic islands and islands close to and far from shore, factors which do not account for the observed patterns tested in this study.

Seabirds thrive in the Gulf, where they have access to nutrient-rich fishes, products of high productivity upwelling in the waters around islands (14). This high productivity is especially concentrated in the Midriff region of the Gulf of California, a desert archipelago that stretches west to east at ca. 29º latitude. While present in other regions of the Gulf, the Midriff region contains the greatest number of seabird islands. This study focused in part on Isla San Pedro Mártir, which is one of the most important seabird rookeries in Mexico, as a model system for the seabird islands and the tropic cascade described. Eighty-five species of birds have been recorded on this island, including eight breeding seabirds (49). The colonies of the Brown Booby (*Sula leucogaster*) and Blue-footed Booby (*S. nebouxii*) are among the world's largest, and the colonies of the Brown Pelican (*Pelecanus occidentalis*) and Red-billed Tropicbird (*Phaethon aethereus*) are among the largest in Mexico (50). Isla San Pedro Mártir's substrate is coated with guano and contains a flora of 28 species (35, 51) with plant biomass dominated by the cardón cactus (Figure 1) and seasonally abundant ephemerals post El Niño or hurricane derived storms. Designation of islands as seabird or not follows Velarde et al. (26) and Wilder et al. (27).

Sample collection

Sample collection took place at two scales. Five steps of the land-sea trophic chain were sampled on Isla San Pedro Mártir in 2017: fish, seabirds, seabird guano, soil, and cardón cactus tissue. Fish were sampled by collecting freshly regurgitated pelagic fish (sardines) from the blue-footed booby. Regurgitation is a common feeding behavior of this species. Seabirds were sampled through collection of recently shed feathers from the blue-footed booby (N = 16). Guano, derived from either the blue-footed or brown booby (N= 15), was collected by scraping off recent excrement from rocks and camping material. The study passively collected excreted guano, dropped feathers from the birds, and excreted fish thrown up by the birds as part of their normal behavior. No experiments were conducted with live vertebrates that needed approval by a named institutional and/or licensing committee. Soil samples obtained were gathered adjacent to the root and at the base of individual cardón cacti by scraping off the top couple centimeters of soil and excavating to ca. six inches belowground (N = 20). Cardón tissue was collected from a small section of a single rib per individual on a stem with recent growth (N = 20). Soil, guano, and feather samples were stored dry at ambient temperature. Fish samples were stored on ice until they could be frozen (after approximately 24 hours) for transport to the lab. Cardón tissues were dried with absorbent paper in a plant press to remove tissue moisture and reduce bacterial degradation.

For comparison, soil and cardón tissue were sampled throughout the range of the species, including other islands of the Gulf of California, both seabird (8, including Isla San Pedro Mártir) and non-bird islands (9), along the Baja California peninsula (11) and in Sonora, MX (3) in 2018 and 2021. In total, 10 soil and 10 cardón collections were made from 31 locations (Figure 3; Table S2).

Lab analysis

Cardón tissue for isotope measurement was limited to the chlorenchyma tissue immediately below the epidermis. Soil samples were prepared by collecting the very fine particles in the soil sample containers, which allowed us to bias the sample toward an average organic matter, avoiding a sample dominated by one large organic particle. Fish samples were collected from muscle tissue and dried overnight in a 50°C oven. Dirt was removed from the bird feathers with soap and water and feathers were dried. Both fish samples and bird feathers were de-oiled using a 2:1 mixture of chloroform:methanol and samples were again dried overnight.

Samples were analyzed in the Environmental Isotope Laboratory in the Geosciences Department of the University of Arizona. The stable nitrogen isotope ratio ($\delta^{15}N$) and nitrogen content were measured on a continuous-flow gas-ratio mass spectrometer (Finnigan Delta PlusXL). Samples were combusted using an elemental analyzer (Costech) coupled to the mass spectrometer. Standardization is based on acetanilide for elemental concentration, IAEA-N-1 and IAEA-N-2 for $\delta^{15}N$. Precision is better than ± 0.15 for $\delta^{15}N$ (1σ), based on repeated internal standards.

Declarations

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Figures

Figure 1

View from summit of Isla San Pedro Mártir, showing the cardón cactus forest. © John Sherman.

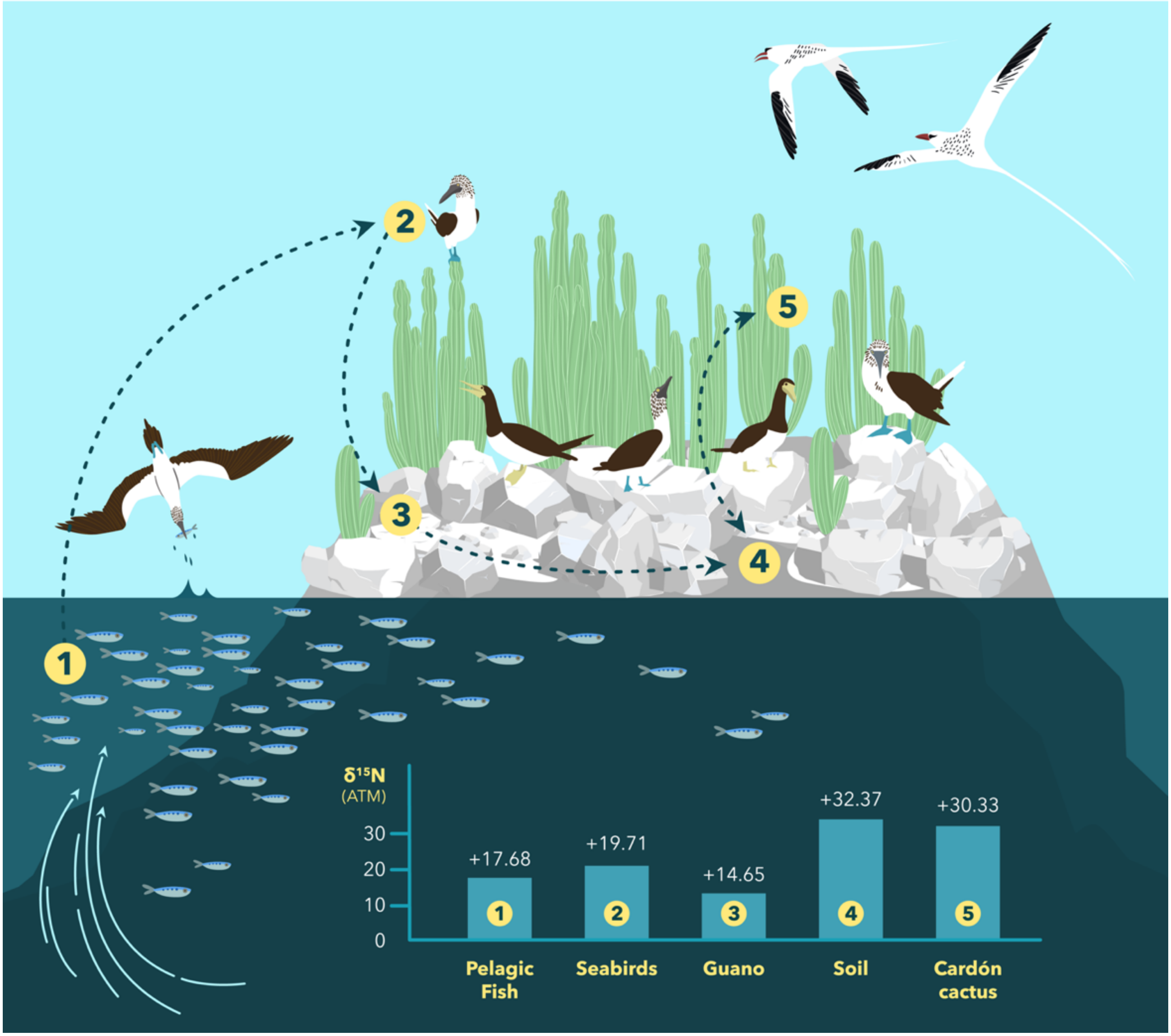

Figure 2

Trophic nutrient transfer across the land-sea interface of Isla San Pedro Mártir. Diagram shows the flow of nitrogen stable isotope values driven by upwelling in the Gulf of California. (1) Pelagic fish that are eaten by (2) seabirds that (3) deposit guano on bird islands, which (4) enter the island soil that is then (5) utilized by the cardón cactus, which returns to the soil upon the death of the cactus. Figure by Paola Ramirez.

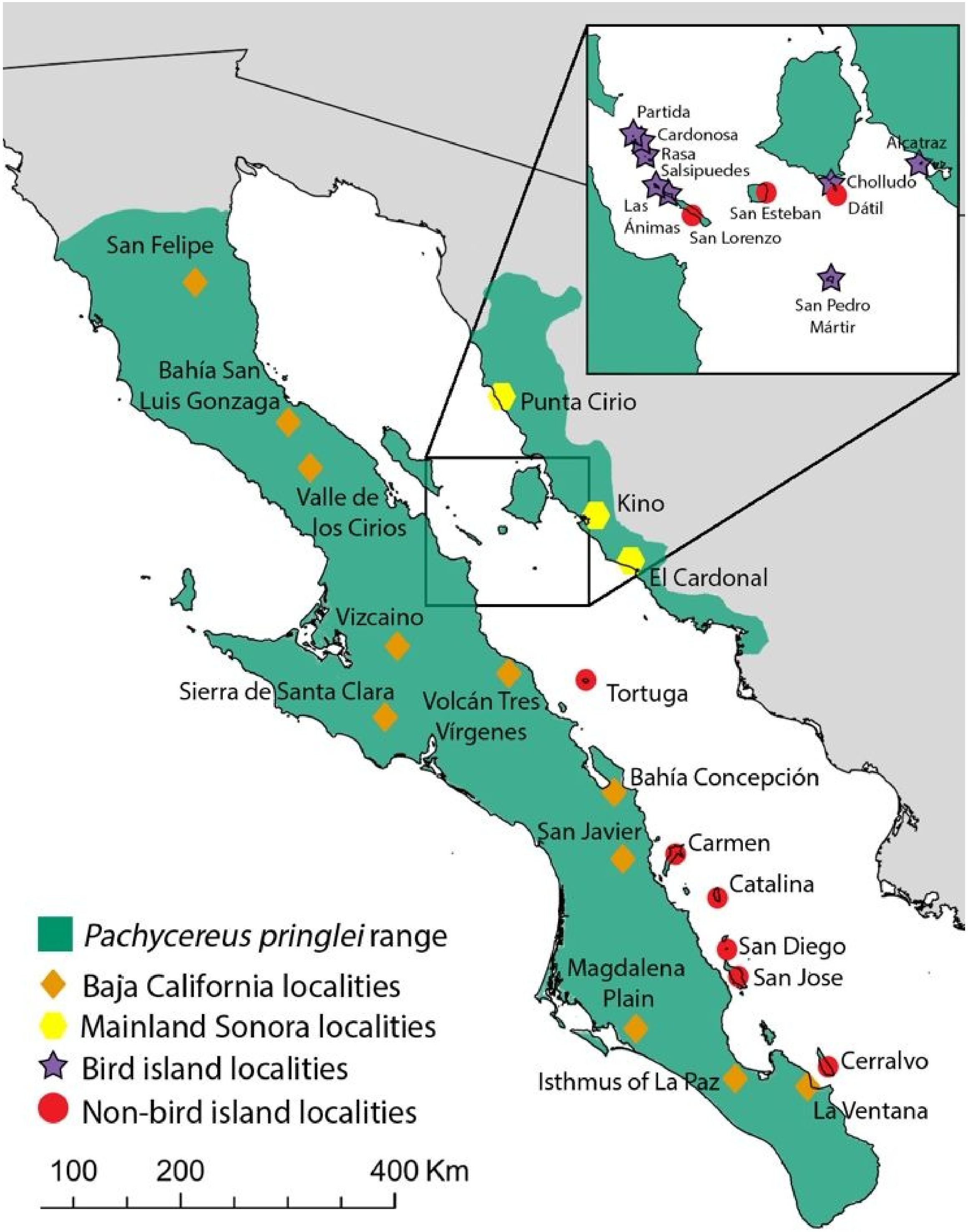

Figure 3

Sampling localities across the range of cardón.

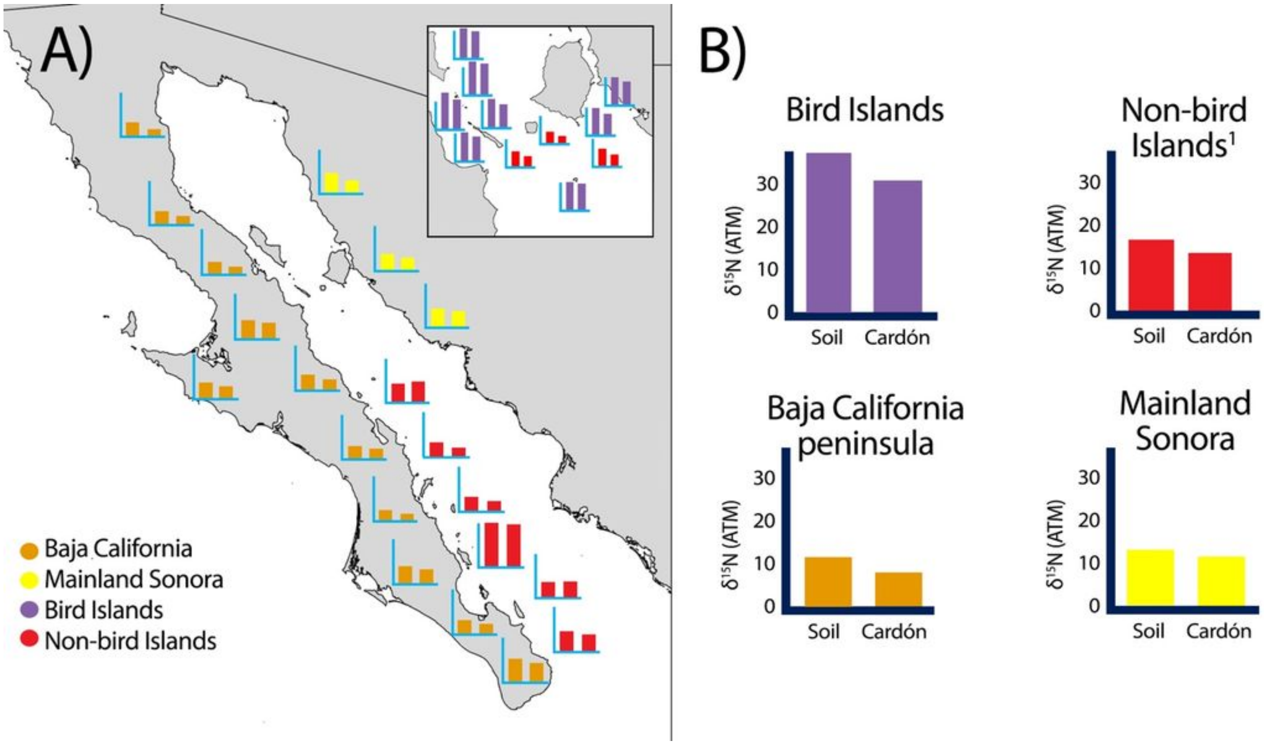

Figure 4

Average δ15N values for soil and cardón across sampling localities. (A) Geographic distribution of soil and cardón δ15N values at each sampling site. (B) Comparison of soil and cardón δ15N values for bird islands, non-bird islands (1 excluding Isla San Diego), Baja California, and Sonora.

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