MARINE SUBSIDIES PRODUCE CACTUS FOREST ON DESERT ISLAND

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AMANDA TARYN BECKER

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Approved by:

Dr. Benjamin Wilder
Desert Laboratory on Tumamoc Hill

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Amanda T. Becker[1], David L. Dettman[2, 3], Benjamin T. Wilder[4]

[1]Department of Ecology and Evolutionary Biology, University of Arizona

[2]Department of Geosciences, University of Arizona

[3]Estuary Research Center, Shimane University, Japan

[4]Desert Laboratory on Tumamoc Hill, University of Arizona

Abstract

Marine nutrient subsidies can impact terrestrial plant biodiversity. In island systems, seabird guano, rich in nitrogen, is a large proponent of such marine subsidies. In the Gulf of California Midriff Islands, seabird guano is commonplace on bird islands, such as San Pedro Mártir, where the large columnar cactus, cardón (*Pachycereus pringlei*), is the dominant plant biomass. We propose that a chain of interactions across the land-sea interface yield an allochthonous input of nitrogen in the form of seabird guano that fuels the production of one of the densest cactus forests in the world. Fish, seabird, guano, soil, and cardón samples were taken from the island for stable $\delta^{15}N$ isotope ratios, which were compared to other Gulf islands and terrestrial ecosystems throughout the range of the cardón. The cactus forest on this seabird island showed elevated marine derived nitrogen isotope ratios relative to mainland and non-bird islands. $\delta^{15}N$ values increased at each trophic level, illustrating a trophic cascade between the marine and island ecosystems driven by marine upwelling. Our findings demonstrate that marine nutrient deposits stimulate terrestrial plant production that is absent in mainland ecosystems and non-seabird islands, elucidating the integral nature of nutrient movement across the land sea interface.

Key words: *nutrient cycling; seabird influence on terrestrial ecosystems; seabird guano; $\delta^{15}N$ isotopes; trophic cascade*

Introduction

Allochthonous subsidies, originating from one location and transported to a disparate environment, often take the form of marine nutrients, an integral aspect of the land-sea interface. Marine derived subsidies, when delivered to coastal regions or islands, can provide nutrient inputs that impact the functioning of terrestrial ecosystems (Bartz and Naiman 2005, Erskine 1998, Hocking and Reimchen 2009). 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 (Hocking and Reynolds 2011).

There are a number of examples of how trophic cascades function across the land-sea interface, with marine or freshwater subsidies impacting the nutrient availability on land. Salmon species can contribute to nutrient levels at their spawning sites, maintaining a large influence on N and C values (Bilby et al.1996). Seabird species can be vectors for nutrients from marine environments, increasing native tree abundance and soil nitrogen (McCauley 2012). Seabird guano, which is deposited on land in coastal regions or island systems, is 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 (Anderson et al. 2008; Bartz and Naiman 2005; Hocking and Reynolds 2011). These inputs can largely impact the nitrogen and carbon found in soils (Mizutani 1988).

Globally, coastal areas represent 20% of oceanic production, while encompassing only 8% of the planet (Talley 2003). Seabirds are present in a wide range of high productivity marine systems around the world and have exhibited potential contributions to marine productivity via guano deposits. Seabirds are essential to nutrient cycling between land-sea systems, because they facilitate the exchange of nitrogen and other chemical subsidies between the two biomes (Rowe

2017; Mizutani and Wada 1988; Anderson et al. 2008; Sanchez-Piñero and Polis 2005; Wait et al. 2004; Stapp et al. 1999). In the San Juan archipelago, guano presence in intertidal regions appears to increase the abundance of certain algal species while simultaneously decreasing intertidal plant biodiversity (Wootton 1991). In coastal areas where native plants create poor bird habitat, nutrient cycling is limited due to decreased seabird guano deposits (Young et al 2010). In Antarctica, penguin rookeries classically exhibit much higher nitrogen isotope ratios than non-penguin systems (Mizutani et al. 1985; Mizutani and Wada 1988). Similarly, in the Gulf of California, areas of seabird influence possess increased nitrogen stable isotope ratios (Stapp et al. 1999).

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 (Lindeboom 1984). 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 d15N values (Mizutani and Wada, 1988). Guano enriched soils have much greater nitrogen isotope ratios than non-guano enriched areas (Anderson et al. 2008) and create spatial variation in the chemical soil composition of island systems (Wait et al. 2004). Areas with high guano content tend to similarly have increased $\delta^{15}N$ values in both soil and surrounding freshwater (Bartz and Naiman 2005).

In years of increased resource availability—termed resource pulse years—where there is an elevated presence of decomposed guano due to increased rainfall, soil exhibits increased nitrogen levels concurrently with an increased plant biodiversity (Anderson et al. 2008). It is suggested that guano deposition in terrestrial ecosystems could increase soil nitrogen content by up to 100 times its original amount (Rowe et. al 2017). Plants growing in areas with higher guano concentrations in their substrate also experience enriched $\delta^{15}N$ values (Erskine 1998; Robinson 2001; Stapp et al. 1999; Wait et al. 2004.

The arid islands in the Gulf of California, Mexico manifest the effects of marine nutrient cycling to terrestrial systems. Bird islands— typically small (<$3km^2$), predator free, with low topography, that occur in high productivity waters are utilized for habitat by a large quantity of seabirds. Guano excreta on bird islands is a significant component of both island appearance and island function, with reported observed guano crusted over rock surfaces as thick as 4 inches in some places (Goss 1888). 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 (Velarde et. al 2005).

These bird islands have also been shown to have significantly reduced plant diversity, likely due to the higher nutrient concentrations (Wilder 2014). However, cacti are seen to occur in both higher diversity and abundance on bird islands (Wilder et. al 2008). What then is the role of the marine nutrients on the structure of these island communities? We focus on the land-sea connections of Isla San Pedro Mártir, the most isolated island in the Gulf of California and one of the most important bird islands in Mexico. This island is distinguished by a forest of the widespread Sonoran Desert columnar cactus *Pachycereus pringlei* (S. Watson) Britton & Rose (*cardón* or *sahueso*, Cactaceae), which covers the island and contributes a shocking amount of plant biomass in such an arid setting (Wilder et. al 2008, Figure 1).

We use stable nitrogen isotope ratios to examine (a) a trophic cascade from the ocean, to sea birds and their guano, into the soil and then the tissue of the cardón is driven by marine upwelling, and (b) that 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.

Methods

Study system

The Gulf of California, also known as the Sea of Cortés, is an ecologically and geologically diverse region (Dolby et al. 2015). 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 and birds. Birds thrive in the Gulf, where they have access to nutrient rich fish, products of high productivity upwelling in the waters around islands (Sanchez-Piñero and Polis 2005). This study focused on Isla San Pedro Mártir, which is one of the most important seabird rookeries in Mexico; 85 species of birds have been recorded there, including eight of breeding seabirds (Tershy and Breese 1997). 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 (Tershy et al. 1997). Isla San Pedro Mártir's substrate is coated with guano and contains a flora of 28 species (Wilder and Felger 2010, Wilder 2014) with plant biomass dominated by the cardón cactus (Figure 1).

Sample collection

Sample collection took place at two scales. Five steps of the land-sea trophic chain were sampled on Isla San Pedro Mártir: fish, seabirds, sea bird 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 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. Both fresh and old guano were taken for sampling. 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).

For comparison, soil and cardón tissue were sampled throughout the range of the species, including other islands of the Gulf of California, along the Baja California peninsula and in Sonora, MX. In total, 10 soil and 10 cardón collections were made at each of 11 populations spread across the Baja California peninsula, seven islands in of Gulf of California (including Mártir), and three locations in mainland Sonora (Figure 2).

Lab analysis

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 ± 0.2 for $\delta^{15}N$ (1σ), based on repeated internal standards.

Results

Stable nitrogen isotope values show a trophic chain from the sea onto the land on Isla San Pedro Mártir (Figure 3; Table 1). Fish samples generally had a mean nitrogen stable isotope content of +17.68 ± 0.88 while seabird feathers—a representation of their consumer—maintained δ1N values with a mean value of +19.71 ± 0.67. Guano deposited by seabirds on the island had a mean value of approximately +14.77 ± 2.12, much lower than soil, δ15N= +32.37 ± 3.55. Cardón specimens ranged in δ1N values of +25.0–37.6.

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 but consistent stable nitrogen isotope values (Figure 4). On average, peninsular localities had values of +8.13 for cacti tissue and values of +11.34 for soil. Likewise, the Gulf island soils ranged from +7.0–35.0 and the cardón cacti had values of +2.1–35.3. One other island, Isla San Diego had significantly higher values of +34.0 and +32.3 for soil and cardón respectively. Mainland Sonora populations showed cacti values that ranged from +7.8–14.9, with soil values in the range of +10.3—21.1.

Discussion

Land sea interface in the Gulf of California

By examining nitrogen isotope ratios across a marine-based trophic cascade, we are able to demonstrate that marine nutrients fuel the establishment of cactus forests on bird islands in the Gulf of California (Figure 3). 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. These birds deposit guano onto island habitats, and as nutrients from guano leech into the soil, they are then able to be utilized by cacti and annual plant species on the island

(Figure 3). As these cacti mature, they tend to topple, potentially because of strong ocean winds and their position in a loose, rocky substrate (Wilder and Felger 2010). Their decomposition propagates the nutrient cycle.

Our research indicates a disparity in the nitrogen content of bird island, non-bird island, mainland, and peninsular populations, with higher mean nitrogen isotope ratios available in bird islands compared to the other localities (Figure 4). Isla San Pedro Mártir, representative of bird island ecosystems, boasts an extensive cardón cactus forest that in the species' range is seen only on a select few other bird islands in the Gulf of California (Medel-Narvaez et al. 2006). The community is dominated by the cardón, which is observed to grow in greater quantities on nitrogen subsidized bird islands. Increased bird activity and presence of guano on Isla San Pedro Mártir set this island apart from other sites in the Midriff Islands system, suggesting that nitrogen subsidies from guano are a likely variable to generate such an increased abundance of cardón cacti on the island.

Lessons from nitrogen

The patterns present on Isla San Pedro Mártir are consistent with previous research; systems subsidized with external nitrogen deposits tend to include fewer species (Wootton 1991; Wilkinson et al. 2005). Species richness and type can be impacted by spatial subsidies (Barrett et al. 2003). It is possible that cacti and other organisms necessitate the development of a physical tolerance to high, "toxic" levels of guano to be successful, and it has been shown that plants on subsidized island systems possess different physiological mechanisms to manage increased resources (Anderson et al. 2008). Therefore, increased guano deposition on Mártir delivers nutrients that may be used uniquely by cardón cacti to increase their population density in a way that is not viewed in other island plant species.

Increased nitrogen deposits have shown to have both beneficial and limiting impacts on plant species (Nobel 1988, Wilder et al. 2008). Cacti utilize nitrogen in a variety of ways, such as components of chlorophyll and nuclei acids, and as a factor in protein synthesis. When there is a greater store of available nitrogen during cacti development, cacti exhibit increased in-soil root growth and shoot growth (Nobel 1988). However, the physiological mechanism by which cacti manage higher nitrogen stores is still relatively unstudied.

The nitrogen isotope values obtained on Isla San Pedro Mártir are consistent with previous research in this region. We obtained $\delta^{15}N$ levels in guano of +14.77 ± 2.12 in comparison to δ15N values of +14.23 ± 2.34 found in the Gulf of California islands by Stapp et al. (1999) and soil levels of δ15N= +32.37 ± 3.55 in comparison to δ15N= +28.26 ± 5.44 (Stapp et al. 1999).

A significant increase in the mean $\delta^{15}N$ values occurs between freshly deposited guano from seabirds and the guano-derived nitrogen in the island's soil. Other studies have also observed this dramatic increase in $\delta^{15}N$ values and argue that the volatilization of ammonia during diagenesis of these nitrogen rich deposits (Mizutani and Wada 1988; Robinson 2001) leads to high $\delta^{15}N$ values, + 28.0 to +35.0 (ATM). Our data show the trophic level increases in nitrogen isotope values as well as the notable increase from guano to soil and cardón samples (Table 1). Nitrogen isotope ratios can show high variance in systems where isotopic fractionation involves significant losses of volatile nitrogen as ammonia (Evans 2001; Robinson 2001; Bilby et al. 1996; Stapp et al. 1999).

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 (Mizutani and Wada 1988, Lindeboom 1984). Guano deposits onto soil substrate allow uric acid to leech into soil and decompose. A study by Mizutani et al. (1985) 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 increase in $\delta^{15}N$ values of nearly 10‰. The soils of Isla San Pedro Mártir, historically covered in seabird guano (Goss 1888) have built an impressive guano-based soil that carries a unique isotopic marker with highly elevated $\delta^{15}N$ values, that allow us to trace the use of these seabird derived nutrients by plants and animals on this island.

Conclusion

The high $\delta^{15}N$ values exhibited in cardón cacti and soil are established by marine nitrogen subsidies deposited via seabird guano and its decay. Isotopic fractionation due to different chemical and biological reactions in the nitrogen cycle—evident in the disparity between guano and soil/cardón $\delta^{15}N$ levels—suggests a method for the uptake of nitrogen from soil by plants, although more research is needed to determine how cardón cacti use excess nitrogen availability so successfully in comparison to other plant species. Nitrogen cycling propagated by seabird guano in the Gulf of California moves nutrients from marine to terrestrial biomes, impacting terrestrial plant production and representing nutrient relationships that transcend the land-sea boundary.

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Table 1. Average δ15N (ATM) values for the four primary sample regions.

Sample	N	δ15N (ATM)	S.D.	Range
San Pedro Mártir				
Fish	11	+17.68	+0.88	+16.6—19.3
Seabird Feather	16	+19.71	+0.67	+18.2—20.5
Guano	15	+14.65	+2.26	+11.4—20.3
Soil	20	+32.37	+3.55	+25.9—37.9
Cardón Tissue	20	+30.33	+3.86	+25—37.6
Non-bird islands				
Sample	N	δ15N (ATM)	S.D.	Range
Soil	65	+16.00	+8.49	+7—36.6
Cardón Tissue	65	+13.72	+9.17	+2.1—35.3
Mainland Sonora				
Sample	N	δ15N (ATM)	S.D.	Range
Soil	30	+13.79	+2.01	+10.3—21.1
Cardón Tissue	30	+11.19	+1.88	+7.8—14.9
Baja California Peninsula				
Sample	N	δ15N (ATM)	S.D.	Range
Soil	99	+11.64	+2.93	+5.5—18.9
Cardón Tissue	110	+8.13	+3.12	+2.5—17.3

Figure 1. View from summit of Isla San Pedro Mártir, showing the cardón cactus forest. Sloped island sides are white-washed with seabird guano deposits. © Benjamin T. Wilder.

Figure 2. Sampling localities across the range of the cardón.

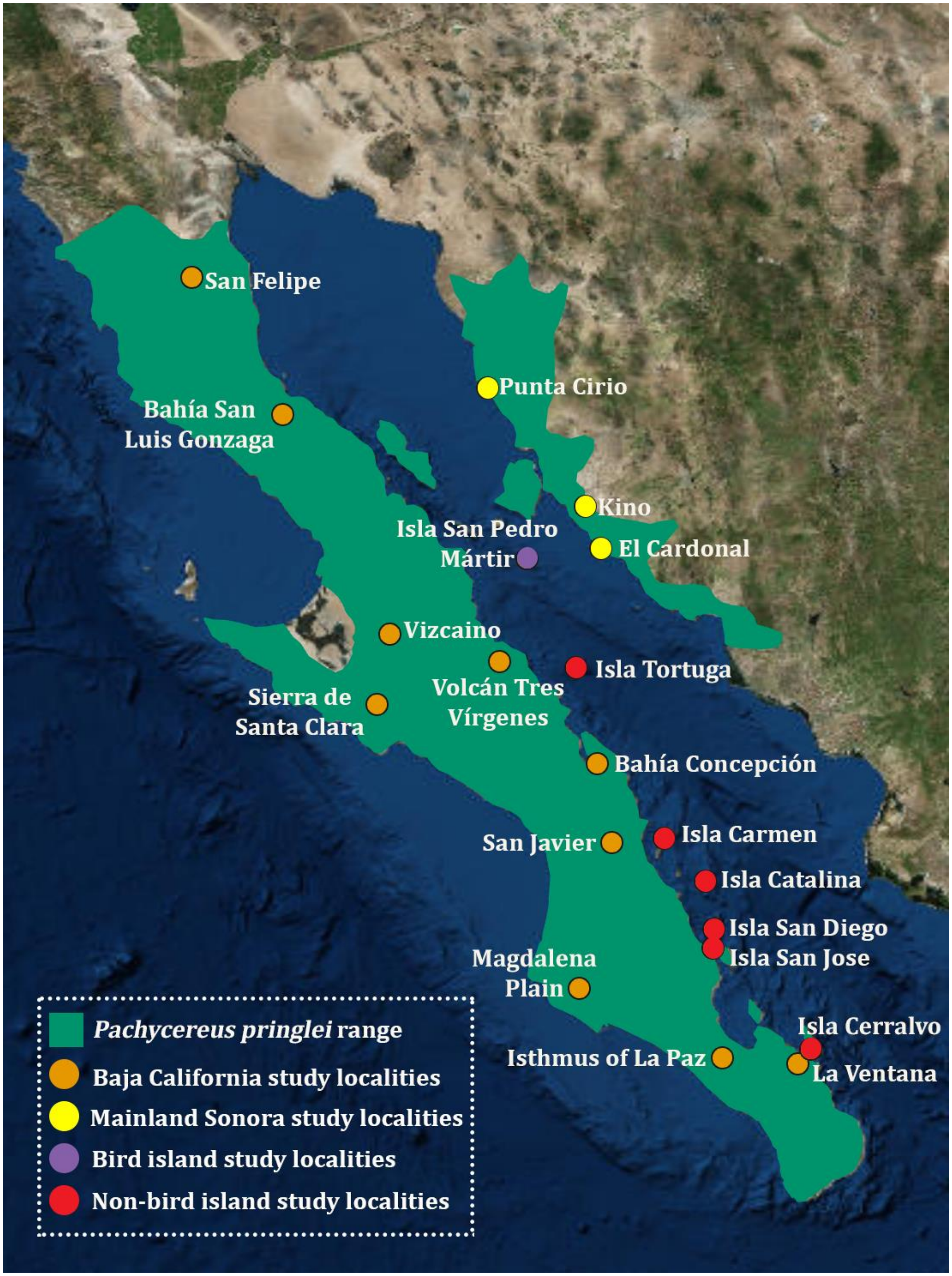
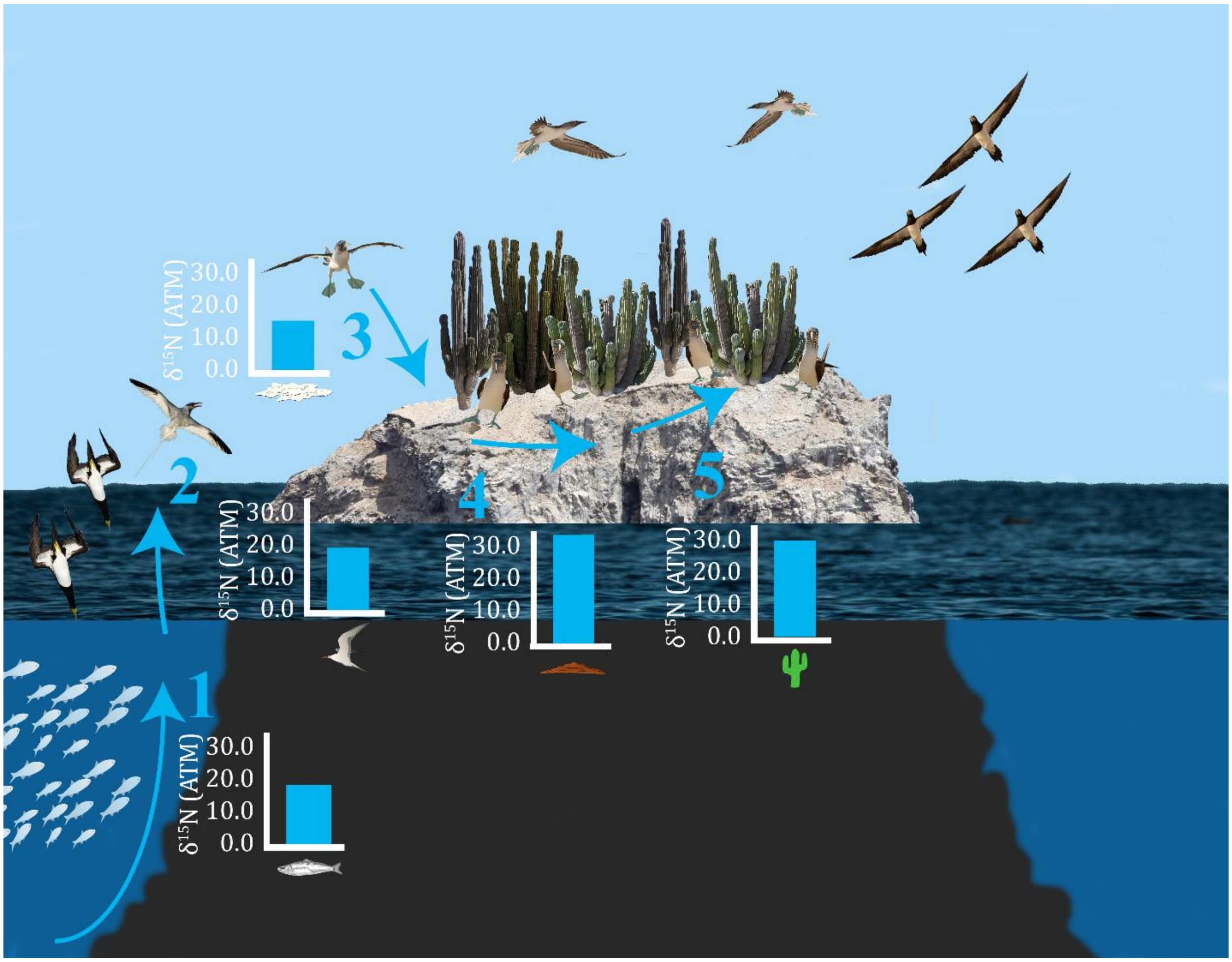


Figure 3. Trophic cascade across the land-sea interface of Isla San Pedro Mártir. Diagram shows the flow of nitrogen stable isotope values driven by upwelling in the Gulf of California. (1) Pelagic fish that are eaten by (2) seabirds that (3) deposit guano on bird islands, which (4) enter the island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



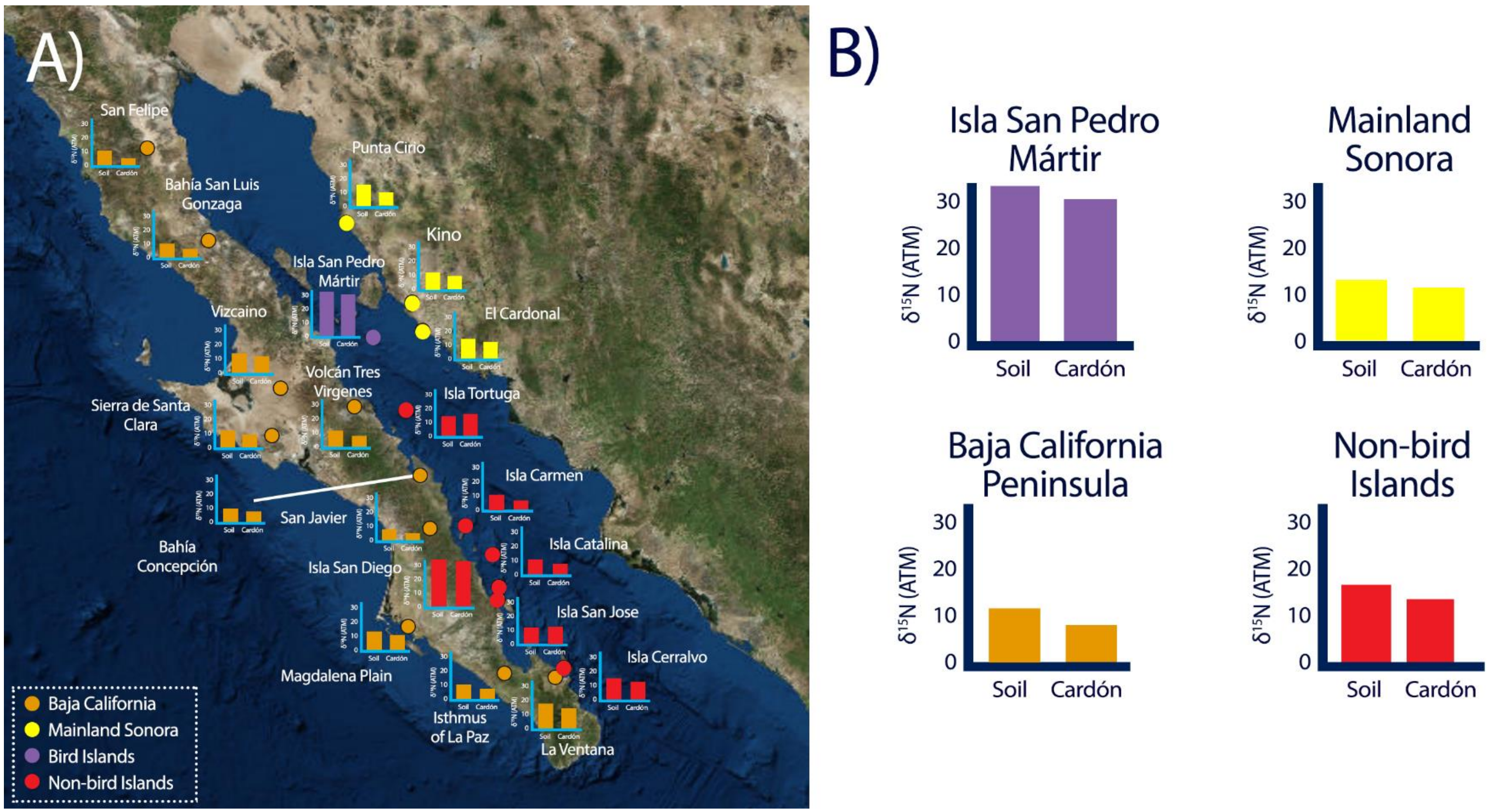


Figure 4. Average δ15N values for soil and cardón across sampling localities. (A) Geographic distribution of soil and cardón δ15N values at each sampling site. (B) Comparison of soil and cardón δ15N values for the four primary sample regions.

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