

Trophic connectivity between the terrestrial and marine ecosystems of Malpelo Island, Colombia, evaluated through stable isotope analysis

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Abstract

Living beings inhabit heterogeneous environments, in which communities that are classified as discrete can be continuous and connected in innumerable ways. The components of food webs can cross borders between ecosystems, and as result, the structure and trophic dynamics of ecosystems can change. The goal of this study was to evaluate trophic connectivity between the terrestrial and marine ecosystems of Malpelo Island, Colombia (4°00'05.63" N; 81°36'36.41" W), based on the isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) assessment of 403 samples (107 terrestrial and 296 marine). Samples were collected in 2017–2021. $\delta^{13}\text{C}_{\text{Terrestrial}}$ values ranged from -30.3‰ to -15.0‰ and $\delta^{13}\text{C}_{\text{Marine}}$ ranged from -24.0‰ to -9.8‰ ; $\delta^{15}\text{N}_{\text{Terrestrial}}$ ranged from 3.7‰ to 21.3‰ and $\delta^{15}\text{N}_{\text{Marine}}$ ranged from 4.5 to 16.9‰ . The mixing model (simmr package) indicated that detritus_{Terrestrial} ($\delta^{13}\text{C} = -18.9 \pm 0.30\text{‰ SE}$) contributed more to the food web than C_3 plants ($-29.4 \pm 0.22\text{‰}$), and reflected high $\delta^{13}\text{C}_{\text{Marine}}$ content. There was high isotopic overlap (65–82%) and a high trophic connection between environments of Malpelo Island due to high similarity between isospaces. These results evidence the role of the donor habitat (marine) on the receptor habitat (terrestrial) and the role of the Nazca booby *Sula granti* regarding nutrient transfers between the two environments. The presence and preservation of this seabird is essential to maintain the balance of this insular ecosystem. The analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ tracers was useful to establish the trophic relationships between small oceanic island environments with presence of large seabird communities.

1. Introduction

Communities categorized as discrete can be open and connected in innumerable ways due to external factors (Holt 1993; Menge 1995; Schindler et al. 1996; Polis et al. 1996; Rooney et al. 2003) that allow the basic components of food webs (i.e., nutrients, detritus, and organisms) to cross the spatial limits of ecosystems (Polis et al. 1997a). This is related to the shape (complexity; Kent and Wong 1982) and size of the ecosystem (Post et al. 2000; Vander Zanden and Vadeboncoeur 2002; McCann et al. 2005; Dolson et al. 2009). The strength of the interactions of mobile generalist predators can be limited (McCann et al. 2005) by the degree of accessibility to different ecosystems (Dolson et al. 2009). These spatial processes impact the trophic structure and dynamics of ecosystems. This is evidenced by allochthonous inputs from different sources (e.g., transport of detritus and nutrients by mobile consumers) that can in turn influence energy, carbon, and nutrient reservoirs (i.e., nitrogen and phosphorus) (Polis and Hurd 1996a; Polis et al. 1997b; Schindler and Scheuerell 2002).

A key element in the trophic dynamics of islands and coastal areas is subsidy from a donor habitat through marine allochthonous inputs (Polis and Hurd 1996a; Polis et al. 1997b). Although islands can have low terrestrial primary productivity (Caut et al. 2012), they can support high abundance and biomass (i.e., secondary production) of consumers, such as spiders, scorpions, lizards, and rodents that are subsidized by marine contributions (Sánchez-Piñero and Polis 2000; Moore et al. 2004). On islands, these allochthonous inputs are mainly incorporated from two sources: 1) seabird colonies and 2) marine detritus transported across beaches (Polis and Hurd 1995, 1996b). This also contributes to combating nutrient limitation (i.e., nitrogen and phosphorus) of primary producers.

Malpelo Island is a small oceanic island (1.2 km²; Graham, 1975) located in the Colombian Pacific. Its geographical isolation and position at the convergence of several marine currents (Fig. 2) mean that this island is an ideal place for the aggregation of species (endemic and migratory). This has led to this island becoming part of the largest marine protected area in the Colombian Pacific, the Malpelo Fauna and Flora Sanctuary (FFS) (Fig. 2) (Ministry of Environment and Sustainable Development, 2017). It is a World Heritage Site (UNESCO) and is included in other important lists for the conservation of species (Management Plan, 2015). These characteristics and its importance for ecological communities mean that Malpelo FFS is an ideal site for the study of trophic interactions between ecosystems and of the input of marine nutrients to the terrestrial environment, due to its low terrestrial primary productivity. Considering its topography, complicated access, and the presence of the largest nesting colony of the Nazca booby *Sula granti* (> 80,000 individuals; López-Victoria and Rozo 2007; García 2013), terrestrial ecosystem structure and trophic dynamics could be directly and/or indirectly affected by the input of marine nutrients in the form of *S. granti* guano, chicks, food remains, and carcasses, denoting high connectivity between ecosystems (Wolda 1975; von Prah 1990; López-Victoria et al. 2009).

Variations in the donor-controlled habitat (i.e., marine ecosystem; Polis et al. 1997a) could cause modifications in the community ecology of Malpelo FFS (Wolda 1975), with drastic consequences on species composition and trophic dynamics at landscape scales (Polis and Hurd 1995; Nakano et al. 1999). Changes in the feeding habits of *S. granti* could result in changes to the role this seabird plays in the trophic connectivity between the two ecosystems (Wolda 1975; von Prah 1990; López-Victoria et al. 2009). Several studies have indicated that of the total energy contributed by *S. granti*, 99% corresponds to guano, 0.64% to eggs and chicks, and 0.06% to carcasses (López-Victoria et al. 2009). These are important dietary components of the dotted galliwasp *Diploglossus millepunctatus*, the Malpelo anole *Anolis agassizi*, the terrestrial crab *Johngarthia malpilensis*, and other invertebrates (López-Victoria 2006, López-Victoria and Werding 2008, López-Victoria et al. 2011).

Trophic studies based on the observation of terrestrial macro-species from Malpelo FFS (e.g., *A. agassizi*, *D. millepunctatus*, *J. malpilensis*, *Phyllodactylus transversalis*; López-Victoria 2006; López-Victoria and Werding 2008; López-Victoria et al. 2011; López-Victoria et al. 2013), including trophic relationships with *S. granti*, have shown the importance of this avian species in the trophic dynamics (López-Victoria et al. 2009) and stability of the terrestrial ecosystem, due to energy input from the sea (Wolda 1975; von Prah 1990; López-Victoria et al. 2009). However, previous trophic studies based on direct observations, as well as stomach contents analysis carried out on several terrestrial species of Malpelo FFS, should be complemented with other methods to strengthen the hypothesis raised by other studies (i.e., Wolda 1975; von Prah 1990; López-Victoria et al. 2009). Stable isotope analysis (SIA) is a complementary approach that counters some of the limitations of previous studies, e.g., use of stomach contents analysis and direct observations, which only provide a temporal snapshot of food ingested. SIA allows the identification of sources of carbon and nitrogen that constitute food assimilated over the short- and long-term (e.g., Kim et al. 2012; Estupiñán-Montaño et al. 2019). The isotopic signal depends on the trophic level and origin of the diet, as well as on ingestion rates, accumulation, turnover rates of assimilated tissue, and growth, among other factors (Fry and Arnold 1982; Tieszen et al. 1983).

Three main objectives were addressed in this study to determine the degree of coupling between the terrestrial and marine environments of Malpelo Island: 1) the assessment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the biological components of the terrestrial and marine environments of Malpelo FFS; 2) the identification of the primary sources that support the terrestrial food web; and 3) the evaluation of the trophic connectivity between the two ecosystems in Malpelo FFS. The general aim was to provide new evidence that *S. granti* is the main mediator in the transfer of matter and energy between the two ecosystems and generate new ideas to clarify some hypotheses, such as: i) the terrestrial food web has a low dependence on terrestrial C_3 plants due to their low abundance; therefore, terrestrial debris should provide the greatest contribution to the different components of the terrestrial food web; ii) the $\delta^{13}\text{C}$ of terrestrial debris is similar and/or varies slightly in relation to $\delta^{13}\text{C}$ of basal sources and consumers at low marine trophic levels, as well as *S. granti* eggs; iii) terrestrial C_3 plants should reflect high values of $\delta^{15}\text{N}$, since N is found in high concentrations in *S. granti* guano; and iv) terrestrial and marine ecosystems should evidence high isotopic overlap as a result of the high connectivity between them.

2. Materials And Methods

2.1. Study area

Malpelo Island (Fig. 1A) is the summit of a submarine mountain range called the Malpelo Ridge, which extends in a NE-SW direction; it is approximately 241.4 km long by 80.5 km wide (Fig. 1B, red polygon). The island has a maximum height of 300 m above sea level and emerges from approximately 4,000 m depth (Fig. 1C).

Malpelo Island constitutes the largest marine reserve in the Colombian Pacific and is commonly referred to as the Malpelo Fauna and Flora Sanctuary (FFS). It is located ~ 390 km from the coast of Buenaventura (4°00'05.63" N; 81°36'36.41" W; Fig. 1B; Management Plan 2015). Malpelo FFS comprises 11 islets (Fig. 1A) and a ~ 2.7 million hectare protected area (Fig. B; yellow polygon; Ministry of Environment and Sustainable Development, 2017). It is influenced by several marine currents due to its geographic location (Fig. 1D). Moreover, there is high productivity as a result of annual upwelling that supplies nutrients from deep waters. This upwelling supports a diverse and abundant community of consumers whose growth is reliant on this productivity (Rodríguez-Rubio and Stuardo 2002).

Despite its physical characteristics (volcanic rock), several plant and animal species inhabit the island (Management Plan 2015). There are 28 plant species on the island, including algae, lichens (i.e., *Caloplaca* sp., *Candelabria* sp., *Lecidea* sp., and *Pyxine* sp.), a moss (*Octoblepharum albidum*), a C_4 grass (*Paspalum* sp.), a legume, a fern (*Pityrogramma calomelanos*), and unidentified shrubs (von Prah 1990; González-Román et al. 2014).

The terrestrial fauna of the island includes ~ 40 species of invertebrates (Wolda 1972; Management Plan 2015), such as ants (*Odontomachus bauri*), beetles (*Platynini* sp.), an endemic decapod crustacean (*J. malpilensis*), three species of endemic reptiles (*A. agassizi*, *D. millepunctatus*, and *Phyllodactylus transversalis*), and a high diversity of migratory and resident birds (> 60 species; Management Plan 2015). The largest *S. granti* nesting colony in the world has been established on Malpelo Island; this is the most abundant bird in the area (López-Victoria and Rozo 2007; García 2013).

2.2. Collection of samples

Samples of 16 terrestrial and 38 marine species/functional groups (Table 1) were collected in 2017–2021 in Malpelo FFS, Colombia (Fig. 1A). All terrestrial samples were collected in October 2018. Samples of terrestrial vertebrates consisted in 1–2 cm of tissue collected from the posterior portion of the tail of *A. agassizi* and *D. millepunctatus*, and body feathers of *S. granti*. For invertebrates such as the land crab *J. malpilensis*, one of the hind limbs was collected, whereas invertebrates (i.e., millipedes, isopods, spiders, worms, crickets, and ants; Table 1) were collected whole.

Table 1

Components of the terrestrial and marine ecosystems of the Malpelo Fauna and Fauna Sanctuary represented by taxa with scientific and common names, number of samples (*n*), and average isotopic values \pm standard deviation (SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Code	Taxa		<i>n</i>	C:N	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)		
	Scientific name	Common name			Mean \pm SD	Min	Max	Mean	SD	Min	Max
Terrestrial Ecosystem											
1	<i>Anolis agassizi</i>	Lizards	8	3.5 \pm 0.10	-18.2	-	-	0.67	13.5	15.5	14.4
2	Araneae	Spiders	8	5.3 \pm 1.31	-21.0	-	-	1.27	16.8	28.4	20.6
3	<i>Diploglossus millepunctatus</i>	Dotted galliwasp	9	3.6 \pm 0.64	-18.3	-	-	1.03	13.6	15.3	14.5
4	-	Detritus	5	5.4 \pm 0.22	-20.1	-	-	0.66	9.5	13.0	10.8
5	Gryllidae	Crickets	5	4.5 \pm 0.42	-20.6	-	-	0.53	9.7	13.4	11.9
6	-	Guano	1	1.2	-	-	-	-	-	-	14.2
7	Hymenoptera		4	4.5 \pm 0.36	-20.3	-	-	0.39	11.0	14.3	13.3
8	<i>Sula granti</i> §	Nazca booby (eggs)†	8	4.3 \pm 0.41	-19.5	-	-	0.44	13.1	14.1	13.6
9	Isopoda	Mealybugs	9	7.0 \pm 0.29	-17.5	-	-	0.82	15.1	17.9	16.8
10	<i>Johngarthia malpilensis</i>	Terrestrial crabs	12	3.2 \pm 0.07	-17.1	-	-	0.45	14.9	17.0	15.8
11	Diplopoda	Millepede	15	6.3 \pm 0.91	-22.9	-	-	1.17	6.4	15.7	11.7
12	Lumbriculidae	Worm	6	4.8 \pm 0.34	-18.7	-	-	0.6	17.2	20.4	19.1
13	Mycrocorifia	Rock jumpers	7	4.1 \pm 0.30	-21.4	-	-	0.6	10.3	19.4	14.1
14	<i>Odontomachus</i> sp.	Ants	12	4.1 \pm 0.41	-18.4	-	-	0.82	15.5	19.2	16.7
15	-	Mosses	8	15.9 \pm 1.71	-30.3	-	-	0.62	3.8	10.1	7.4
16	<i>Sula granti</i> §	Nazca booby (feathers)	9	3.3 \pm 0.05	-16.7	-	-	0.2	13.5	15.2	14.3
Marine Ecosystem											
1	-	Green algae	6	14.6 \pm 2.71	-21.0	-	-	1.58	4.6	5.6	5.
2	<i>Padina</i> sp.	Brown algae	4	13.3 \pm 1.42	-18.1	-	-	0.93	6.5	7.8	7.
3	Arcidae	-	1	3.6	-	-	-	-	-	-	9.
4	Balanidae‡	-	2	4.2 \pm 0.35	-18.1	-	-	1.70	9.5	10.0	9.
5	Balistidae	Triggerfishes	3	3.3 \pm 0.00	-18.1	-	-	0.19	12.1	13.1	12.
6	-	Unidentified shrimp	8	4.8 \pm 0.45	-18.7	-	-	0.69	8.2	11.6	9.
7	Carangidae‡	Jacks	12	3.4 \pm 0.20	-18.3	-	-	0.19	11.9	13.7	12.

§ Species present in both ecosystems.

† $\delta^{13}\text{C}$ values corrected with Elliot et al. (2014).

‡ $\delta^{13}\text{C}$ values corrected with Kiljunen et al. (2006).

Code	Taxa		n	C:N	δ ¹³ C (‰)			δ ¹⁵ N (‰)			
	Scientific name	Common name			Mean ± SD	Min	Max	Mean	SD	Min	Max
8	Carcharhinidae	Requiem sharks	12	3.0 ± 0.07	-16.7	-16.1	-16.3	0.21	14.8	15.9	15.3
9	Chaetodontidae [‡]	Butterflyfishes	2	3.5 ± 0.21	-17.5	-17.3	-17.4	0.12	12.7	14.3	13.5
10	-	Unidentified crustaceans	3	6.2 ± 1.55	-19.0	-11.7	-16.4	4.03	7.1	9.1	8.1
11	Dendrophylliidae [‡]	Anthozoos	3	3.6 ± 0.70	-23.0	-21.8	-22.5	0.60	4.7	6.6	5.7
12	Epialtidae [‡]	Crabs	1	7.5	-	-	-13.2	-	-	-	7.5
13	-	Sponges [‡]	5	4.0 ± 0.20	-16.3	-14.9	-15.7	0.58	4.9	9.4	7.1
14	Exocoetidae [‡]	Flyingfishes	4	3.6 ± 0.10	-17.8	-16.8	-17.5	0.47	9.6	10.9	10.3
15	-	Unidentified gastropods [‡]	5	4.1 ± 0.36	-19.1	-15.4	-16.9	1.58	7.1	13.5	10.3
16	Gecarcinidae [‡]	Crabs	2	6.2 ± 0.85	-15.7	-14.9	-15.3	0.60	8.2	8.2	8.2
17	Grapsidae [‡]	Cangrejos anfibios	21	5.3 ± 1.58	-19.6	-10.0	-14.6	3.45	6.9	16.9	10.3
18	Inachidae [‡]	Spider crabs	3	6.2 ± 0.55	-15.0	-12.6	-14.2	1.41	8.7	9.4	8.6
19	Lophiidae [‡]	Rapes	5	4.2 ± 0.33	-18.9	-18.1	-18.6	0.36	8.6	13.3	11.5
20	Lutjanidae [‡]	Snappers	36	3.5 ± 0.28	-19.3	-16.4	-17.4	0.62	9.8	15.0	13.5
21	-	Macroplankton [‡]	23	6.6 ± 1.28	-23.2	-17.8	-21.4	1.02	4.6	10.8	7.1
22	Malacanthidae	Tilefishes	8	3.3 ± 0.04	-18.8	-18.0	-18.5	0.27	11.7	14.0	12.9
23	-	Microplankton [‡]	9	7.9 ± 0.72	-20.7	-15.5	-18.6	1.79	4.8	8.3	6.1
24	Myliobatidae	Eagle rays	1	3.5	-	-	-15.2	-	-	-	15.2
25	Ommastrephidae [‡]	Squids	5	4.1 ± 0.13	-18.1	-17.4	-17.7	0.31	10.1	10.8	10.4
26	Ostreoida [‡]	Oysters	9	4.0 ± 0.53	-20.1	-18.3	-19.4	0.46	4.8	7.8	6.3
27	Palinuridae [‡]	Lobsters	4	4.0 ± 0.06	-16.2	-15.8	-15.9	0.16	12.2	12.6	12.4
28	Parthenopidae [‡]	Crabs	2	8.2 ± 0.35	-17.0	-11.5	-14.2	3.90	5.9	6.5	6.2
29	Penaeidae [‡]	Shrimp	12	4.5 ± 0.48	-20.1	-17.7	-19.7	0.65	7.5	9.5	8.5
30	Pomacanthidae	Angelfish	3	3.3 ± 0.06	-18.1	-18.0	-18.0	0.03	12.4	13.7	12.6
31	Scombridae [‡]	Tunas	12	3.6 ± 0.43	-17.9	-15.9	-17.1	0.56	12.0	14.6	13.3
32	Scorpaenidae	Scorpion fish	2	3.3 ± 0.07	-17.8	-17.8	-17.8	0.04	14.8	15.0	14.9

§ Species present in both ecosystems.

† δ¹³C values corrected with Elliot et al. (2014).

‡ δ¹³C values corrected with Kiljunen et al. (2006).

Code	Taxa		n	C:N		δ ¹³ C (‰)			δ ¹⁵ N (‰)		
	Scientific name	Common name		Mean ± SD	Min	Max	Mean	SD	Min	Max	Mean
33	Serranidae [‡]	Groupers	34	3.7 ± 0.59	-21.5	-	-18.1	1.20	8.4	15.0	12
34	Sphyrnidae	Hammerhead sharks	14	3.1 ± 0.07	-16.6	-	-16.0	0.50	15.0	16.4	15
35	Squillaidae [‡]	Mantis shrimp	1	4.7	-	-	-16.4	-	-	-	11
36	Stromatidae	Butterfishes	1	3.3	-	-	-17.3	-	-	-	12
37	Sulidae [†]	Nazca booby	17	3.8 ± 0.60	-20.0	-	-17.5	1.35	13.1	15.2	14
38	Synodontidae [‡]	Lizardfish	1	4.3	-	-	-18.3	-	-	-	8.
39	Xanthidae [‡]	Crabs	1	7.7	-	-	-11.8	-	-	-	6.

§ Species present in both ecosystems.

† δ¹³C values corrected with Elliot et al. (2014).

‡ δ¹³C values corrected with Kiljunen et al. (2006).

Marine samples were obtained at different depths (between 10–30 m) by scuba diving at different sites around Malpelo Island. Muscle tissue of teleost fishes and rays was obtained with a harpoon and/or Hawaiian hook, and from fish that had been illegally caught and seized by the authorities. Scalloped hammerhead (*Sphyrna lewini*) and silky shark (*Carcharhinus falciformis*) muscle tissue was obtained from Estupiñán-Montaño et al. (2017).

Plankton samples were collected around Malpelo Island with a “bongo” type net of 68, 90, and 294 µm mesh size; surface tows were conducted from the M/N Seawolf inflatable boats for 10 min at each sampling site around the island. Samples of the other marine species/groups (e.g., algae, crustaceans, gastropods, and oysters; Table 1) were collected by hand.

All collected samples (terrestrial and marine) were placed in pre-labeled zip-lock plastic bags, except for the plankton samples, which were stored in 250 ml plastic bottles. Samples were kept frozen on board the Pacific Diving Company’s M/N Seawolf for subsequent transfer to the laboratory. Sampling procedures were endorsed by Parques Nacionales de Colombia, through Memorandum 20177730007973 of 30 May 2017, issued by the Planning and Management Group.

2.3. Sample preparation and analysis

Samples were washed with distilled water, freeze-dried in an oven at 60 °C for 24 h, and ground to a fine powder with an agate mortar. Approximately 0.23 to 0.97 mg of powder were obtained for each terrestrial sample and packed in 3.2 × 4-mm tin capsules.

The C:N ratio was estimated and compared to reference values; a C:N value ≤ 3.5 indicates no effect of lipid contents (Post et al. 2007), whereas values > 3.5 suggest high lipid content. δ¹³C values of terrestrial and marine samples (Table 1) with C:N values > 3.5 were mathematically normalized according to Kiljunen et al. (2006):

$$\delta^{13}\text{C}_{\text{adjusted}} = \delta^{13}\text{C}_{\text{measured}} + D \times \left(I + \frac{3.90}{14^{287/L}} \right) \quad (\text{Eq. 1})$$

Where δ¹³C_{adjusted} is the δ¹³C after normalization and δ¹³C_{measured} is the δ¹³C obtained from the sample without lipid removal. D= 7.018, I= 0.048, and L is the proportional lipid content of the sample, estimated as L = - 20.54 + (7.24 × C:N) (Post et al. 2007).

Arthropods (i.e., ants, isopods, and millipedes; Table 1) were analyzed without extracting lipids because these organisms have an exoskeleton characterized by high chitin contents (e.g., Liu et al. 2019), which are reflected in high C:N values (> 3.5). Therefore, δ¹³C values of arthropods with C:N values < 7.0 were not normalized mathematically (Schimmelmann and DeNiro 1986; Webb et al. 1997; Pringle and Fox-Dobbs 2008). Otherwise, δ¹³C values were normalized according to Post et al. (2007) (Eq. 1).

S. granti feathers were cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol solution, followed by two successive methanol rinses (Jaeger et al. 2009). The δ¹³C values of *S. granti* eggs were mathematically normalized because lipid extraction can alter δ¹⁵N by washing out nitrogenous compounds. In this case, the formula proposed by Elliot et al. (2014) was used:

$$\delta^{13}\text{C}_{\text{lipid-extracted}} = \delta^{13}\text{C}_{\text{non-extracted}} + 1.47 - 2.72 \times \text{Log}_{10}(\text{C:N}) \quad (\text{Eq. 2})$$

Where $\delta^{13}\text{C}_{\text{lipid-extracted}}$ is the $\delta^{13}\text{C}$ after normalization and $\delta^{13}\text{C}_{\text{non-extracted}}$ is the $\delta^{13}\text{C}$ obtained from the sample without lipid removal.

Extraction of lipids and urea from elasmobranch muscle samples (i.e., sharks and rays; Table 1) was performed following the procedure described by Kim and Koch (2012). Stable isotope analyses were carried out in the Stable Isotope Laboratory of the Instituto Andaluz de Ciencias de la Tierra in Granada (CSIC-UGR), Spain. The isotopic composition (i.e., carbon and nitrogen) of terrestrial specimens was obtained using an online Carlo Erba NA 1500 NC elemental analyzer coupled online via ConFlo III interface to a Delta Plus XP mass spectrometer (EA-IRMS; ThermoQuest). Stable isotopes were reported as δ values per mil (‰) based on the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \text{ (Eq. 3)}$$

where R is the isotopic ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) of the sample or the standard (V-PDB and AIR for carbon and nitrogen, respectively). Commercial CO_2 and N_2 were used as the internal standard for isotopic analyses. Internal standards of -30.6‰ and -11.7‰ (V-PDB) were used for $\delta^{13}\text{C}$ analysis and internal standards of -1.0‰ and $+16.0\text{‰}$ (AIR) were used for $\delta^{15}\text{N}$. Standards were systematically interspersed among analytical batches; daily drift of the mass spectrometer was corrected and a precision factor $< \pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was calculated. Reference gases and in-house standards (with different C:N ratios and isotopic composition) were calibrated against International Reference Materials for carbon (USGS-24 and IAEA-C6) and nitrogen (IAEA-N1, IAEA-N2, and IAEA-N3).

2.4. Relative contribution of potential basal sources

The relative contribution of potential terrestrial basal sources to the diet of terrestrial consumer groups was estimated with the package *simmr* (version 0.3) in R (R Core Team 2018). This model uses a Bayesian isotopic framework based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to estimate the proportional contribution of potential prey (in this case, basal sources) to a consumer's diet (Parnell et al. 2013), including variability in model inputs such as trophic discrimination factor (TDF) values of consumers.

The following four steps were implemented (Supplementary material S1): 1) we selected two potential basal sources: terrestrial C_3 plants and terrestrial detritus (sources that consist of decomposing organic matter [DOM] and seabird feces; López-Victoria et al. 2009); 2) all terrestrial organisms were considered potential prey, due to feeding preferences (López-Victoria 2006; López-Victoria and Werding 2008; López-Victoria et al. 2011), and also consumers (i.e., mixing), except C_3 plants and detritus (basal sources); 3) due to the lack of specific TDFs for each terrestrial organism, we used the estimated mean TDF for terrestrial ecosystems ($\Delta^{13}\text{C} = 0.5 \pm 0.19\text{‰}$ SD and $\Delta^{15}\text{N} = 2.3 \pm 0.24\text{‰}$ SD; McCutchan et al. 2003), to minimize sources of uncertainty (i.e., environmental and physiological factors, trophic position, metabolic rates, growth rates; Phillips et al. 2014), to which mixing models are highly sensitive (Bond and Diamnon 2011, Phillips et al. 2014); and 4) the mixing model was adjusted to verify that the TDFs, potential prey, and consumers were consistent with the assumptions of the model (Smith et al. 2013). The mixing model adjustment was run with 10^3 iterations with a 95% probability for the mixing polygon (Smith et al. 2013). The model was considered adequate if isotopic values were within 1% of the mixing model polygons (Reum et al. 2020). Finally, if the model was correctly adjusted, we ran the mixing model with the isotopic values of terrestrial Malpelo FFS consumer groups (Table 1). The mixing model was run with 10^6 iterations, 10^4 burn-in period, 100 thinning period, and 4 Markov Chain Monte Carlo (MCMC).

The basal $\delta^{13}\text{C}_{\text{detritus}}$ of the terrestrial ecosystem was compared to the $\delta^{13}\text{C}$ values of the following five marine groups: macroalgae, marine crabs, zooplankton, *S. granti* eggs, and flying fish. The values of the marine groups were corrected with the mean TDF for marine environments ($\Delta^{13}\text{C} = 0.4 \pm 0.17\text{‰}$ SD; McCutchan et al. 2003) and compared statistically with a non-parametric paired test (Wilcoxon rank sum test).

2.5. ^{15}N enrichment

^{15}N enrichment of terrestrial components was estimated using $\delta^{15}\text{N}$ values of detritus, eggs, and feathers of *Sula granti* as reference, as this species provides marine nutrients to the terrestrial ecosystem (García and López-Victoria 2007; López-Victoria et al. 2009). Relative ^{15}N enrichment was calculated using the algorithm proposed by Estrada et al. (2006):

$$\text{Enrichment in } Y = \left(\frac{\delta^z Y_x - \delta^z Y_{S. granti \text{ eggs and/or feathers}}}{\delta^z Y_{S. granti \text{ eggs and/or feathers}}} \right) \text{ (Eq. 4)}$$

where: Y is the element of interest (^{15}N), z is the atomic mass of the element, and x are the terrestrial components (i.e., plants, *A. agassizi*, *J. malpilensis*, *D. millepunctatus*, ants, millipedes, and Isopoda; Table 1) relative to the reference component (i.e., *Sula granti* eggs and feathers).

2.6. Niche amplitude and isotopic overlap

To quantify the isotopic niche and isotopic overlap between ecosystems (terrestrial [with and without C_3 plants] vs. marine), we used the Stable Isotope Bayesian Ellipses (SIBER, Jackson et al. 2011) method available in the R package (R Development Core Team 2008). This analysis estimates ellipses that represent the "core isotopic niche" (Standard Ellipse Corrected Area, SEA_C) using a Bayesian approach and calculating covariance matrices that define the shapes and areas of the ellipses (Jackson et al. 2011).

The ellipses were corrected using a posteriori randomly replicated sequences (SEA_C = standard ellipse area correction, Jackson et al. 2011) and they represent the isotopic niche width of consumers. In addition, this method allows the estimation of the isotopic niche overlap of the consumer (in this study, isospace), based on the overlap between ellipses (Newsome 2007).

SIBER results were supported by the nicheROVER package in R (Lysy et al. 2014), which uses a probabilistic method to calculate niche regions and pairwise niche overlap using multidimensional niche indicator data. The niche regions are defined as the joint probability density function of the multidimensional niche indicators at a user-defined probability α (95%), while the package provides directional estimations of niche overlap (x vs y and y vs x), according to the species-specific distributions in the multivariate niche space (Lysy et al. 2014).

3. Results

A total of 403 samples were collected in Malpelo FFS, 26.6% of which ($n = 107$) corresponded to the terrestrial ecosystem and 73.4% ($n = 296$) to the marine ecosystem (Table 1).

3.1. Carbon and nitrogen stable isotopes

$\delta^{13}C$ values of the terrestrial ecosystem ranged from -30.3‰ to -15.0‰ and $\delta^{15}N$ ranged from 3.7‰ to 21.3‰ (Table 1). Terrestrial C_3 plants (mosses) had the lowest average $\delta^{13}C$ value (-30.3‰) and the dotted galliwasp *Diploglossus millepunctatus* had the highest average value (-15.0‰), with a total range in $\delta^{13}C$ values of 15.3‰ (Fig. 2). The lowest $\delta^{15}N$ value corresponded to the terrestrial C_3 plants (3.7‰), whereas the highest value was obtained for arthropods from the family Araneae (21.3‰), with a $\delta^{15}N$ range of 17.6‰ (Fig. 2).

The carbon isotopic space of the marine ecosystem ranged from -23.2‰ to -10.0‰ for $\delta^{13}C$ and from 4.5‰ to 16.9‰ for $\delta^{15}N$ (Table 1). In this ecosystem, corals Dendrophylliidae had the lowest average $\delta^{13}C$ value (-22.5‰) and the scalloped hammerhead shark *Sphyrna lewini* (Sphyrnidae; -14.8‰) had the highest average value, with a range of 7.7‰ (Fig. 3). Brown algae (Dictyotaceae) showed the lowest $\delta^{15}N$ values (4.5‰), while the scalloped hammerhead shark had the most positive value (16.4‰), with a range of 11.8‰ (Fig. 3).

3.2. Contribution of terrestrial basal sources to the trophic web

The fitted model (i.e., mixing polygons, subsequent predictive validations; Supplementary material S2A), suggested that these results explained the uncertainty of the TDFs and of the isotopic values of the 13 consumer groups (Supplementary material S2A). Therefore, the implementation of the mixing model was adequate to estimate the relative contribution of the different basal sources, confirmed by the Gelman-Rubin (Rhat) convergence diagnostic statistics, which was 1.00 for all parameters and suggested that there was convergence.

The organic matter present in the soil ($\delta^{13}C = -20.1\text{‰}$ to -17.3‰) (Figs. 4 and 5), reflected the isotopic signal of organic matter transferred from marine primary production. These results suggest a high input of $\delta^{13}C$ from detritus towards the lizard *Anolis agassizi*, the crab *Johngarthia malpilensis*, and the dotted galliwasp *D. millepunctatus*. Terrestrial C_3 plants contributed mainly to the Orders Hymenoptera, Diplopoda, and Microcoryphia, which presented low $\delta^{13}C$ values, resulting in a greater contribution probability from terrestrial C_3 plants (Fig. 4, Table 2).

Table 2
Compación de la probabilidad de contribución relativa de dos fuentes basales terrestres del Santuario de Fauna y Flora Malpelo, con respecto todos los grupos de consumidores terrestres.

Consumers	Contribution probability (%)	
	C_3 Plants	Detritus
Hymenoptera	78.0	22.0
Isopoda	29.5	70.5
<i>Odontomachus</i> sp.	25.3	74.7
Gryllidae	54.2	45.8
Araneae	67.0	33.0
Microcoryphia	93.6	6.4
Lumbriculidae	41.7	58.3
Diplopoda	78.5	21.5
<i>Anolis agassizi</i>	10.4	89.6
<i>Diploglossus millepunctatus</i>	9.8	90.2
<i>Johngarthia malpilensis</i>	9.2	90.8

The basal $\delta^{13}\text{C}_{\text{detritus}}$ of the terrestrial ecosystem was contrasted with the $\delta^{13}\text{C}_{\text{Corrected*TDF}}$ values of five marine groups: $\delta^{13}\text{C}_{\text{macroalgae}}$ (Wilcoxon rank sum test, $W = 14$, $P = 0.21$), $\delta^{13}\text{C}_{\text{phytoplankton}}$ (Wilcoxon rank sum test, $W = 24$, $P = 90$), $\delta^{13}\text{C}_{\text{marine crabs}}$ (Wilcoxon rank sum test, $W = 84.5$, $P = 0.37$), and $\delta^{13}\text{C}_{\text{S. granti eggs}}$ (Wilcoxon Rank sum test, $W = 33$, $P = 0.07$), with statistically significant differences between the basal source of detritus and $\delta^{13}\text{C}_{\text{zooplankton}}$ (Wilcoxon rank sum test, $W = 110$, $P = 0.002$) (Fig. 5).

3.3. ^{15}N enrichment

The range of $\delta^{15}\text{N}$ values indicated that terrestrial C_3 plants, as well as crickets, millipedes, and Hymenoptera, presented values compatible with terrestrial primary production (Craine et al. 2009; Amundson et al. 2003). However, species such as *A. agassizi*, *D. millepunctatus*, *J. malpilensis*, Isopoda, Araneae, Lumbricullidae, and *Odontomachus* sp. were enriched in ^{15}N , presenting values incompatible with a diet based on the primary productivity of the island (i.e., C_3 plants) and with some groups associated with organic matter decomposition processes (e.g., consumption of detritus) (Fig. 6). High $\delta^{15}\text{N}$ levels of terrestrial animals could be related to the high trophic level of *S. granti* (trophic level = 4.2 [3.9–4.4, CI 95%]; Estupiñán-Montaño et al. unpublished), due to prey consumed in the marine environment.

3.4. Isotopic niche and isotopic overlap

The wide isotopic range of carbon, and especially of nitrogen, in the terrestrial ecosystem reflected an isospace ($\text{TA}_{\text{Terrestrial}}$) of 134.7‰^2 and an isotopic niche ($\text{SEA}_{\text{C}_{\text{terrestrial}}}$) of 30.4‰^2 (Fig. 6A). After excluding terrestrial C_3 plants, the isospace and the isotopic niche were 65.1‰^2 and 17.3‰^2 , respectively (Fig. 6B). The isospace and isotopic niche of the marine ecosystem ($\text{TA}_{\text{marine}} = 117.2\text{‰}^2$ and $\text{SEA}_{\text{C}_{\text{marine}}} = 21.0\text{‰}^2$) were very similar to those of the terrestrial ecosystem, excluding C_3 plants (Fig. 7A, B).

Taking into account the low contribution of terrestrial C_3 plants to the terrestrial trophic web, two isotopic overlap scenarios were considered: one including C_3 plants and one excluding them. The terrestrial (C_3 plants; red box, Fig. 6A) and marine isospaces reflected an isotopic overlap of 0.85 (SIAR overlap; Fig. 7A), suggesting an overlap probability of 65% (nicheROVER) between the two ecosystems. In contrast, the marine isospace indicated a higher overlap probability with the terrestrial isospace (76%; Fig. 7A). In the second scenario, the estimated isotopic overlap between the terrestrial and marine isospaces was 0.71 (SIAR overlap; Fig. 7B), corresponding to 82% (terrestrial vs. marine) and 70% (marine vs. terrestrial) overlap between the two isospaces (Fig. 7B).

4. Discussion

Some isolated systems, such as oceanic islands, can support relatively complex food webs due to the input of nutrients via seabirds (Polis and Hurd 1996; Polis et al. 1997a; Ellis 2005). This allows a connection between low-productivity habitats (“receptor habitats”) and environments with higher primary productivity (“donor habitats”); these processes drive the trophic and ecological dynamics of connected ecosystems (Polis and Hurd 1995; 1996a, Polis and Strang 1996; Polis et al. 1996, 1997a; Anderson and Polis 1999; Caut et al. 2012).

The terrestrial ecosystem of Malpelo FFS is a small insular system with a limited capacity for atmospheric nitrogen fixation; it is therefore highly dependent on external nitrogen. *Sula granti* plays an important role in supplying nitrogen from the marine environment (Wolda 1975; López-Victoria et al. 2009), resulting in an increase in the isotopic nitrogen concentration of the terrestrial environment. This seabird provides high quantities of nutrients in the form of guano, feathers, eggs, carcasses, chick remains, juveniles, and adults, in addition to food waste of marine origin, such as fish and squid (López-Victoria and Werding 2008; López-Victoria et al. 2009, 2013). This highlights its importance in the transport of nutrients from the marine to the terrestrial ecosystem (Burger et al. 1978; López-Victoria et al. 2009). The same seabird-dependent process of transfer of energy and matter has been observed in the islands of the Gulf of California, Mexico (Anderson and Polis 1999; Sánchez-Piñero and Polis 2000), in Baccalieu Island, Canada (Duda et al. 2020), the Pacific and Indian Oceans, as well as in the Mediterranean Sea (Caut et al. 2012).

Terrestrial macro-species (i.e., *A. agassizi*, *D. millepunctatus*, and *J. malpilensis*) had similar $\delta^{13}\text{C}$ values to those of the marine ecosystem; they were supported by the presence of seabirds as nutrient assimilators from the marine to the terrestrial ecosystem (Caut et al. 2012). This could be due to: 1) the similarity in isospace amplitude between the terrestrial (excluding terrestrial C_3 plants) and marine ecosystems; 2) the high isotopic overlap between the two ecosystems; and 3) the similarity between the $\delta^{13}\text{C}$ of terrestrial detritus, *S. granti* eggs, marine macroalgae, and marine crustaceans. The high contribution of detritus to terrestrial consumers (Fig. 4B) suggests that the carbon in terrestrial organisms comes from the marine environment (Table 1). Their $\delta^{13}\text{C}$ signals are similar to those of marine primary producers in Malpelo FFS (i.e., macroalgae: -21.0‰ to -16.0‰ ; phytoplankton: -20.7‰ to -15.5‰ [this study]), as a result of transport and deposition of nutrients by *S. granti* and its “byproducts” (López-Victoria and Werding 2008; López-Victoria et al. 2009, 2013), and not from terrestrial primary producers (i.e., terrestrial C_3 plants). Conversely, grasses (i.e., *Paspalum* sp.) are C_4 plants, and similarly to C_3 plants, they have a high C:N ratio (C_3 Malpelo Island = 13.5–18.7); thus, they would not be the main source of protein of the terrestrial ecosystem. However, it should be noted that no samples of C_4 or CAM plants were collected, mainly due to the reduced plant cover in the study area.

On the contrary, the orders Diplopoda (millipedes) and Microcoryphia reflected a higher contribution of terrestrial C_3 plants (Fig. 4B), which is consistent with the food preferences of these taxa (Bueno-Villegas 2012; Bach de Roca et al. 2015). These results reinforce the hypothesis that suggests a high reliance and trophic interaction between the marine and terrestrial ecosystems of Malpelo FFS (Wolda 1975; López-Victoria et al. 2009).

The decomposition of naturally ^{15}N -enriched guano and seabird tissue (Anderson and Polis 1999) could be further ^{15}N enriched due to the volatilization of ^{14}N (Lindeboom 1984; Mulder et al. 2011) and to the fast mineralization of uric acid to ammonium (NH_4^+) from guano (Wainright et al. 1998). This leads to greater isotopic fractionation, provoking ^{15}N -enrichment of the residual NH_4^+ reservoir (Mizutani and Wada 1988; Wainright et al. 1998). Plants fertilized with

guano have ^{15}N -enriched values (Anderson and Polis 1999), similar to the soil (Croll et al. 2005; Maron et al. 2006). Conversely, organisms that consume guano and those who include other seabird byproducts in their diet (i.e., feathers, eggs, carcasses; Barrett et al. 2005; López-Victoria et al. 2009) have higher $\delta^{15}\text{N}$ values; consequently, they have a higher trophic position than their prey (e.g., seabirds) or present higher tissue ^{15}N -enrichment.

In this regard, terrestrial C_3 plants of Malpelo FFS should reflect ^{15}N -enrichment, as has been documented for islands in the Gulf of California (C_3 plants = $24.5 \pm 1.1\text{‰}$, C_4 = $24.3 \pm 1.4\text{‰}$; Barrett et al. 2005). However, terrestrial C_3 plants of Malpelo FFS evidenced a different pattern (low $\delta^{15}\text{N}$ values; Fig. 2). Values found for these plants are consistent with atmospheric nitrogen fixation, and were impoverished in ^{15}N relative to the eggs and feathers of *S. granti* (Fig. 7). Similar results were reported for Possession Island in the Indian Ocean (plants = $5.2 \pm 1.05\text{‰}$ SD, seabirds = $9.34 \pm 0.45\text{‰}$ SD, enrichment = -0.44 ; Caut et al. 2012). Therefore, it seems that terrestrial C_3 plants of Malpelo FFS do not obtain N indirectly from guano nor from the solids of seabirds (Caut et al. 2012). Primary consumers (i.e., Isopoda and ants *Odontomachus* sp.) and terrestrial secondary consumers (i.e., *A. agassizi*, *D. millepunctatus*, and *J. malpilensis*), incorporate ^{15}N directly from the consumption of *S. granti* and its byproducts (López-Victoria and Werding 2008; López-Victoria et al. 2009, 2013). This indicates ^{15}N -enrichment relative to the eggs and feathers of *S. granti* (Fig. 6).

The *S. granti* colony positively impacts terrestrial communities of Malpelo FFS due to the high contributions of guano and other “byproducts” that terrestrial species consume directly (Polis and Hurd 1996; Sánchez-Piñero and Polis 2000). This is reflected in the high abundances of *J. malpilensis* (estimated population: 833,000 individuals; López-Victoria and Werding 2008), *D. millepunctatus* (12,000–18,000 individuals; López-Victoria et al. 2011), and *A. agassizi* (60,000–102,000 individuals; López-Victoria et al. 2011) present in Malpelo FFS. In contrast, the large *S. granti* colony could negatively affect the population of terrestrial C_3 plants (28 species; González-Román et al. 2014) by reducing their cover on the island.

This phenomenon has been observed on Malpelo island (S. Bessudo Lion, *personal communication*). It could be related to: 1) the high concentrations of guano during the dry season that could exceed the concentration limits of essential nutrients and eventually toxify the soil and limit the development of plants; this could also prevent the establishment of native plants in places where there is a high density of seabirds (Boutin et al. 2011; Sánchez-Piñero and Polis 2000) and 2) the reduction of nutrients due to guano washing off during the rainy season, which limits soil formation and affects the adequate development of plants (Caita and Guerrero 2000).

There is a high input of nutrients (mainly from marine origin) from the terrestrial environment (e.g., organic matter, seabird guano, etc.) into the sea at Malpelo FFS, due to runoff from frequent and abundant rains between May and December (annual precipitation $\sim 2,500$ mm; von Prael 1990; López-Victoria and Estela 2007). Terrestrial nutrients could affect primary producers locally, altering the typical values of marine primary productivity surrounding Malpelo FFS and modifying seasonal marine trophic dynamics (Ishida 1996; Wait et al. 2005); as a result, this would be reflected in their isotopic values. Despite the contributions of terrestrial nutrients to the sea and the effects that these contributions may have on the dynamics of this ecosystem, more studies are necessary to validate these hypotheses and identify other trophic connectivity routes between the terrestrial and marine ecosystems of Malpelo FFS.

Finally, an important control by the “donor” habitat (marine ecosystem) over the “receptor” habitat (terrestrial habitat) was evidenced by the transport and contribution of matter and energy between ecosystems (Polis et al. 1997a). The transport of nutrients from sea to land in Malpelo FFS is governed mainly by *S. granti*. However, there are other inputs in the sea-land interface, which are generated in the intertidal zone when *J. malpilensis* and *D. millepunctatus* consume marine algae and marine crabs (*Grapsus grapsus*), respectively (López-Victoria et al. 2009, 2013). Nevertheless, this source of input of marine nutrients into the terrestrial ecosystem has not been studied in detail. More studies are necessary to estimate the contribution of the intertidal zone and terrestrial ecosystem in Malpelo FFS. In turn, this would improve ecological knowledge regarding the dynamics of this small oceanic island.

Given the impact exerted by the donor habitat on the receptor habitat, it is possible that an eventual disturbance of marine populations may alter food webs, due to the transitional interphase between the marine and insular environment (Sullivan and Manning 2019). The present study documented trophic interactions between marine and terrestrial ecosystems, providing support to how diverse species can cross the limits of distinct environments (e.g., terrestrial and aquatic). Furthermore, this study evidenced how stable isotope analysis constitutes a useful tool in the identification of trophic interactions between terrestrial and marine ecosystems.

Declarations

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Ethics approval All procedures performed in this study were in accordance with Parques Nacionales Naturales de Colombia in Memorandum 20177730007973 of May 30, 2017 by the Planning and Management Group.

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Figures

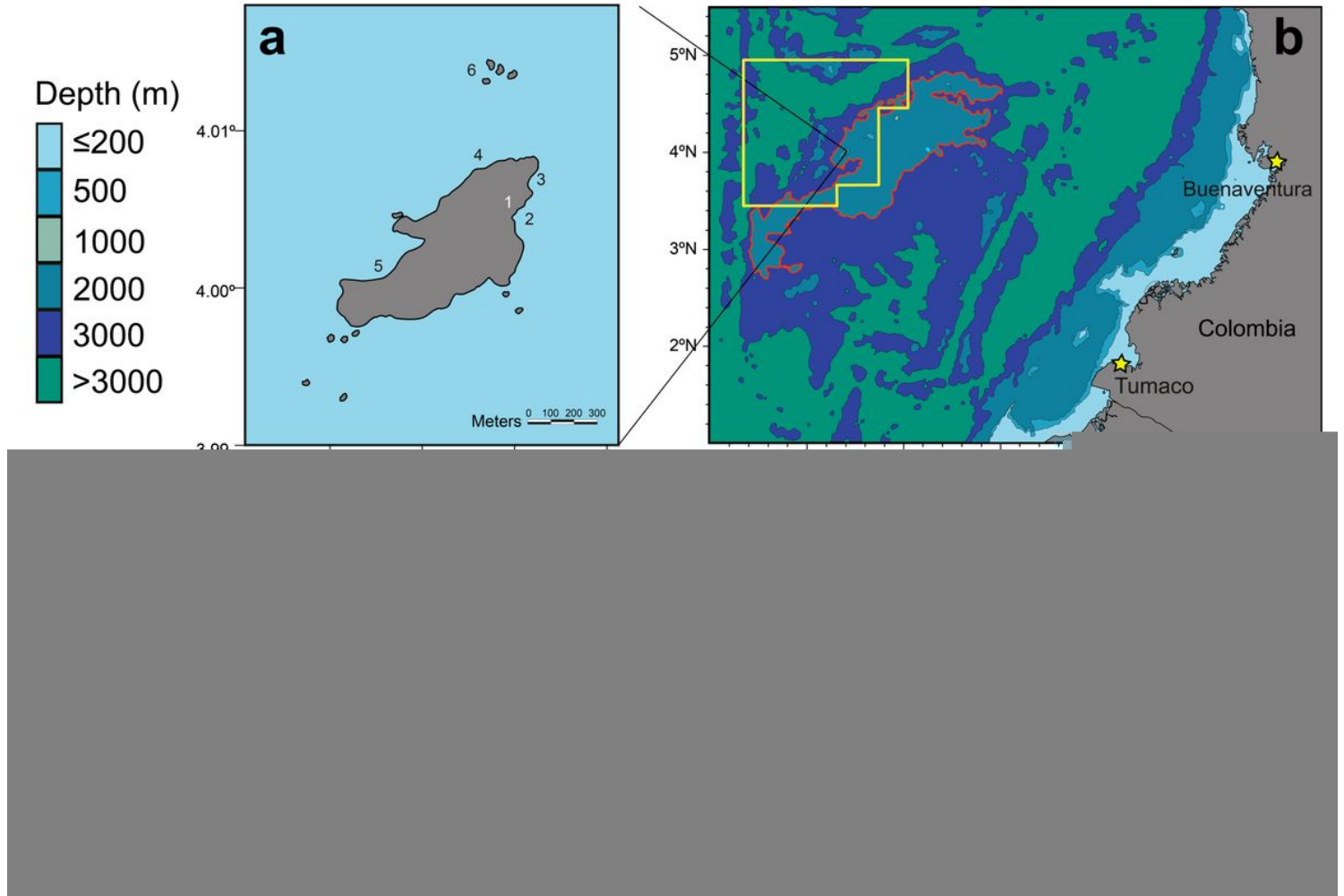


Figure 1
 Study area in the Eastern Pacific Ocean. **A)** Geographic location of the Malpelo Fauna and Flora Sanctuary. **B)** Polygon showing the marine protected area (yellow) of the Malpelo Fauna and Flora Sanctuary and polygon of the Malpelo Ridge (Red). **C)** Lateral view of the bathymetric profile of Malpelo Island (Management Plan, 2015). **D)** Marine currents that influence the dynamics of Malpelo Island. *Currents near the surface* (Yellow arrows, dotted lines), *geostrophic currents in the upper layer* (Blue arrows, solid lines) **CC:** California Current, **NEC:** North Equatorial Current, **NECC:** North Equatorial Countercurrent, **SEC:** South Equatorial Current, **CRCC:** Costa Rica Coastal Current, **HC:** Humboldt Current, **COLC:** Colombian Current (*and subsuperficial currents*) **ESC:** Equatorial subcurrent, **N/SSCC:** North/South subsuperficial countercurrent, **EMC:** Eastern Mexican Current, **PCS:** Peru-Chile subcurrent. **Taken and modified from:** Kessler (2006).

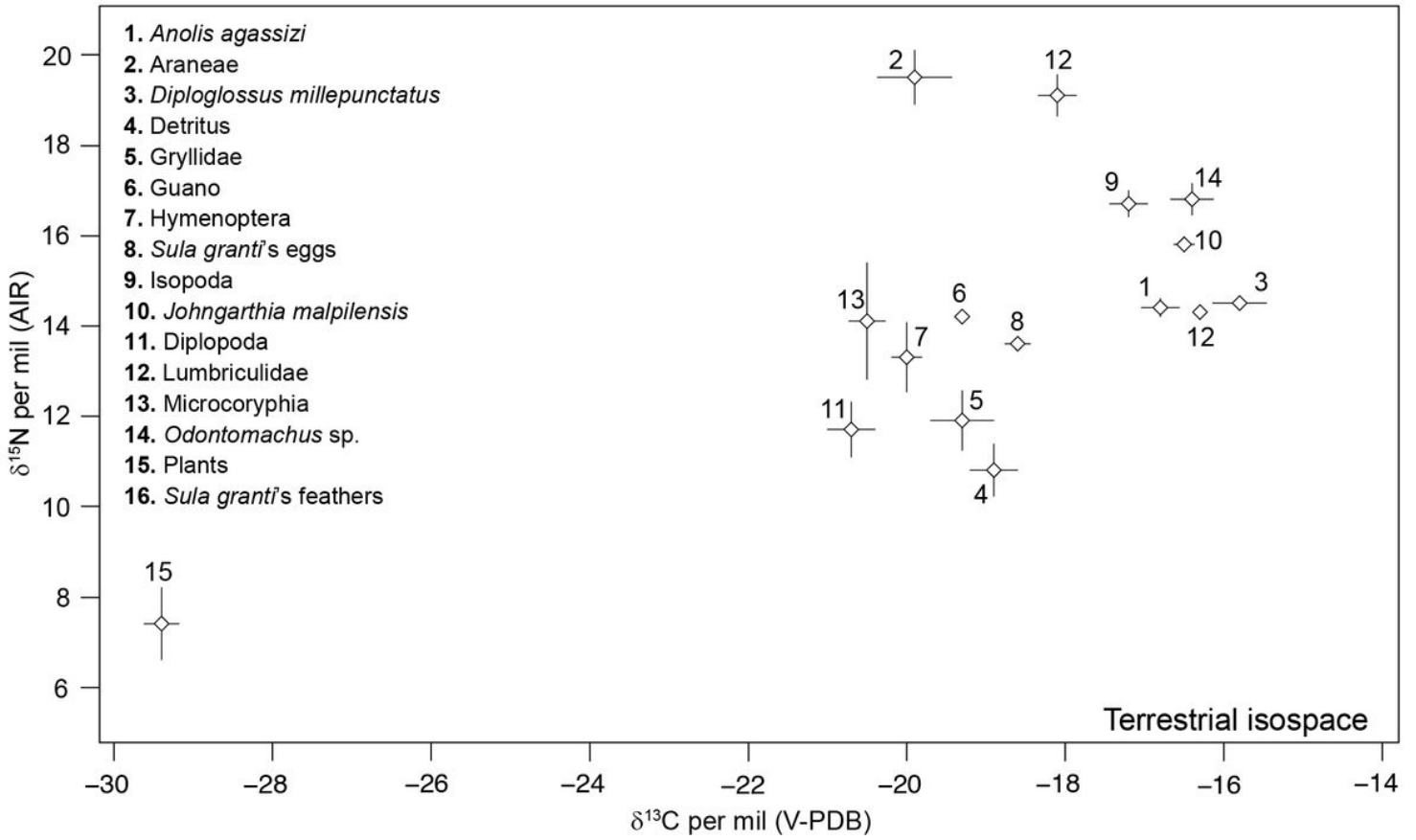


Figure 2

Terrestrial isospace of the Malpelo Fauna and Flora Sanctuary, Colombia, represented by the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm standard deviation) of 16 components of its trophic web. **Note:** The numbers correspond to each species identified.

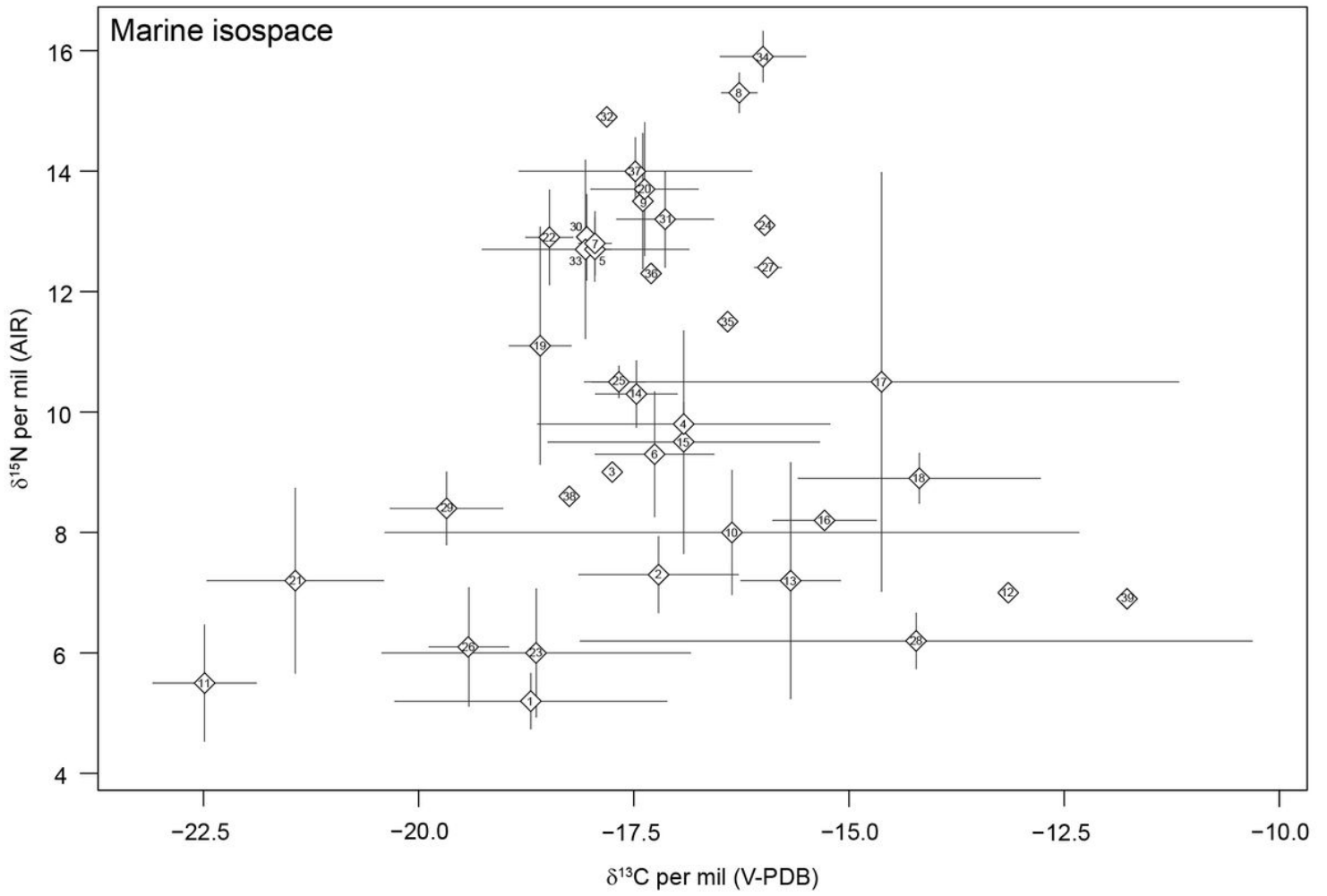


Figure 3
 Marine isospace of the Malpelo Fauna and Flora Sanctuary, Colombia, represented as average values (\pm SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for 39 different consumer groups (species/families/orders) of the marine trophic web.

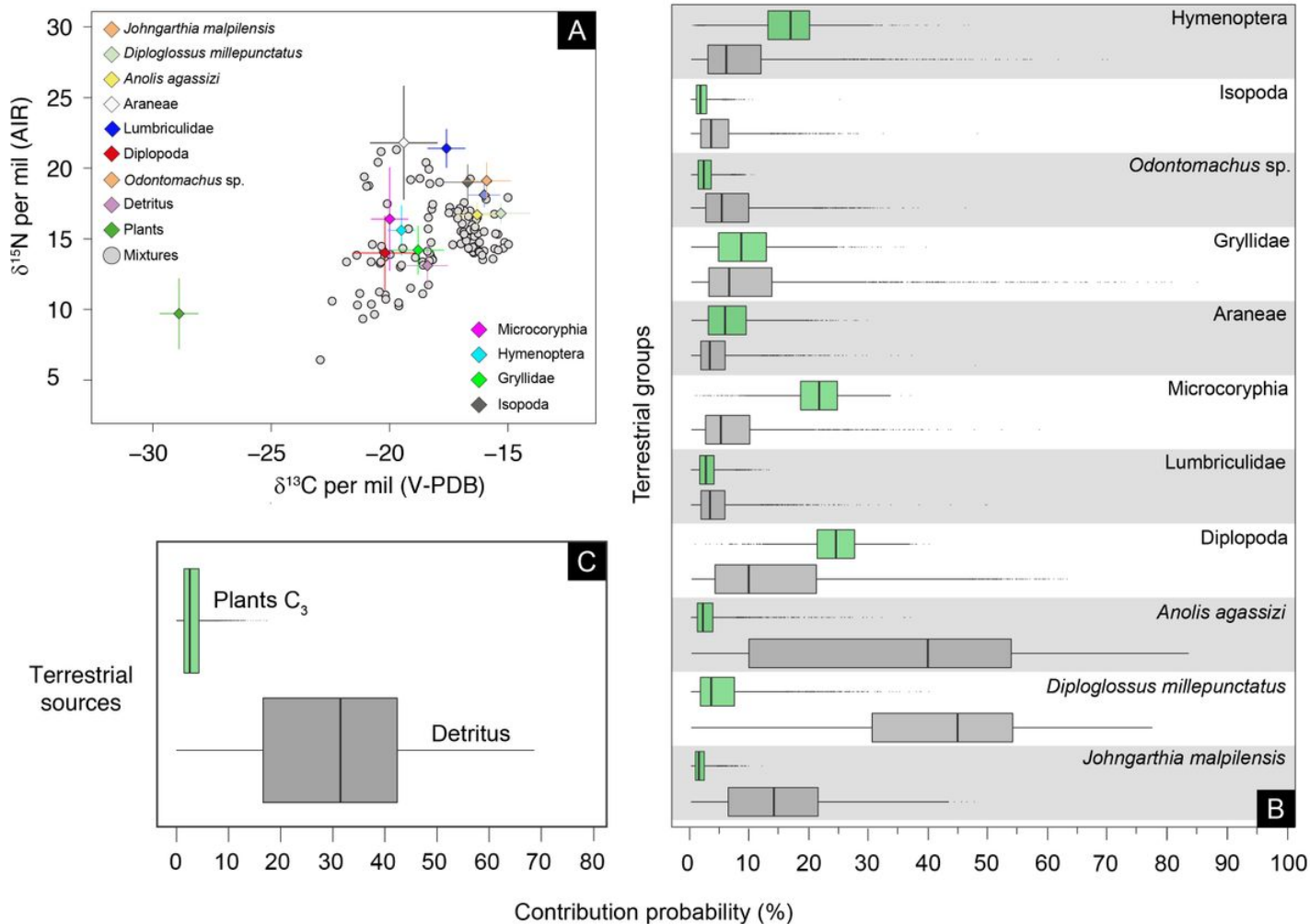


Figure 4

A. Information of the sources used in the stable isotope mixing models. **B.** Estimate of the relative contribution of the terrestrial basal sources to the diet of secondary consumers of the terrestrial ecosystem. **C.** Estimation of the contribution probability (in %) of the terrestrial basal sources to the terrestrial ecosystem in Malpelo Fauna and Flora Sanctuary, Colombia.

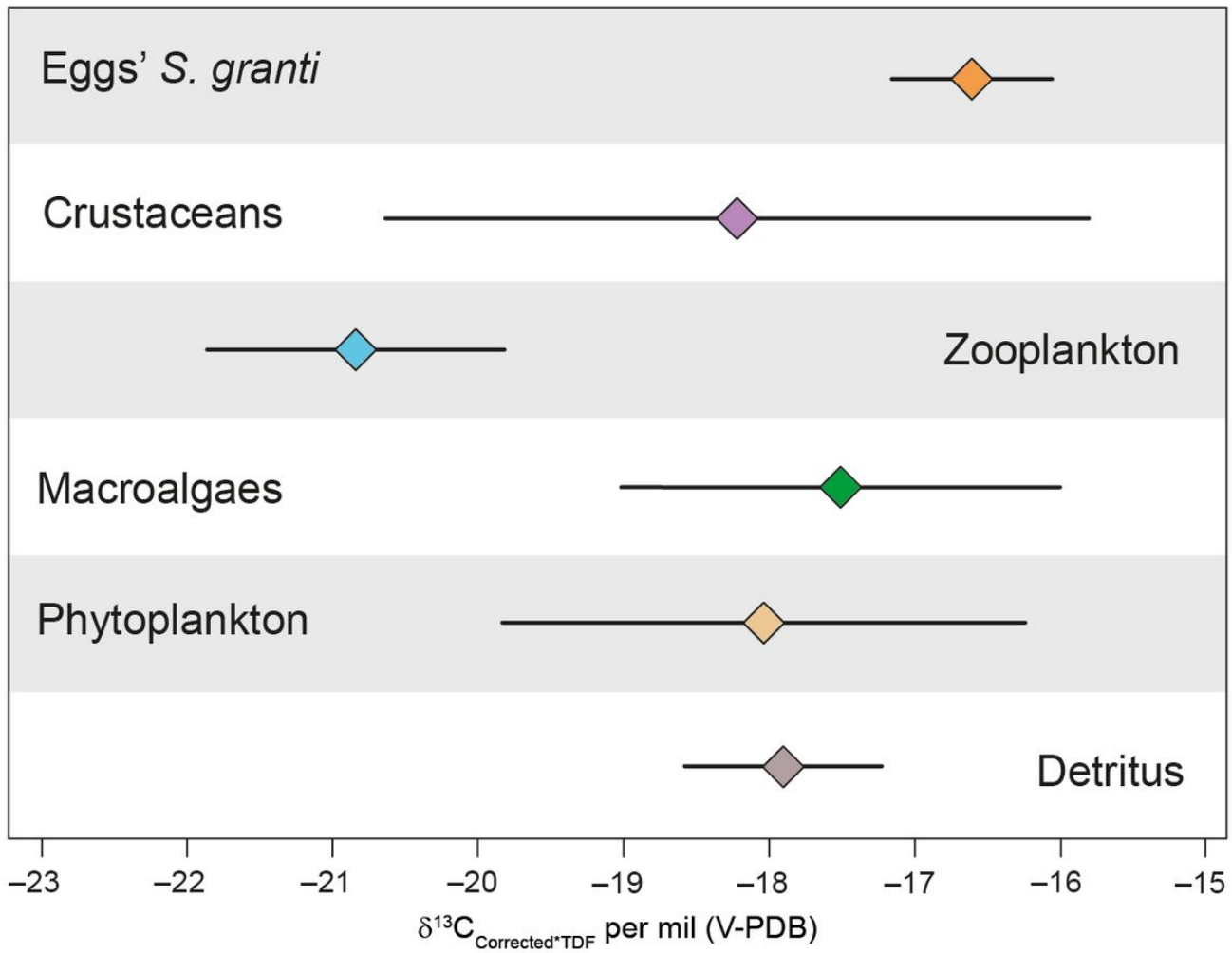


Figure 5
 Statistical comparison of the $\delta^{13}C$ values (mean \pm SD) of the terrestrial detritus with respect to the basal sources and organisms of low marine trophic levels of the Malpelo Fauna and Flora Sanctuary, Colombia.

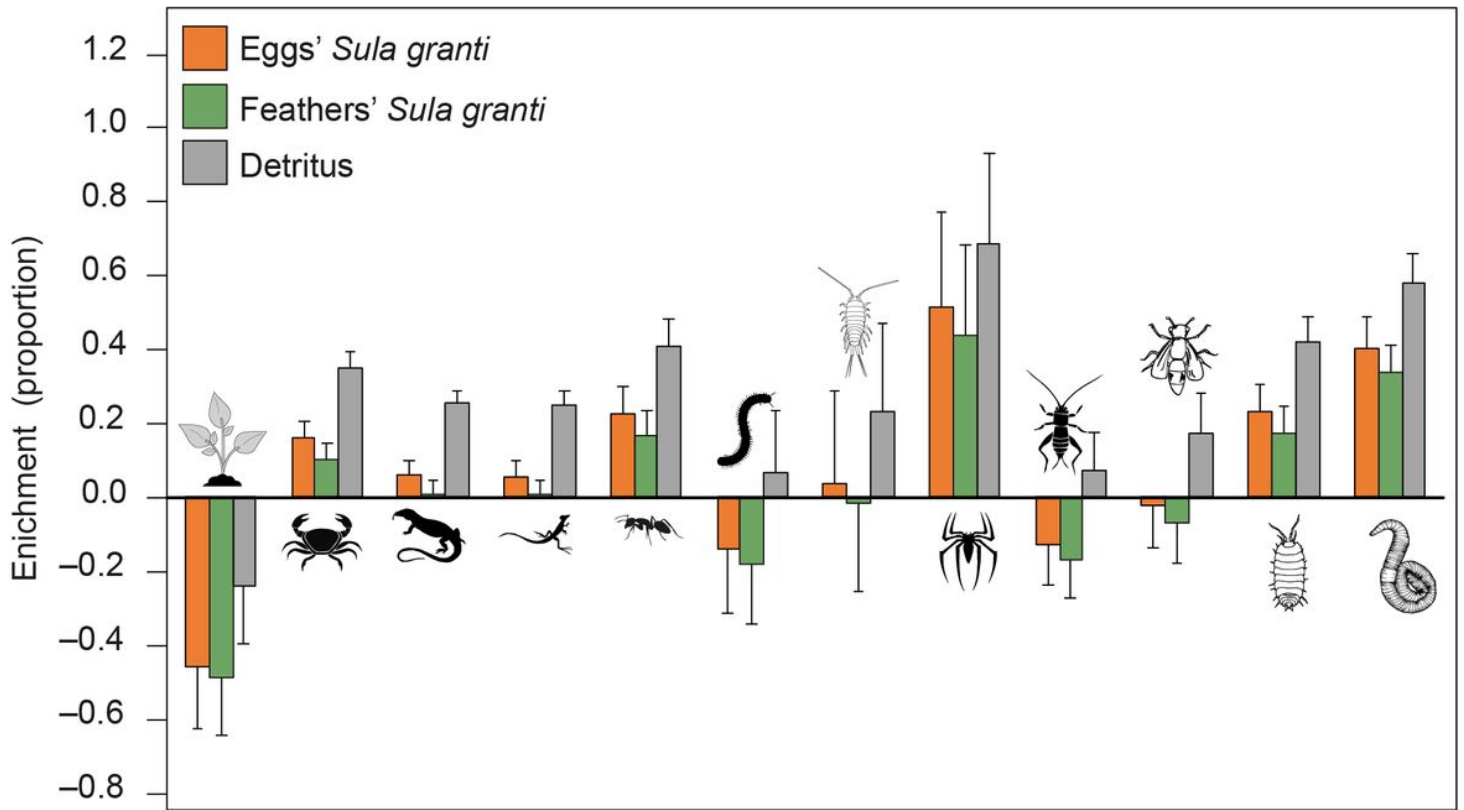


Figure 6
Isotopic enrichment (mean \pm SD) in ^{15}N of the various components of the terrestrial ecosystem of the Malpelo Fauna and Flora Sanctuary, Colombia, related to feathers (green), eggs (orange) of *Sula granti*, and detritus (grey).

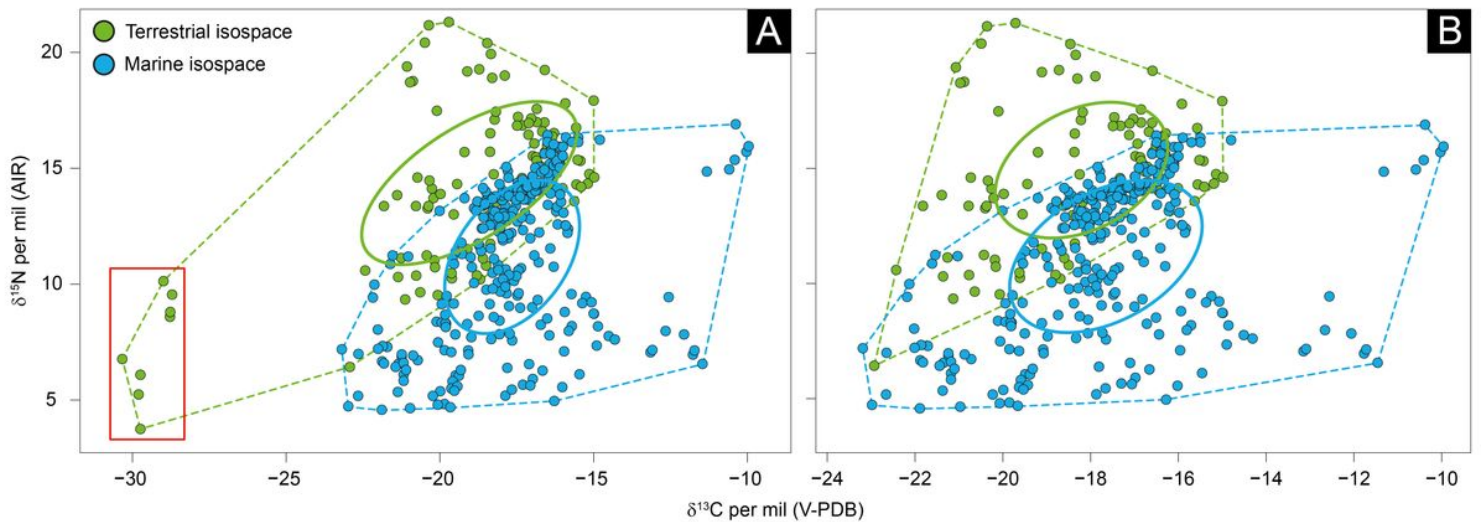


Figure 7
Isotopic overlap between the terrestrial and marine ecosystems of the Malpelo Fauna and Flora Sanctuary, Colombia, represented by two scenarios **A**. Terrestrial isospace including terrestrial C_3 plants vs. marine isospace. **B**. Terrestrial isospace excluding terrestrial C_3 plants and the marine isospace.

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