



Nutrient Input from Green Turtle Eggs and Hatchlings in a West Africa Island and Its Nearshore Environment

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Received: 17 October 2024 / Revised: 24 January 2025 / Accepted: 30 January 2025 / Published online: 15 February 2025
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Abstract

Sea turtle nesting brings marine-derived nutrients into sandy beach ecosystems, potentially influencing their dynamics. We investigated nutrient input from green turtle *Chelonia mydas* eggs and hatchlings into coastal habitats in Guinea-Bissau, West Africa. We assessed two islands within the João Vieira-Poilão Marine National Park ('JVPMNP'), with contrasting sea turtle nesting density: very low (João Vieira) and very high (Poilão). On each island, we analyzed stable isotopes of carbon and nitrogen in one pair of plant species (coinvine *Dalbergia ecastaphyllum* bush/baobab *Adansonia digitata* tree) and two pairs of predator species (tufted ghost crab *Ocypode cursor*/African rainbow crab *Cardisoma armatum* and sea catfish *Carlarius* spp./crevalle jack *Caranx hippos*). The first species in each pair is distributed closer to nesting sites, while the second is found further inland or offshore. Stomach content analysis was also conducted for fishes. Results supported nutrient input from turtle clutches benefiting the species living near nesting sites. Shoreline coinvines at Poilão had higher $\delta^{15}\text{N}$ ($5.1 \pm 3.2\text{‰}$) compared to João Vieira ($\approx 0\text{‰}$), suggesting assimilation of turtle-derived ^{15}N . Shoreline tufted ghost crabs at Poilão had enriched $\delta^{15}\text{N}$ ($15.2 \pm 0.7\text{‰}$ vs. João Vieira's $12.2 \pm 1.1\text{‰}$) and $\delta^{13}\text{C}$ ($-13.4 \pm 0.7\text{‰}$ vs. João Vieira's $-18.7 \pm 1.4\text{‰}$), likely reflecting predation upon eggs and hatchlings. Sea catfishes at Poilão frequently consumed unhatched turtle eggs washed into the sea (17% frequency of occurrence) and hatchlings (up to 27%). This study suggests that nutrient availability from turtle nests influences and supports shoreline plants and consumers at JVPMNP.

Keywords Nutrient transport · Nutrient input · Sea turtles · Ecosystems · Stable isotope analysis · Producers and secondary consumers

Communicated by Paul A. Montagna

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Introduction

Nutrients can be transported across ecosystem boundaries, connecting them (Doughty et al., 2016). While physical vectors like wind and water contribute to nutrient transport between spatially distinct ecosystems, biotic vectors such as animals can also play an important role (Bauer & Hoye, 2014; McInturf et al., 2019; Polis et al., 1997; Vanni, 2002). Nutrient transport by animals can significantly influence nutrient cycling, ecosystem productivity, food web functioning, and support consumer populations within the recipient ecosystem (Subalusky & Post, 2019). For instance, animal-mediated nutrient transport from ocean to land is well described for seabirds (e.g. Adame et al., 2015; Anderson & Polis, 1998; González-Bergonzoni et al., 2017; Hawke & Holdaway, 2005; Sánchez-Piñero & Polis, 2000) and anadromous fish (e.g. Ben-David et al., 1998; Gende et al., 2002;

Helfield & Naiman, 2001; Koshino et al., 2013; Reimchen et al., 2003).

The range and relative nutrient input into the recipient ecosystem are influenced by the composition of its plant and animal communities. From a well-known example, in Alaska, salmon-derived nitrogen dispersed via brown bear *Ursus arctos* urine was detected up to 500 m from the stream in the foliage of white spruce trees *Picea glauca*, with nitrogen concentration decreasing with distance from the stream (Hilderbrand et al., 1999). Terrestrial nitrogen gain (foliage total nitrogen) via salmon biomass along a 500-m stream-to-forest transect was almost 20% (Hilderbrand et al., 1999). Riparian trees near anadromous Pacific salmon *Oncorhynchus* spp. spawning streams derive significant foliar nitrogen from salmon carcasses, with the highest values found within 25 m of streams and detectable up to 100 m (Helfield & Naiman, 2001, 2002). In the opposite direction, terrestrial invertebrates can contribute nutrients that sustain stream fish (Mason & Macdonald, 1982; Nakano et al., 1999). This dual cross-system nutrient flux can impact multiple trophic levels (e.g. Hocking & Reimchen, 2002).

In tropical, subtropical, and warm temperate coastal regions, sea turtles are known to be important biotic vectors of nutrients between marine and coastal terrestrial ecosystems (Bouchard & Bjorndal, 2000). Nutrients derived from sea turtle eggs contribute to enhance vegetation growth along nesting beaches, aiding in shoreline stabilization and erosion control (Moss, 2017). Furthermore, the consumption of sea turtle eggs by terrestrial predators redistributes nutrients as these are subsequently dispersed through the predators' faeces, thus fostering ecosystem health and resilience (Moss, 2017). Previous research has highlighted the important role of sea turtle-mediated nutrient transport from marine to terrestrial ecosystems (Bouchard & Bjorndal, 2000; Hannan et al., 2007; Madden et al., 2008; Maros et al., 2006; Vander Zanden et al., 2012). For example, studies conducted on the east central coast of Florida, USA (Hannan et al., 2007), and in Tortuguero, Costa Rica (Vander Zanden et al., 2012), investigated nutrient incorporation by different plants at beaches used by nesting green *Chelonia mydas* or loggerhead *Caretta caretta* turtles. These studies showed positive correlations between nest density and vegetation nitrogen isotopic signatures. Another study observed nitrogen enrichment in mole crickets *Scapteriscus didactylus*, terrestrial insects known to perforate leatherback turtle *Dermochelys coriacea* eggs (Maros et al., 2006); this increase was observed in individuals collected from nesting beaches compared to those collected near human settlements, suggesting that they had fed on turtle eggs (Maros et al., 2006). At Melbourne Beach, Florida, USA, it was estimated that 40% of the nitrogen derived from loggerhead turtle clutches was accessible to plants, detritivores, and decomposers, while 26% was consumed by nest predators (Bouchard & Bjorndal,

2000). On Australia's north-west coast, an estimated 13% of the energy supplied by loggerhead turtle clutches into the beach environment became available to plants, detritivores, and decomposers, 70% to terrestrial predators, and 8% returned to the ocean as hatchlings (Avenant et al., 2024).

The intricate ways in which nutrients are transported and assimilated within ecosystems can be investigated through indirect and direct methods, or a combination of both. Stable isotope analysis (SIA) is a valuable tool for investigating the flow of energy or mass through trophic levels and ecosystems (Ehleringer et al., 1986; Post, 2002). This technique relies on the premise that the isotopic ratios of consumers reflect those of their dietary sources through reasonably predictable patterns (Fry, 2006). SIA typically combines nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopic ratios. Nitrogen serves as a proxy for the consumer's trophic position as it gradually accumulates through the food chain, while carbon undergoes negligible changes along the food chain and is often used to distinguish original sources of dietary carbon, particularly when distinct carbon isotopic signatures characterize the sources (DeNiro & Epstein, 1978, 1981; Peterson & Fry, 1987; Post, 2002).

SIA is also useful for tracking nutrient uptake by plants, including over different spatial and temporal scales (Dawson et al., 2002; Snyder et al., 2022). The $\delta^{15}\text{N}$ is generally used to identify the sources of nitrogen used by plants, such as atmospheric nitrogen fixed by nitrogen-fixing plants vs. soil nitrogen. In contrast, the $\delta^{13}\text{C}$ is commonly used to determine photosynthetic pathways (with C3 plants exhibiting lower $\delta^{13}\text{C}$ values than C4 plants) and to estimate water use efficiency, as well as to identify the sources of assimilated carbon (Dawson et al., 2002; Snyder et al., 2022).

While SIA can provide an integrated perspective on the assimilated dietary sources in animals over longer periods, stomach content analysis (SCA) offers direct evidence of recently ingested food items (Hyslop, 1980; Pinnegar & Polunin, 2000; Stergiou & Karpouzi, 2002). The integration of SIA and SCA can offer a comprehensive approach to trophic studies, providing complementary insights into dietary patterns and enhancing the taxonomic resolution and reliability of dietary assessments (e.g. Gonzalez et al., 2021; Mantel et al., 2004; Parkyn et al., 2001).

The João Vieira-Poilão Marine National Park (hereafter 'JVPMNP'), located in the Bijagós Archipelago of Guinea-Bissau, West Africa, is an important marine protected area (MPA) that hosts one of the primary breeding aggregations of green turtles globally (Cтры et al., 2009; Patrício et al., 2019). The park encompasses islands with undisturbed tropical seasonal forests immediately bordering the beach dunes, with zero to low human occupation, and heterogeneous green turtle nest densities (Raposo et al., 2024). These densities range from very high, with a mean of 2.04 nests m^{-2} on Poilão Island, to very low,

with approximately 0.002 nests m^{-2} on João Vieira Island (Raposo et al., 2024). It is estimated that an average of 33,065 female turtles nested at Poilão each year between 2020 and 2022, laying around 3,912,960 eggs each year, yielding a total of 2,656,900 hatchlings (IBAP, unpublished data). In contrast, these estimates are much lower for João Vieira, with an average of 242 nests and 29,040 eggs per year (2020–2021, IBAP, unpublished data). Hatching success in João Vieira is unquantified, but clutch predation by Nile monitors *Varanus niloticus* is very high, affecting 76% of the clutches (Raposo et al., 2024). These discrepancies make this MPA an ideal location to study the nutrient contributions of sea turtles to sandy beach ecosystems. Here, we aimed to examine the input of nutrients from green turtle nesting activities into the coastal communities of the João Vieira-Poilão Marine National Park. We used two types of comparisons: (i) of organisms of the same species collected on the islands with the lowest and highest sea turtle nest concentrations in the park; (ii) of pairs of related species, one distributed along the shoreline and the second occurring both on the shoreline and further inland or, in the case of fishes, on offshore areas. We hypothesized that nutrient transport would be evident only in Poilão and would primarily be observed in the species occurring in closest proximity to sea turtle nesting sites.

Materials and Methods

Study Site

This study was conducted at the João Vieira-Poilão Marine National Park (JVPMNP), which lies on the southeast of the Bijagós Archipelago, in Guinea-Bissau, West Africa ($N11^{\circ}17'$, $W15^{\circ}58'$, Fig. 1). The JVPMNP consists of four main islands: Poilão, João Vieira, Meio, and Cavalos, characterized by low-lying sandy beaches and widely varying levels of green turtle nesting activity (Raposo et al., 2024). Poilão ($10^{\circ}52'N$, $15^{\circ}43'W$, Fig. 1), covering an area of 43 ha, is the smallest island of the park and hosts the largest green turtle breeding aggregation in the entire archipelago (Cstry et al., 2002, 2009), ranking among the top six globally (Patrício et al., 2019). At 900 ha in size, João Vieira ($11^{\circ}02'N$, $15^{\circ}38'W$, Fig. 1) is the largest island but ranks lowest in number of nests among the JVPMNP islands (Barbosa et al., 2018). We selected João Vieira and Poilão as sites of low and high nest densities within the JVPMNP, respectively. At these sites, monitoring of sea turtle nesting activities is conducted annually by the Instituto da Biodiversidade e das Áreas Protegidas (IBAP) of Guinea-Bissau (Barbosa et al., 2018), the governmental institution responsible for biodiversity monitoring and management.

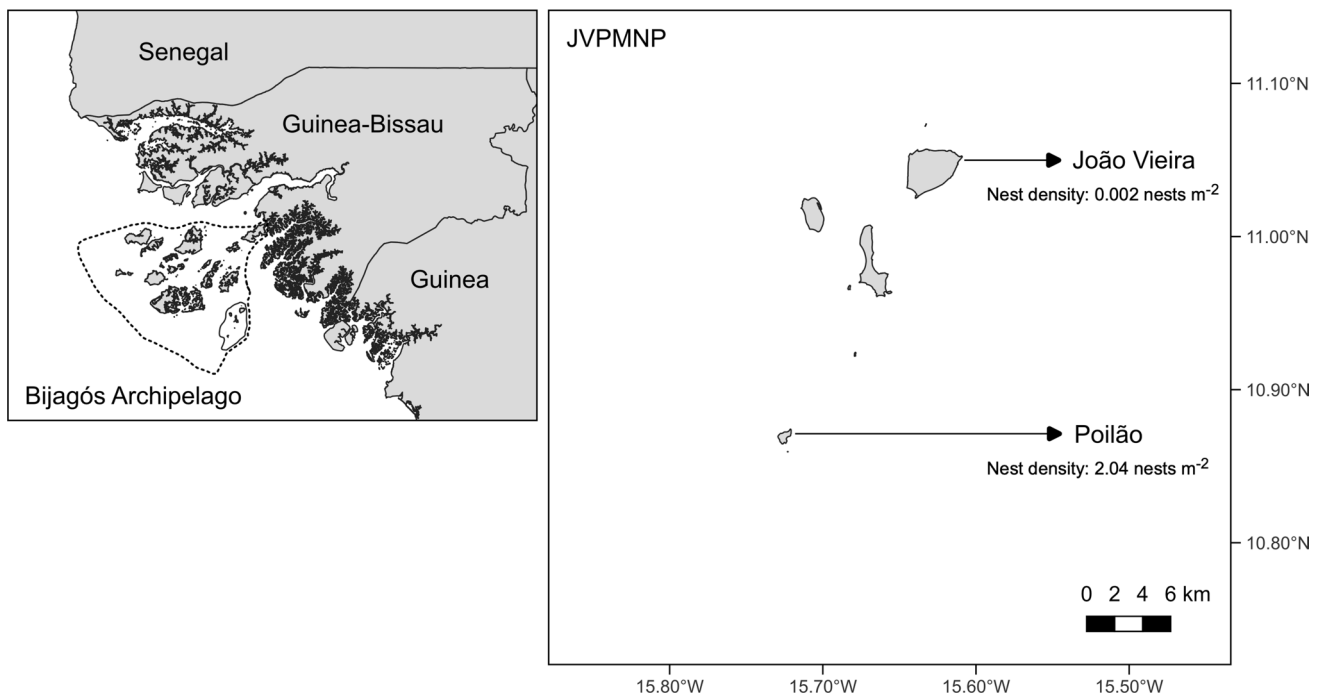


Fig. 1 Location of the João Vieira-Poilão Marine National Park (JVPMNP) depicted by the solid line within the Bijagós Archipelago, Guinea-Bissau, whose limits are shown by the dashed line. Green turtle nest densities were obtained from Raposo et al. (2024)

Sampled Species

At the JVPMNP, terrestrial predators of sea turtle eggs include crabs (e.g. ghost crabs *Ocypode* spp.), reptiles (e.g. Nile monitors), and birds (Palm-nut vultures *Gypohierax angolensis* and pied crows *Corvus albus* (Catry et al., 2002; Sampaio et al., 2022)), while hatchlings are preyed upon by crabs (e.g. ghost crabs) and birds (Palm-nut vultures and pied crows (Catry et al., 2010; Rebelo et al., 2012; Carneiro et al., 2017)). Marine predators of hatchlings include several species of fish (e.g. sea catfishes *Carlarius* spp., crevalle jack *Caranx hippos*, snappers *Lutjanus* spp., and Guinean barracuda *Sphyræna* spp. (Catry et al., 2010; IBAP, pers. comm.)). To investigate the nutrient input from green turtle eggs and hatchlings into the coastal environment, we collected samples from three groups representing primary producers and terrestrial and marine predators of sea turtle eggs and hatchlings: two plant species, two crab species, and two fish species.

We chose the plant species coinvine (*Dalbergia ecastaphyllum*, Fabaceae, $N=36$, Table 1) and baobab (*Adansonia digitata*, Malvaceae, $N=36$, Table 1), due to their abundance along the beaches of both islands. Coinvines occupy littoral sand dune environments, whereas baobabs occur further inland, right behind the dune vegetation, where sea turtles also nest. Coinvine is a large shrub known to establish symbiosis in its root system with rhizobia for nitrogen fixation (Saur et al., 2000; Sotuyo et al., 2022). In contrast, baobab is a non-nitrogen-fixing tree.

The selection of crab species was guided by their habitat preferences. Tufted ghost crabs (hereafter ‘ghost crabs’, *Ocypode cursor*, Ocypodidae, $N=30$, Table 1) live and build their burrows on sandy beach littoral habitats typical of sea turtle nesting areas, whereas African rainbow crabs (*Cardisoma armatum*, Gecarcinidae, $N=12$, Table 1) occur along the dunes as well as further inland. Ghost crabs are opportunistic omnivores and known predators of sea turtle eggs and hatchlings (Marco et al., 2015; Martins et al., 2021; Rae et al., 2019). A previous study documented the predation of green turtle hatchlings by this species at Poilão (Rebelo et al., 2012). African rainbow crabs are generally reported as herbivores (Lawal-Are & Gbewa, 2015; Ngo-Massou et al., 2021), but can also exhibit opportunistic omnivorous diets (Olalekan & Lawal-Are, 2013; Etchian et al., 2016; N’zi & Coulibaly, 2021), and are known to prey on sea turtle hatchlings (Kamel & Mrosovsky, 2005). On Poilão, this species is found in forested areas along the beaches where green turtles nest (Patrício et al., 2018), where they have been observed to prey on hatchlings (Catry et al., 2010).

Two predatory fish species, sea catfishes (*Carlarius* spp., Ariidae, $N=75$, Table 1) and crevalle jack (*Caranx hippos*, Carangidae, $N=47$, Table 1), were selected based on their ecology: sea catfishes are benthic and are frequently found

nearshore, while crevalle jacks are highly mobile swimmers, usually found further offshore, although they also regularly forage in shallow coastal areas. Both species have been observed preying green turtle hatchlings at Poilão (IBAP, pers. comm.).

Sampling Period

We collected samples of green turtle eggs and hatchlings, plants, crabs, and fishes for SIA. Additional fish samples were collected for SCA. The main green turtle breeding season in the JVPMNP runs from mid-June to mid-December, with peak nesting activity in August and September (Catry et al., 2002), while green turtle hatching takes place from mid-August to mid-February, with a peak between September and November. Sample collection of plants, crabs and fishes was conducted on both islands towards the end of the breeding season (October/November). This timing aimed to maximize the incorporation of the annual turtle clutches-derived nutrients into plant tissues and the turtle egg or hatchling nutrients into consumer tissues. Fishes were captured for SCA at both islands during the same period.

Green turtle eggs and hatchlings were exclusively collected at Poilão, considering previous research indicating that breeding turtles move between JVPMNP islands to nest (Raposo et al., 2023). Therefore, these samples are representative of the eggs and hatchlings of João Vieira. Sampling took place in 2021, 2022, and 2023.

Green Turtle Eggs and Hatchlings

We collected addled green turtle eggs (hereafter ‘eggs’), i.e. eggs containing yolk but exhibiting no visible signs of development (Hannan et al., 2007), as well as muscle tissue from dead hatchlings. During early morning beach surveys, we scoured the sand on Poilão for scattered turtle eggs and dead hatchlings that had not reached the ocean the previous night and were untouched by predators. Nest destruction by subsequent nesting turtles frequently result in eggs found exposed on the beach surface (Catry et al., 2009), a common occurrence at Poilão (Raposo et al., 2024).

Eggshells were removed using a sterile scalpel blade and only undeveloped egg contents were analyzed. A small muscle sample from the flipper of each dead hatchling was also collected.

Vegetation

In 2021 and 2022, we selected five sampling sites per plant species per island, while in 2023, we selected eight sampling sites. The selection of sampling sites was based on the existence of green turtle nests nearby; this corresponded to the entire Poilão shoreline, while in João

Table 1 Number of samples collected per sampling group and species. Plant species include coinivines (*Dalbergia ecastaphyllum*) and baobabs (*Adansonia digitata*), crab species include tufted ghost crabs (*Ocypode cursor*) and African rainbow crabs (*Cardisoma armatum*), and fish species include sea catfishes (*Carlarius* spp.) and crevalle jacks (*Caranx hippos*)

Group	Species	Year	Location	Mouth gape	<i>n</i>
Green turtle eggs	<i>Chelonia mydas</i>	2021	Poilão	NA	19
		2022			20
		2023			5
Green turtle hatchlings	<i>Chelonia mydas</i>	2021	Poilão	NA	19
		2022			20
Plants	<i>Dalbergia ecastaphyllum</i>	2021	João Vieira	NA	5
			Poilão	NA	5
		2022	João Vieira	NA	5
			Poilão	NA	5
		2023	João Vieira	NA	8
			Poilão	NA	8
	<i>Adansonia digitata</i>	2021	João Vieira	NA	5
			Poilão	NA	5
		2022	João Vieira	NA	5
			Poilão	NA	5
		2023	João Vieira	NA	8
			Poilão	NA	8
Crabs	<i>Ocypode cursor</i>	2021	João Vieira	NA	0
			Poilão	NA	6
		2022	João Vieira	NA	12
		Poilão	NA	12	
	<i>Cardisoma armatum</i>	2021	João Vieira	NA	6
			Poilão	NA	6
2022		João Vieira	NA	0	
Fishes	<i>Carlarius</i> spp.	2021	João Vieira	Restricted	8
				Wide	8
			Poilão	Restricted	1
			Wide	30	
		2022	João Vieira	Restricted	0
				Wide	7
	<i>Caranx hippos</i>	2021	João Vieira	Restricted	1
				Wide	20
			Poilão	Restricted	4
			Wide	16	
		2022	João Vieira	Restricted	0
				Wide	6
<i>Sardinella maderensis</i>	2021	João Vieira	Restricted	4	
			Wide	12	
		Poilão	NA	10	
	2022	João Vieira	NA	10	
			NA	10	
		Poilão	NA	0	

Vieira we selected sites along the nesting areas. At each sampling site, we gathered three leaves from each plant species, ensuring consistency in leaf maturity and absence of herbivory. From these collected leaves, we randomly

selected pieces and then combined them according to species and site. This process resulted in a single, finely mixed composite sample for each species at each site each year (Vander Zanden et al., 2012).

Crabs

Crabs were collected by hand from the beach in 2021 and 2022 during nightly exploratory surveys at non-fixed locations, with the exception of ghost crabs in João Vieira in 2022, which were sampled by digging their burrows due to difficulty in finding them active on the beach. All crabs were measured with a vernier caliper to the nearest 0.1 mm for carapace width ('CW', cm). Sex was not identified. Leg muscle tissue was collected from up to two legs, and all individuals were released shortly after handling.

Fishes

Fishes were captured from the beach in 2021 and 2022 using artificial bait (lures), cut bait, hook and line, and nets over 50 (October 31 to November 21, 2021) and 22 (October 30 to November 20, 2022) days in 2021 and 2022, respectively. During these periods, fishes were opportunistically caught. Net mesh sizes were 2.5 × 2.5 cm at Poilão and 1 × 1 cm or 2.5 × 2.5 cm at João Vieira. Shortly after capture and death by oxygen deprivation, we measured the fork length (FL, cm) of each fish to the nearest 1 mm using a flexible measuring tape.

Within the *Carlarius* genus, two species were identified through dental plate examination: rough-head sea catfish (*Carlarius laticutatus*, Ariidae) and Guinean sea catfish (*Carlarius parkii*, Ariidae). These species have broadly similar diets consisting of crabs, fish, molluscs, and shrimp, but with different preferences for specific prey types, particularly crabs for *C. laticutatus* and bivalves for *C. parkii* (Simier et al., 2021). However, since it was not possible to identify every individual at the species level, we present data for both species combined instead of estimating relative frequency. Prior research indicated Madeiran sardinella (*Sardinella maderensis*, Clupeidae) as a primary food source for crevalle jacks (Correia et al., 2017), so samples of this prey fish species were collected to assess differences between its isotopic ratios and the ones from green turtle eggs and hatchlings.

To ensure that we were capturing individuals capable of preying on turtle hatchlings, we classified predatory fish individuals into 'restricted gape' or 'wide gape' by determining the minimum size (i.e. FL) at which a hatchling could fit their mouth.

We collected samples of dorsal white muscle (hereafter 'muscle') of all fishes (Pinnegar & Pollunin, 1999) and, when possible, blood from the heart region. We directly collected blood using a sterile syringe or a disinfected pointed spoon.

Stomach contents of sea catfishes were carefully removed and examined on-site. Identifiable contents were recorded in

the field. Non-identifiable contents were preserved in 96% ethanol, transported to the laboratory, and classified using a stereomicroscope. Prey items were identified to the lowest taxonomic level possible using morphologic characteristics, and comparing them with a reference collection of vertebrae and other bones from a wide range of species compiled by different researchers at the Bijagós Archipelago (Correia et al., 2017). We examined the stomach contents of crevalle jacks on-site and concluded that these were highly digested, making SCA impossible for this species.

Stable Isotope Analysis

Both plant and animal (muscle and blood) tissues were thoroughly air-dried on-site for immediate preservation and stored in microvial tubes until subsequent processing to determine their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Tissue samples were oven-dried in the laboratory at 60 °C for 24–48 h to remove moisture content. Vegetation samples were ground using a ball mill. As animal tissues were too sticky for the ground mill, they were ground into powder using a mortar and pestle. Since animal tissues with high lipid content frequently have more negative $\delta^{13}\text{C}$ values (Post et al., 2007), introducing a potential bias in the interpretation of $\delta^{13}\text{C}$ and trophic relationships, all animal samples underwent lipid extraction, a chemical process used to physically remove lipids from samples (Post et al., 2007). This began with the immersion of each sample in a 2:1 chloroform/methanol solution at a volume approximately five times that of the sample. After mixing for 30 s, the samples were allowed to settle for 30 min and then centrifuged for 10 min at 3400 rpm. The supernatant, which held solvent and lipids, was carefully removed. This process was repeated three to five times for each sample, until the supernatant was clear after centrifugation. Following lipid extraction, the samples were further dried in an oven at 60 °C for 48 h to remove any residual solvent. A total of 4 to 5 mg and 0.75 to 1 mg of ground plant and animal tissue sample, respectively, were individually weighted into tin cups. The isotopic ratios were determined through continuous flow isotope mass spectrometry (CF-IRMS; (Dunn & Carter, 2018)), on a Sercon Hydra 20–22 (Sercon, UK) stable isotope ratio mass spectrometer, coupled to a EuroEA (EuroVector, Italy) elemental analyzer for online sample preparation by Dumas-combustion. Delta values were calculated following the formula $\delta = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] * 1000$, where R represents the ratio between the heavier isotope and the lighter one (i.e. $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratio). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were calibrated against atmospheric nitrogen (N_2) and the Pee Dee Belemnite (PDB) scale, respectively. The reference materials used included IAEA N1, IAEA N2, USGS26, Glucose BCR no. 657,

IAEA-CH7, and IAEA-C3. For plant samples, the laboratory quality control check used was rice flour, while for animal samples, it was bovine liver powder (commercial food additive). The uncertainty of the isotope ratio analysis, calculated using values from 6 to 9 replicates of laboratory standard interspersed among samples in every batch of analysis, was $\leq 0.2\%$. The major mass signals of carbon and nitrogen were used to calculate total carbon (%C) and nitrogen (%N) contents for both plant and animal samples.

The timescale of isotopic incorporation, or turnover rate, reflects how quickly the consumers' tissues assimilate the dietary isotopic signal (Martínez del Rio et al., 2009; Thomas & Crowther, 2015). Vertebrate turnover rates vary widely, from a few days or weeks to months (Layman et al., 2012), influenced by tissue type, body size, growth, and taxon (Martínez del Rio et al., 2009; Vander Zanden et al., 2015). For example, blood generally exhibits a rapid turnover rate compared to muscle (Thomas & Crowther, 2015). Knowledge of the turnover rates is therefore essential for interpreting stable isotope signatures, and selecting the appropriate biological tissue is key to investigate the period of interest (Carter et al., 2019). For crabs, we considered a muscle turnover rate (isotopic half-life) ranging from 4 to 6 months, based on a timeframe established by previous research on marine arthropods (Bopp et al., 2023). There is a lack of isotopic turnover studies specific to our fish species (e.g. Papastamatiou et al., 2015)). As proxies, we used turnover rates (isotopic half-life) from the muscle of sub-adult whitemouth croakers *Micropogonias furnieri* ($\delta^{15}\text{N}$, 22.3 days; $\delta^{13}\text{C}$, 17.7 days; (Mont'Alverne et al., 2016)). Considering these values, and the fact that in ectotherms blood has a rapid turnover rate compared to muscle (Buchheister & Latour, 2010; Warne et al., 2010), it is likely that the turnover rate of fishes blood will be faster.

Data Analysis

Two-way analyses of variance (two-way ANOVAs) were performed to evaluate the effects of location (= island), year, and their interaction on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of all tissues of all species except African rainbow crabs. For fishes, this analysis was performed only for the 'wide gape' individuals. For African rainbow crabs, there is data from a single year, and we tested for differences in the isotopic signatures of African rainbow crabs between islands using Welch two-sample *t*-tests.

For each plant species, we also used Welch two-sample *t*-tests to compare %N and %C between João Vieira and Poilão islands, considering data from all years. We examined the relation between $\delta^{15}\text{N}$ and %N of the plant tissues using simple linear regressions.

Since crabs with larger CW usually have larger chelae (Divine et al., 2017), we hypothesized that individuals with larger CW would potentially exhibit $\delta^{15}\text{N}$ values closer to those of green turtle hatchlings, as they are likely to capture and subdue larger prey items. The non-parametric Spearman's rank correlation was applied to test the associations between $\delta^{15}\text{N}$ and CW for both crab species.

We compared the isotopic signatures of crabs to those of their main purported prey—green turtle eggs and hatchlings, combined into one single group—using a method adapted from Meier et al. (2017). We applied the published mean trophic enrichment factor estimates of 3.4‰ for $\delta^{15}\text{N}$ and of 0.4‰ for $\delta^{13}\text{C}$ per trophic level (Post, 2002) to the mean isotopic signatures of turtle eggs and hatchlings. This allowed drawing, in the 2-dimensional isotopic space, the region occupied by 'theoretical' crabs that would have been exclusively consuming this prey for longer than their isotopic turnover rate (Layman et al., 2012; Newsome et al., 2007). It is worth noting that the estimation of discrimination factors (i.e. the difference between the stable isotope values of an animal's tissue and its diet (Martínez del Rio et al., 2009)) can be uncertain due to several factors like species, taxon, tissue, diet quality and isotopic composition, and the form of nitrogenous waste excretion (Martínez del Rio et al., 2009; Vander Zanden & Rasmussen, 2001; Vanderklift & Ponsard, 2003). Although species-specific estimates were not available, the broadly applicable estimates used in this study are suitable across various aquatic species and ecosystems (Post, 2002); still, our results should be interpreted with caution.

We evaluated the associations between $\delta^{15}\text{N}$ and FL for each predatory fish species annually, using both muscle and blood tissue samples from all sampled fishes, including both 'restricted gape' and 'wide gape', with the non-parametric Spearman's rank correlation. Subsequent analysis focused solely on 'wide gape' fishes.

To visually compare the isotopic signatures of both predatory fishes to those of green turtle eggs and hatchlings, as well as to those of Madeiran sardinella, we applied the same methodology used for the crab species (see above), using previously published trophic enrichment factors (Post, 2002).

SCA was used to ascertain the importance of each prey item in the diet of both 'restricted gape' and 'wide gape' sea catfishes and facilitate comparisons between João Vieira and Poilão. Results were presented as frequency of occurrence (%) of each prey type, which represents the number of stomachs containing a particular prey item relative to the total number of sampled stomachs. In order to estimate the number of individuals of each prey item in the sea catfish's stomachs (hereafter 'numerical frequency'), we counted all discernible structures of each prey item. For example, a stomach containing one whole green turtle hatchling and

35 scutes was counted as containing 4 hatchlings—the whole individual and 3 more based on the 35 scutes, as each hatchling typically has 13 scutes. This allowed us to avoid over-representation of prey items in the sea catfish's diet. To assess potential size-related changes in the consumption of 'green turtle items' (i.e. the sum of green turtle eggs and hatchlings), 'benthic fauna' (i.e. the combined count of crabs not identified, marbled swimcrabs *Callinectes marginatus*, shrimps not identified, ophiuroids not identified, sea cucumbers not identified, and ball sea cucumbers *Phyllophorus* sp.), and 'nektonic fauna' (i.e. the total number of fish not identified, Madeiran sardinella *Sardinella maderensis*, and Lesser African threadfin *Galeoides decadactylus*), we used the non-parametric Spearman's rank correlation to evaluate the association between the numerical frequency of each of these prey items groups observed in the stomachs of sea catfishes and fish FL.

All statistical analyses were performed using R v4.2.2 software (R Core Team, 2022). Data are presented as mean \pm standard deviation.

Results

Vegetation

There was a distinctly different interspecies pattern in $\delta^{15}\text{N}$ values. While coinvines displayed $\delta^{15}\text{N}$ values of approximately 0‰ in João Vieira and higher values in Poilão, baobabs exhibited similar values on both islands (Table S1, Fig. 2).

Regarding coinvines, only the location had a significant effect on $\delta^{15}\text{N}$ (two-way ANOVA $F(1,30)=40.97, p<0.001$) and $\delta^{13}\text{C}$ (two-way ANOVA $F(1,30)=4.39, p=0.045$). For baobabs, both the year (two-way ANOVA $F(2,30)=6.98, p=0.003$) and the interaction between location and year (two-way ANOVA $F(2,30)=4.31, p=0.023$) significantly influenced their $\delta^{15}\text{N}$ values. Moreover, location (two-way ANOVA $F(1,30)=7.56, p=0.010$), year (two-way ANOVA $F(2,30)=3.67, p=0.038$), and their interaction (two-way ANOVA $F(2,30)=5.05, p=0.013$) significantly affected their $\delta^{13}\text{C}$ values.

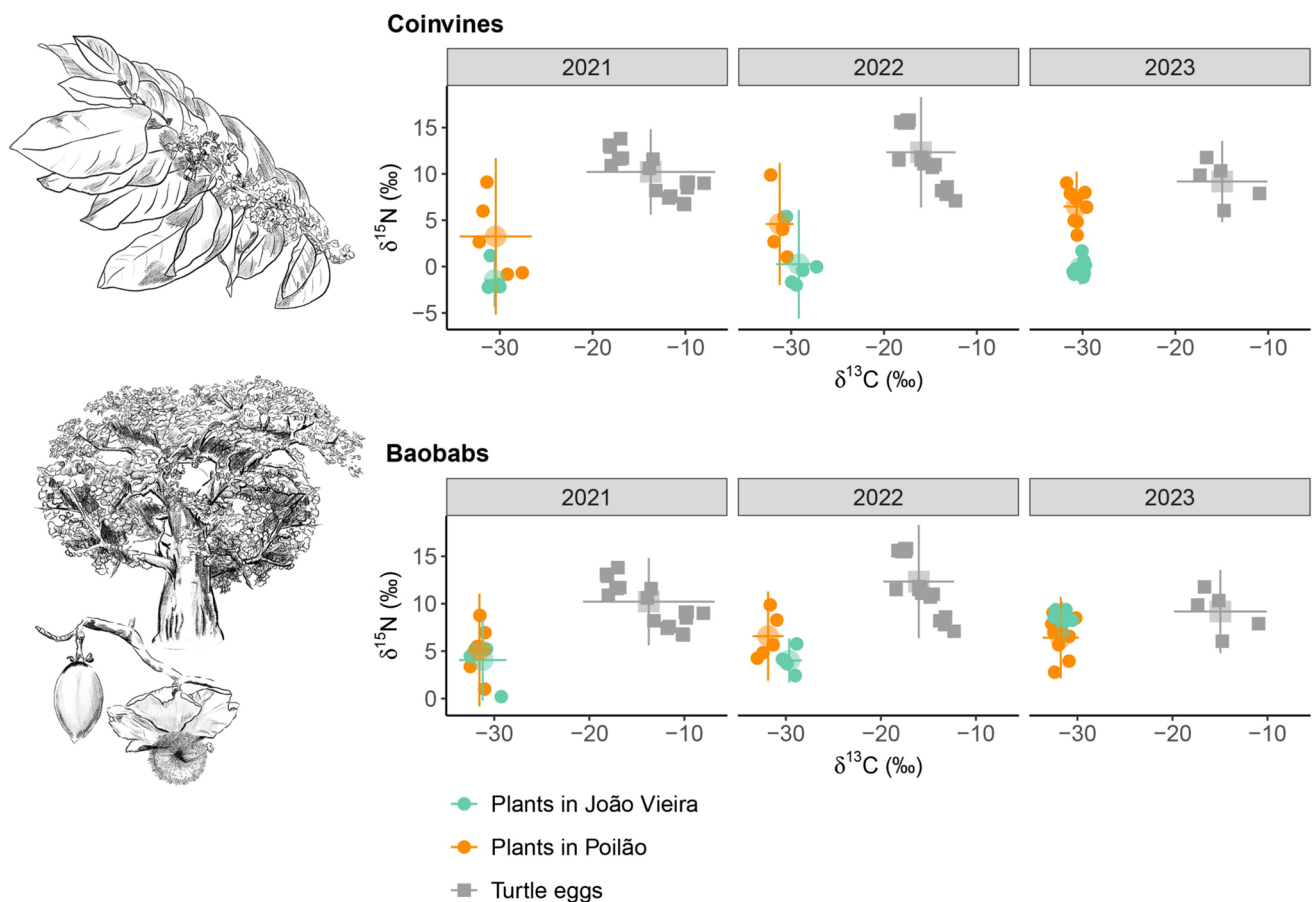


Fig. 2 Biplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for coinvines *Dalbergia ecastaphyllum* and baobabs *Adansonia digitata*, along with green turtle *Chelonia mydas* eggs, by year at João Vieira and Poilão

There were no differences in %N (coinvines: $t(32.77) = -0.66$, $p = 0.26$; baobabs: $t(27.35) = 1.35$, $p = 0.91$) and %C (coinvines: $t(34.00) = -0.66$, $p = 0.26$; baobabs: $t(30.01) = -0.48$, $p = 0.32$) between islands for either plant species. Overall, increases in foliar %N did not correspond to significant increases in $\delta^{15}\text{N}$, with the exception of coinvines in Poilão in 2021 (adjusted $r^2 = 0.78$, $n = 5$, $F(1,3) = 14.98$, $p = 0.031$, Table S2, Fig. 3) and baobabs in João Vieira that same year (adjusted $r^2 = 0.80$, $n = 5$, $F(1,3) = 17.42$, $p = 0.025$, Table S2, Fig. 3). However, there was also a significant negative relation between $\delta^{15}\text{N}$ and %N for baobabs in Poilão in 2021 (adjusted $r^2 = 0.90$, $n = 5$, $F(1,3) = 35.17$, $p = 0.010$, Table S2).

Crabs

Overall, ghost crabs had a mean (\pm standard error, SE) CW of 4.6 ± 0.1 cm (range 2.4–5.8 cm), while African rainbow crabs had a mean (\pm SE) CW of 8.3 ± 0.5 cm (range 5.9–12.5 cm).

Ghost crabs exhibited enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in Poilão, compared to João Vieira (Table S1, Fig. 4), whereas African rainbow crabs showed lower ratios of both isotopes than green turtle eggs or hatchlings on both islands (Table S1, Fig. 4). Location significantly affected both $\delta^{15}\text{N}$ (two-way ANOVA $F(1,27) = 80.95$, $p < 0.001$) and $\delta^{13}\text{C}$ (two-way ANOVA $F(1,27) = 182.84$, $p < 0.001$)

for ghost crabs. On the other hand, there were no significant differences in $\delta^{15}\text{N}$ (two sample t -test = 0.75, $p = 0.76$) and $\delta^{13}\text{C}$ (two sample t -test = -1.04, $p = 0.17$) between islands for African rainbow crabs. The isotopic signatures of ghost crabs in Poilão in both years were contained within the isotopic niche of a theoretical green turtle consumer (Fig. 4). The isotopic niches of ghost crabs in João Vieira and African rainbow crabs on both islands did not overlap with that of a turtle consumer (Fig. 4). In 2022, we found a significant positive correlation between $\delta^{15}\text{N}$ and CW for ghost crabs (Spearman rank correlation, $r_s = 0.46$, $n = 24$, $p = 0.025$, Table S3). In 2021, we did not find significant correlations between $\delta^{15}\text{N}$ and CW for either crab species (Table S3).

Fishes

In 2021 and 2022, a total of 75 sea catfishes were sampled, with a mean FL of 34.4 cm (range 24.8–66.1 cm). Of these, 65 individuals met the ‘wide gape’ criterion (Table 1), with a minimum FL of 29.6 cm. Among these, 17 (26.2%) were found to have green turtle eggs (eroded or unhatched yet intact eggs likely washed out into the sea) and/or hatchlings in their stomachs. In the same years, 47 crevalle jacks were caught, with a mean FL of 47.1 cm (range 30.7–88.0 cm). Of these, 37 crevalle jacks were classified as ‘wide gape’ (Table 1), with a minimum FL of 37.0 cm, of which only one (2.7%) had green turtle hatchling remains in its stomach. None of the fishes from either species that were classified as ‘restricted gape’ had turtle contents in their stomachs.

In 2021, a significant positive correlation was observed between $\delta^{15}\text{N}$ and FL for blood samples of the entire sea catfish sample (Spearman rank correlation, $r_s = 0.73$, $n = 12$, $p = 0.007$, Table S4). Conversely, a significant negative correlation was found in blood samples of crevalle jacks (Spearman rank correlation, $r_s = -0.52$, $n = 17$, $p = 0.031$, Table S4). When considering only ‘wide gape’ fishes, both predatory fish species exhibited higher mean $\delta^{15}\text{N}$ values and similar mean $\delta^{13}\text{C}$ values compared to those of green turtle eggs and hatchlings, whether for muscle or blood samples (Table S1, Figs. 5 and 6). In sea catfish muscle tissue, both $\delta^{15}\text{N}$ (two-way ANOVA $F(1,61) = 117.07$, $p < 0.001$) and $\delta^{13}\text{C}$ (two-way ANOVA $F(1,61) = 15.50$, $p < 0.001$) were significantly influenced by the year, but not by location, while in blood samples, $\delta^{15}\text{N}$ was affected by location (two-way ANOVA $F(1,29) = 7.19$, $p = 0.012$). For crevalle jacks, $\delta^{13}\text{C}$ in both muscle (two-way ANOVA $F(1,33) = 14.70$, $p < 0.001$) and blood samples (two-way ANOVA $F(1,26) = 7.06$, $p = 0.013$) were significantly influenced by location. Sea catfishes shared the isotopic niche of an exclusive green turtle consumer on both islands, whether muscle or blood samples were assessed, except for muscle samples of

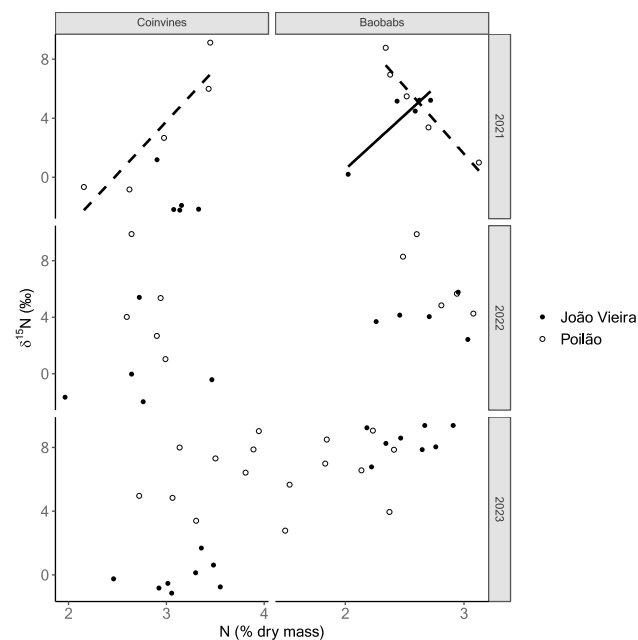
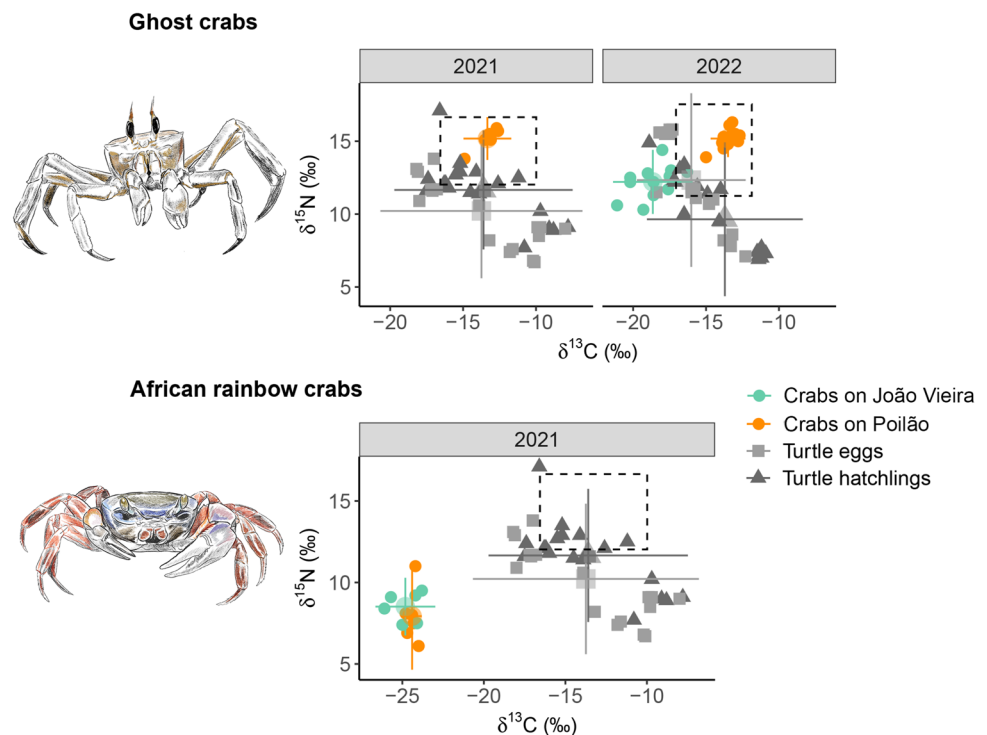


Fig. 3 Scatterplot showing the relation between foliar nitrogen isotopic ratio ($\delta^{15}\text{N}$) and nitrogen content (%N) for coinvines *Dalbergia ecastaphyllum* and baobabs *Adansonia digitata*, by year in João Vieira and Poilão. The solid and dashed lines indicate significant relations in João Vieira and Poilão, respectively

Fig. 4 Biplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for tufted ghost crabs *Ocypode cursor* and African rainbow crabs *Cardisoma armatum*, along with green turtle *Chelonia mydas* eggs and hatchlings, by year at João Vieira and Poilão. The dotted boxes represent the expected range in isotopic values of a consumer feeding on green turtle eggs and hatchlings, based on mean trophic enrichment factors of 3.4‰ for $\delta^{15}\text{N}$ and 0.4‰ for $\delta^{13}\text{C}$



individuals captured on both islands in 2021 (Fig. 5). In contrast, crevalle jacks' isotopic signatures did not overlap with that isotopic niche (Fig. 6). In both years, crevalle jacks captured at Poilão had isotopic signatures that corresponded with those of a theoretical Madeiran sardinella consumer (Fig. 6).

The majority of sea catfish stomach contents exhibited either partial or advanced digestion, posing challenges for precise identification of contents. Unidentified crabs and fish species (including not identified fish, Madeiran sardinella, and the Lesser African threadfin) were the dominant prey for 'restricted gape' and 'wide gape' sea catfishes captured at João Vieira and Poilão (Figs. 7 and 8). Additionally, 'wide gape' sea catfishes captured at Poilão exhibited a high frequency of consumption of green turtle eggs and hatchlings (Fig. 8). We found a significant positive correlation between the numerical frequency of green turtle items in their stomachs and FL in 2021 (Spearman rank correlation, $r_s = 0.60$, $n = 38$, $p < 0.001$, Table S5).

Discussion

We examined the nutrient input from green turtle eggs and hatchlings into some of the commonest species of the coastal communities of the João Vieira-Poilão Marine National Park in Guinea-Bissau. We compared sites with low and high sea turtle nest densities and pairs of organisms from the same species group (plants, crabs, and fishes)—one with a closer

to shore distribution and the other frequenting more inland or further offshore areas. Our objective was to examine the importance of sea turtle nutrients across the coastal terrestrial and marine habitats. We found evidence of nutrients very probably derived from green turtle clutches over time, but only in species that reside directly or very near sea turtle nesting sites and at the highest sea turtle nest density island.

Green Turtle Nutrient Uptake by Plants

Green turtles in Poilão nest towards the top of the frontal dune, with a significant proportion of clutches laid either on the vegetation border or under the vegetation (36%, (Patrício et al., 2018)), especially under coinvine bushes and baobab trees. In general, the observed differences in foliar $\delta^{15}\text{N}$ and %N patterns between the two species are consistent with previous findings. Nitrogen-fixing plants, such as coinvines, typically have $\delta^{15}\text{N}$ values approaching 0‰ due to symbiotic atmospheric nitrogen fixation (Craine et al., 2015; Evans, 2001; Robinson, 2001), whereas their %N is often higher than that of non-fixing plants (Evans, 2001). This pattern differs from baobabs, which rely only on soil-derived nitrogen sources.

The contrasting $\delta^{15}\text{N}$ values of coinvines between the low and the high sea turtle nest density sites suggest that nitrogen was acquired from different sources across islands. Approximately 70 to 80% of the nitrogen in a nitrogen-fixing plant is fixed by the rhizobia, while the remainder is absorbed by the root system (Bruning & Rozema, 2013).

Fig. 5 Biplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for muscle and blood samples of sea catfish *Carlarinus* spp., along with green turtle *Chelonia mydas* eggs and hatchlings, by year at João Vieira and Poilão. Only fish classified as ‘wide gape’ were used here. The dotted boxes represent the expected range in isotopic values of a consumer feeding on green turtle eggs and hatchlings, based on mean trophic enrichment factors of 3.4‰ for $\delta^{15}\text{N}$ and 0.4‰ for $\delta^{13}\text{C}$

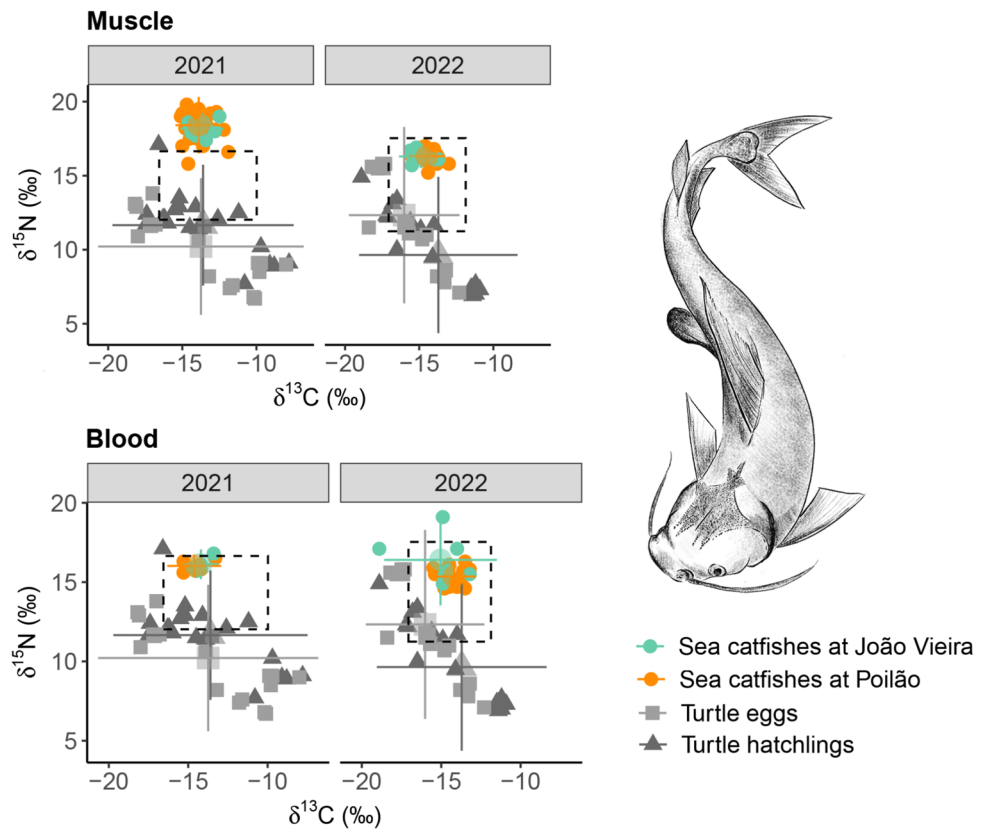
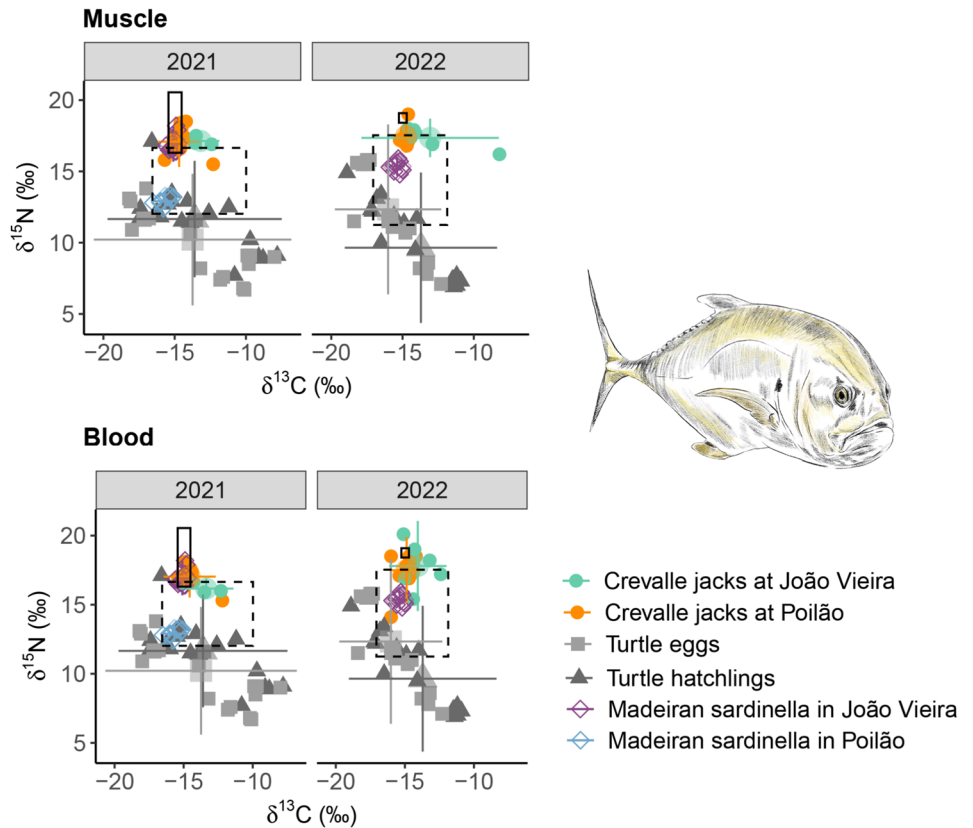


Fig. 6 Biplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for muscle and blood samples of crevalle jack *Caranx hippos*, along with green turtle *Chelonia mydas* eggs and hatchlings, and Madeiran sardinella *Sardinella maderensis*, by year at João Vieira and Poilão. The Madeiran sardinella is a locally present year-round species often consumed by jacks. Only fish classified as ‘wide gape’ were used here. The boxes represent the expected range in isotopic values of a consumer feeding on green turtle eggs and hatchlings (dotted boxes) and on Madeiran sardinella (solid boxes), based on mean trophic enrichment factors of 3.4‰ for $\delta^{15}\text{N}$ and 0.4‰ for $\delta^{13}\text{C}$. The relatively small sample size used in this study most likely limits the narrow region defined in the isotopic biplot for Madeiran sardinella



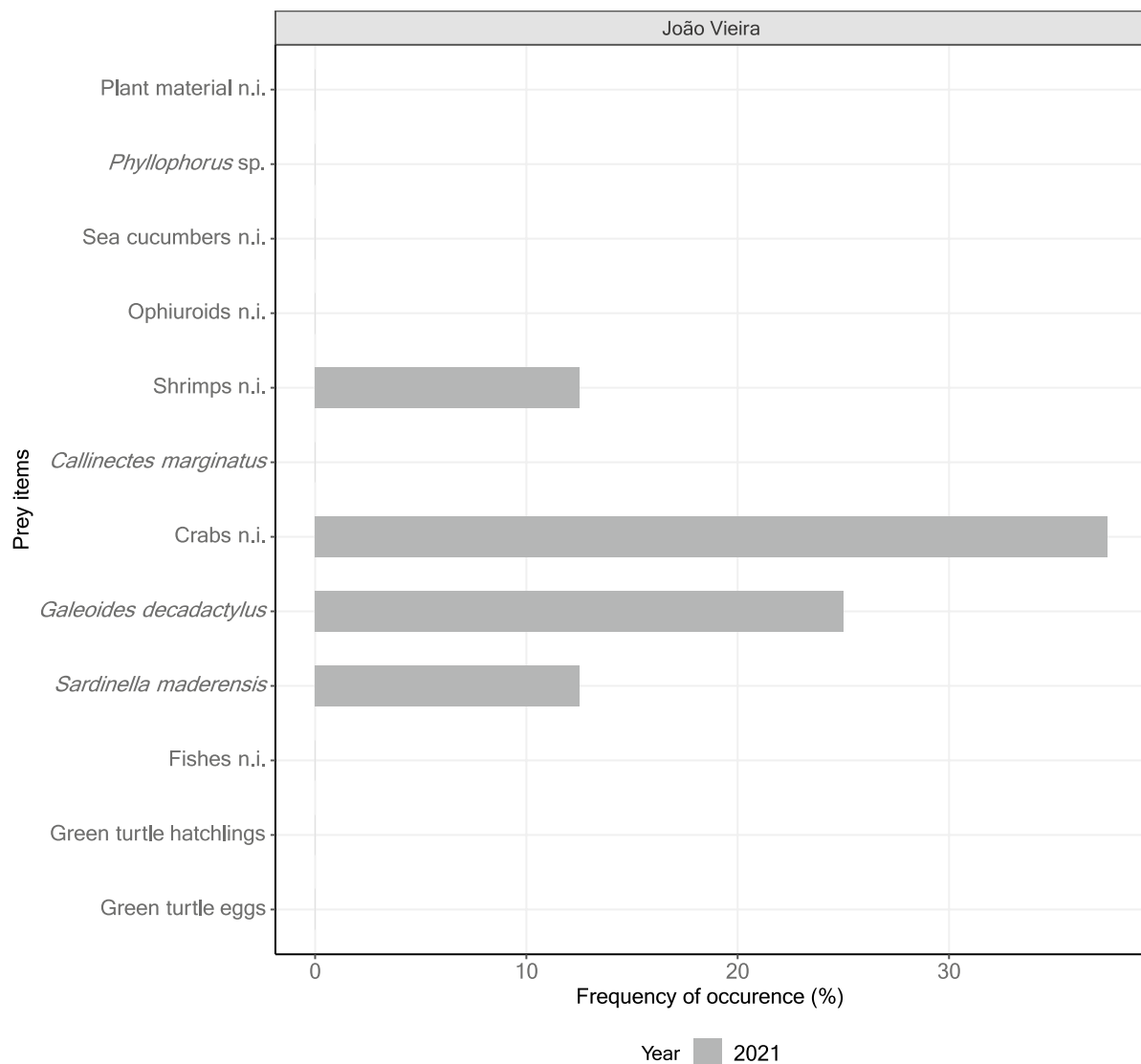


Fig. 7 Frequency of occurrence (%) of prey items in the stomachs of sea catfishes *Carlarinus* spp. classified as ‘restricted gape’. ‘n.i.’ denotes not identified

Thus, the higher $\delta^{15}\text{N}$ values of coinvines in Poilão may have been influenced by the isotopic composition of nitrogen sources in the soil, such as nutrients derived from green turtle clutches. Research has shown that the roots of the beachgrass *Ammophila breviligulata* can absorb nutrients exuded from the eggs of the diamondback terrapin *Malaclemys terrapin* (Stegmann et al., 1988), and that plant roots invaded 23% of loggerhead turtle nests in Melbourne Beach, Florida, USA (Bouchard & Bjorndal, 2000). Nitrogen fixation by plants may be more energy-consuming than using soil nitrogen, as symbiotic bacteria need carbohydrates from the host plant for ammonia production (Hannan et al., 2007). Hence, in nutrient-poor environments like sandy beaches, coinvines may benefit from the increased availability of marine-derived nitrogen from sea turtles. Here, coinvines’

$\delta^{15}\text{N}$ values were enriched at the high-density sea turtle nest location. Similarly, enriched foliar $\delta^{15}\text{N}$ values were observed in nitrogen-fixing plants in other studies comparing high to low density sea turtle nesting sites (Hannan et al., 2007).

Biotic nitrogen input typically promotes plant growth in nutrient-limited environments (Leghari et al., 2016). In terrestrial ecosystems, bird guano-derived nutrients enhance plant growth (e.g. Burger et al., 1978; Magnússon et al., 2014; Sánchez-Piñero & Polis, 2000), and salmon-derived nutrients promote riparian forest growth along the aquatic-terrestrial interface (e.g. Helfield & Naiman, 2001, 2002). Furthermore, nitrogen availability often limits productivity in several ecosystems (Elser et al., 2007; LeBauer & Treseder, 2008; Vitousek &

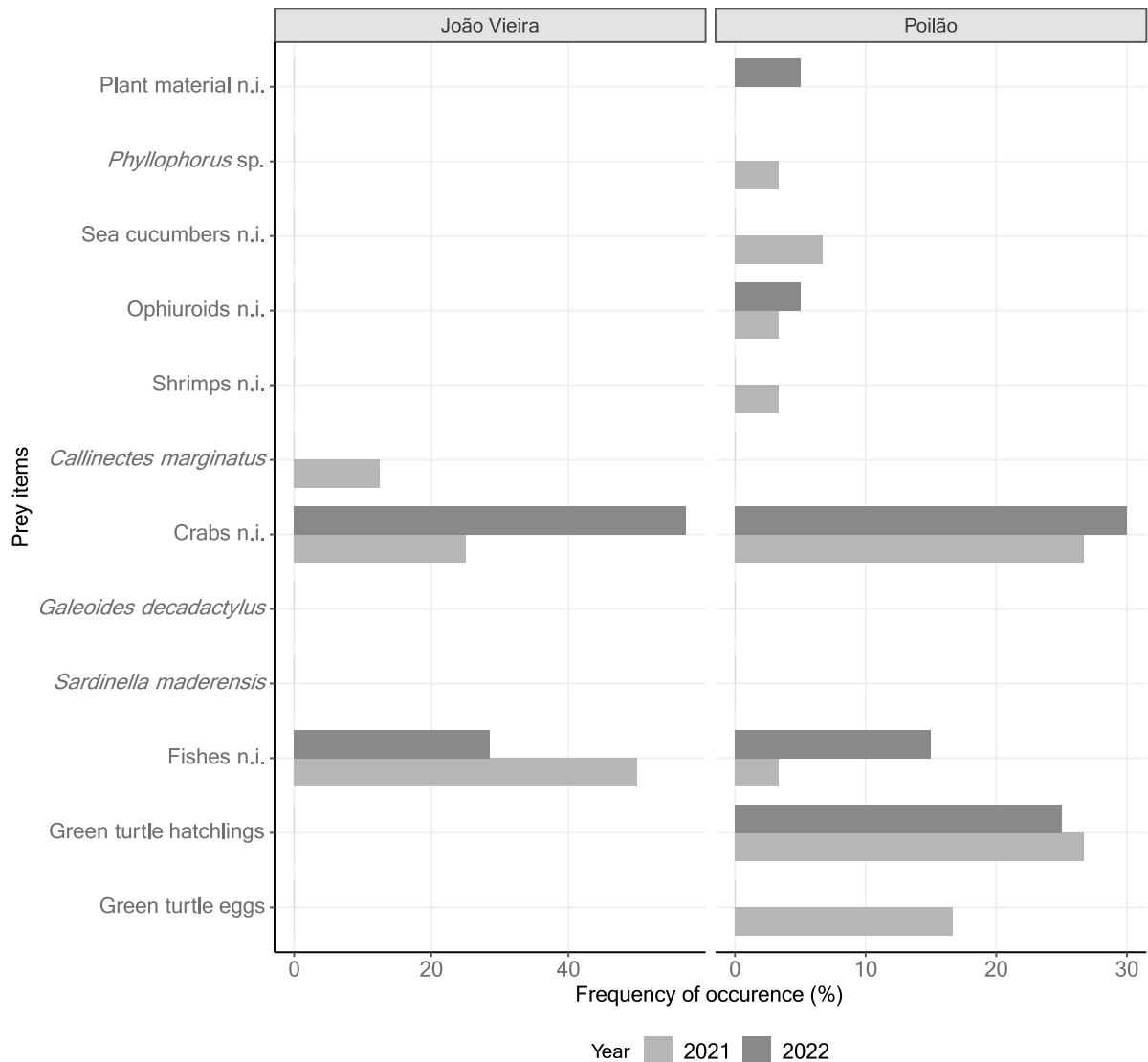


Fig. 8 Frequency of occurrence (%) of prey items in the stomachs of sea catfishes *Carlarius* spp. classified as ‘wide gape’. ‘n.i.’ denotes not identified

Howarth, 1991). However, despite the potential availability of nitrogen from the high density of sea turtle nesting sites, with the exception of coinivines in Poilão in 2021, there was no correlation between $\delta^{15}\text{N}$ and %N in either of the plant species studied. This may happen, for example, if plants responded to the highest nitrogen availability by growing more leaves, flowers, and/or fruits, rather than enriching their leaf nutrient content.

Green Turtle Nutrient Uptake by Crabs

Ghost crabs’ $\delta^{15}\text{N}$ values, and their alignment with the trophic niche of a theoretically exclusive green turtle consumer in Poilão, but not in João Vieira, indicate extensive

feeding on green turtle eggs and/or hatchlings on the first island, where these resources are highly abundant. Our results were expected, since ghost crabs have been documented preying on sea turtle eggs and hatchlings on several sea turtle nesting sites (e.g. Playa Grande, Costa Rica (Santidrián Tomillo et al., 2010), Onslow Beach, North Carolina, USA (Peterson et al., 2013), Boa Vista Island (Marco et al., 2015; Martins et al., 2022), Diego Garcia, Chagos Archipelago, Indian Ocean (Stokes et al., 2024) and on the north-west coast of Australia (Avenant et al., 2024)), including Poilão (Rebello et al., 2012). Additionally, as hypothesized, ghost crabs with larger carapace width had higher $\delta^{15}\text{N}$ values, suggesting their increased potential to capture and subdue larger prey, such as green turtle hatchlings.

On the other hand, the isotopic ratios of African rain-bow crabs on both islands suggest that they do not often rely on green turtle eggs or hatchlings as food sources (although they have been confirmed to predate or scavenge hatchlings, at least occasionally (Catry et al., 2010)). Furthermore, the relatively low $\delta^{15}\text{N}$ signatures, similar to those of green turtle eggs, suggest that they are mainly primary consumers at the JVPMNP.

It should be noted, however, that the isotopic signatures of crabs captured in October and November possibly reflect dietary information since April or June, which falls before the peak of green turtle nesting activity at the JVPMNP. Therefore, the isotopic signal of crabs may partly reflect the assimilation of sea turtle-derived carbon and nitrogen, diluting their effect and yielding a conservative isotopic signature for ghost crabs.

Green Turtle Nutrient Uptake by Fishes

The blood $\delta^{15}\text{N}$ values of sea catfishes differed between João Vieira and Poilão but both matched the isotopic niche of a green turtle consumer. This match with both the low- and high-density sea turtle nesting sites raises the possibility that other prey (untested) may be responsible for this overlap. Thus, sea catfishes perhaps feed on a range of prey at both islands that have isotopic signals similar to those of green turtle eggs and hatchlings. Earlier studies highlighted the importance of crabs and fishes in the diet of generalist predator sea catfishes (Faye et al., 2012; Simier et al., 2021). Similarly, stomach contents of sea catfishes at Poilão showed reliance on crabs and fishes, and the positive correlation between $\delta^{15}\text{N}$ and fork length suggests that larger sea catfishes consumed prey at higher trophic levels. Among that diversity of prey, other fish or crabs may be the providers of isotopic signatures similar to those of sea turtles, hindering the ability to differentiate sea turtle hatchling consumption between both islands. Nevertheless, stomach contents confirmed that sea catfishes at Poilão consume a high quantity of green turtle hatchlings, not observed at João Vieira. Importantly, the availability of turtle resources may be essential for other local predatory fish, for example snappers, as they are known to feed on green turtle hatchlings (Catry et al., 2010).

Crevalle jacks are described as large predators primarily preying on other fishes (Fagade & Olaniyan, 1973; Jefferson et al., 2022; Kwei, 1978), mainly clupeids within the Bijagós Archipelago (Correia et al., 2017). Their $\delta^{13}\text{C}$ values varied by location, suggesting different resource use between islands. Overall, their isotopic signatures did not match those of an exclusive sea turtle predator at either island. However, the overlap between their isotopic signatures and those of an exclusive Madeiran sardinella predator was high on both islands (and higher than of an exclusive

sea turtle predator), suggesting that this prey may be much more frequently consumed than sea turtle hatchlings. This preference for Madeiran sardinella was reported by Correia et al. (2017). Crevalle jacks with larger body sizes, however, had lower $\delta^{15}\text{N}$ values, suggesting that they were feeding at a lower trophic level. This can be due to the consumption of hatchlings by larger specimens. However, generally our stable isotope results suggested that crevalle jacks do not extensively rely on green turtle eggs and hatchlings at the JVPMNP. Furthermore, we only found sporadic consumption of green turtle hatchlings at Poilão based on on-site stomach content observations.

In this study, we used different tissue types (muscle and blood) to represent distinct timeframes of dietary information. Like crabs, the isotopic signatures of fishes are also likely conservative, as they partly reflect the diet consumed prior to the integration of sea turtle isotopes. Crevalle jacks showed a high dietary overlap between short-term (blood) and long-term (muscle) signatures. This may be related to a diet dominated by clupeids (e.g. Madeiran sardinella (Correia et al., 2017)) that are highly abundant year-round in the Bijagós Archipelago. In contrast, sea catfishes exhibited variation in short-term and long-term consumption in 2021, though the causes for this variation remain to be ascertained.

Final Considerations

Our results, along with prior research, indicate that sea turtles play an important role in supplying nitrogen to coastal plants, which may be particularly significant in nutrient-depleted sandy beach environments. Additionally, we observed that turtle eggs and hatchlings make an important contribution to the local food web. These ecological functions should be considered in management strategies. For instance, clutch relocation is a widely practiced and globally prevalent conservation method. However, the ecological importance of sea turtle clutches for coastal ecosystems should be taken into account if relocations become extensive. Green turtles transport nutrients from the ocean to the land at Poilão. While we did not quantify the extent of this shoreward transport along a coast-to-forest transect, our findings demonstrate that turtle-derived nutrients are concentrated near the coastal dune habitat. This is evident from the isotopic signals detected in coin vines and ghost crabs. Although not observed during this study, the assimilation of these nutrients could promote plant growth, contributing to shoreline stabilization (Moss, 2017), and influence the abundance of herbivorous invertebrates (Ebeling et al., 2022; Martínez et al., 2024; Tomasula et al., 2023).

Nitrogen input from green turtle clutches can potentially affect plant community composition (Avolio et al., 2014; Firn et al., 2019; Harpole et al., 2016). Green turtle nesting

at Tortuguero, Costa Rica, has been shown to affect the dominant plant species, with different species prevailing in areas of low and high sea turtle nest densities (Vander Zanden et al., 2012). Plant growth, in turn, can benefit sea turtles. Sea turtles exhibit temperature-dependent sex determination, with high incubation temperatures yielding more females and low incubation temperatures yielding more males (Jensen et al., 2018; Santidrián Tomillo & Spotila, 2020; Tanner et al., 2019). A healthy coinvine population along the dunes of Poilão may help provide cooler incubation conditions, promoting the production of male hatchlings (Patrício et al., 2017). This can be particularly important in the context of future global warming (Patrício et al., 2021).

Green turtles also directly provide nutrients to consumers, influencing community dynamics. The availability of green turtle eggs and hatchlings shapes the foraging behaviour of ghost crabs in the JVPMNP, and potentially sea catfishes, as local reports indicate an increase in sea catfish abundance at Poilão during the green turtle breeding season (IBAP, pers. comm.). A study by Carneiro et al. (2017) found that Palm-nut vultures prey on green turtle eggs or hatchlings at Poilão and João Vieira. The vultures appear to migrate from João Vieira to Poilão during the green turtle breeding season to capitalize on the temporal abundance of green turtle resources (Carneiro et al., 2017). Comparing the relative abundance of predators (e.g. ghost crabs and sea catfishes) between islands and assessing the level of predation would provide valuable insights into hatchling survival, supporting conservation and management efforts at Poilão.

The number of green turtle nests in Poilão has increased in the last 20 years (Barbosa et al., 2018; Broderick & Patrício, 2019), with an average annual estimate of 32,608 nests over a recent 3-year period (Raposo et al., 2024). As sea turtles introduce substantial nutrients to sandy beaches (Bouchard & Bjorndal, 2000), these nutrients may have further effects throughout the sandy beach ecosystem. On Poilão Island, the $\delta^{15}\text{N}$ values of green turtle eggs and hatchlings may have a limited geographic range, but their ecological impact likely extends beyond this spatial range. Nutrients derived from turtle eggs and hatchlings probably not only contribute to the isotopic signature of their predators, such as ghost crabs, but also to increased biomass production and progeny among those predators. This, in turn, creates a secondary effect, as the progeny of predators—who may exhibit diluted or absent $\delta^{15}\text{N}$ turtle signatures—distributes nutrients more broadly across the ecosystem. Such secondary nutrient redistribution supports increased food availability and enriches the ecosystem beyond the spatial extent directly indicated by the $\delta^{15}\text{N}$ values of green turtle eggs and hatchlings. On the other hand, nutrient redistribution by sea turtles should be increasingly considered. By supporting

a variety of organisms through nutrient redistribution, as observed in seabirds (Hentati-Sundberg et al., 2020), sea turtles help maintain high biodiversity levels. Therefore, their conservation contributes to the thriving of other species in the ecosystem.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-025-01500-9>.

Acknowledgements The Instituto da Biodiversidade e das Áreas Protegidas (IBAP), Dr. Alfredo Simão da Silva of Guinea-Bissau granted research permits and logistical assistance. This research was conducted following all applicable guidelines for the care and use of animals approved by the IBAP and meets the legal requirements of the country it was carried out. The protocols were approved by Órgão Responsável Pelo Bem-estar Animal of Ispa—Instituto Universitário (ORBEA-Ispa), which aims to ensure the compliance of ethical standards and animal welfare rules. We thank the members of the Bijagós community, the IBAP technicians, and rangers for the support during fieldwork. Our gratitude extends to Catarina Monteiro and Seco Leão for their invaluable collaboration and contribution during sampling. The stable isotope analyses were performed on the CRIE (Center for Resources in Stable Isotopes) of the Center for Ecology, Evolution, and Environmental Change (ce3c) of the Faculty of Sciences of the University of Lisbon (FCUL).

Author Contribution CR, PC, ARP, and RR conceived and designed the study. AR facilitated fieldwork logistics and research permits. CR, CB, and AC conducted the fieldwork. CR led the data analysis and wrote the first draft of the article. ARP, PC, and RR commented previous versions of the article.

Funding Open access funding provided by FCTIFCCN (b-on). This work was funded by the MAVA Foundation through the project ‘Consolidation of sea turtle conservation at the Bijagós Archipelago, Guinea-Bissau’; the Regional Partnership for Coastal and Marine Conservation (PRCM), through the project ‘Survie des Tortues Marines’; the ‘La Caixa’ Foundation (ID 100010434) through a fellowship awarded to ARP (LCF/BQ/PR20/11770003); and the Fundação para a Ciência e a Tecnologia, Portugal, through a grant (UIDB/04292/2020 and UIDP/04292/2020) awarded to MARE, the project LA/P/0069/2020 granted to the Associate Laboratory ARNET, the grant UIDB/00329/2020 with <https://doi.org/10.54499/UIDB/00329/2020> awarded to Centro de Ecologia, Evolução e Alterações Ambientais (ce3c); and a PhD grant (2020.08549.BD) awarded to CR.

Data Availability All data analyzed during the current study will be made available upon reasonable request submitted to the corresponding author.

Declarations

Ethics Approval The Instituto da Biodiversidade e das Áreas Protegidas (IBAP), Dr. Alfredo Simão da Silva of Guinea-Bissau provided research permits. The research protocols were conducted in accordance with all the applicable guidelines for the care and use of animals for scientific purposes approved by the IBAP, as well as the legal requirements of the country in which they were carried out. The protocols were approved by Órgão Responsável Pelo Bem-estar Animal of Ispa—Instituto Universitário (ORBEA-Ispa), which aims to ensure the compliance of ethical standards and animal welfare rules.

Conflict of Interest The authors declare no competing interests.

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