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Species-specific ontogenetic isotopic niche dynamics in Amazon River turtles

Gabriel Costa Cardozo-Ferreira
gabrielccf@gmail.com

Ecology and Conservation in the Anthropocene Lab
Giullia Esther Magalhães
Ecology and Conservation in the Anthropocene Lab
Letycia M. M. Acioli
Ecology and Conservation in the Anthropocene Lab
Larissa J. Benevides
Ecology and Conservation in the Anthropocene Lab
Camila Duarte Ritter
Instituto Juruá
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Programa Pé de Pincha – Universidade Federal do Amazonas
Hugo C. M. Costa
Instituto Juruá
João Vitor Campos-Silva
Instituto Juruá
Robson Guimarães dos Santos
Ecology and Conservation in the Anthropocene Lab

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Abstract

The partitioning of the available resources is a key to species' coexistence. Ontogenetic changes in resource use can alter ecological roles within species, yet such trajectories remain poorly resolved for Amazonian freshwater turtles. We used stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) to evaluate ontogenetic and spatial variation in the isotopic niches of *Podocnemis expansa* and *P. sextuberculata* in floodplain lakes of the Middle Juruá River, Brazilian Amazon. *P. expansa* showed substantial isotopic niche overlap among ontogenetic classes (57.1–70.8%) and little evidence of size-related change in $\delta^{13}C$ or $\delta^{15}N$. In contrast, *P. sextuberculata* showed lower overlap between sampled age classes (49.1%) and a size-related shift in $\delta^{13}C$, indicating stronger ontogenetic differentiation in assimilated resource pathways. *P. sextuberculata* also exhibited higher $\delta^{15}N$ values than *P. expansa*. These results indicate that trophic ecology in *Podocnemis* emerges from the interaction among species identity, ontogenetic stage, and the spatial and temporal structure of floodplain resource landscapes. Moreover, the conservation of Amazonian turtles is centred on ontogenetic resource landscapes with its unique habitats, hydrological and ecological processes and resource pathways that support individuals as they grow.

Introduction

Ecological niches are not necessarily fixed throughout an organism's lifetime. As individuals grow, changes in body size, morphology, energetic demands, habitat use, and foraging capacity can alter the resources they exploit and the ecological roles they perform (Zhao et al. 2014; Nakazawa 2015). Ontogenetic shifts in resource use can therefore generate substantial intraspecific niche variation, sometimes reducing overlap among life stages and modifying interactions within ecological communities. Among closely related or ecologically similar species, such variation is especially relevant because the degree of niche overlap may depend not only on species identity but also on developmental stage (Hutchinson 1961; Mcgill et al. 2006; Weber et al. 2023).

Ontogenetic dietary change is particularly common in herbivorous vertebrates. Early life stages may rely more heavily on animal-derived or protein-rich resources, whereas increasing digestive capacity and the ability to mechanically process plant material can support a greater reliance on herbivory later in development (Day et al. 2011; German et al. 2014). Freshwater turtles frequently show size- and age-related changes in diet and habitat use, although the timing and magnitude of these shifts can vary among species and populations (Ramirez et al. 2015; Eisemberg et al. 2017; Tomaszewicz et al. 2017). Ontogenetic transitions may also be facultative: adults of predominantly herbivorous species can consume animal matter opportunistically, and individuals within the same population may follow different resource-use trajectories when environmental conditions or resource availability vary (Clark and Gibbons 1969; Ramirez et al. 2015).

Stable isotope analysis (SIA) provides a complementary way to investigate these patterns because it reflects assimilated resources over time rather than only recently ingested food. Carbon and nitrogen

isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) has been used to describe and explore niche relationships within communities in different environments and/or across ontogenetic stages (Newsome et al. 2007; Andrades et al. 2019a, b; Cardozo-Ferreira et al. 2026). In chelonians, SIA has helped reveal trophic relationships that may not be apparent from stomach-content analyses alone, while also allowing comparisons of niche width and overlap among groups (McClellan et al. 2010; Medeiros et al. 2015). Isotopic niches should nevertheless be interpreted as proxies for assimilated resource pathways, because similar isotope values can arise from different diets and because local isotopic baselines (e.g. primary producers' signatures) can influence consumer signatures (Newsome et al. 2007; Vander Zanden et al. 2013).

Amazonian river turtles of the genus *Podocnemis* provide a useful system in which to examine ontogenetic variation in resource use. These species are widespread in the Amazon basin and generally consume large amounts of fruits, seeds, and other plant material, while animal matter can also contribute to their diets and some species have been described as omnivorous (Teran et al. 1995; Rueda-Almonacid et al. 2007; Cunha et al. 2020; Hinderaker 2021). Previous studies indicate that diet composition can vary with body size, season, habitat, and species identity, including ontogenetic changes in the relative importance of seeds and other food items (Eisemberg et al. 2017; Cunha et al. 2020). However, comparatively little is known about how these dietary changes translate into assimilated isotopic niches across development in freshwater turtles, particularly when closely related species occur within the same floodplain landscape (Lara et al. 2012; Hinderaker 2021).

This question is especially relevant in Amazonian floodplains, where the annual flood pulse continually reorganizes habitats and resource availability. Seasonal inundation connects rivers, oxbow lakes, and flooded forests and influences the production and availability of fruits, seeds, aquatic vegetation, and other potential food resources (Hawes and Peres 2016; Hinderaker 2021). As water levels recede, floodplain lakes become increasingly isolated until they reconnect during the following flood season. Consequently, isotopic niches may reflect both ontogenetic differences in resource use and spatial variation in basal resources among habitats. Evaluating these two sources of variation together is important for distinguishing species- and life-stage-specific trophic patterns from local environmental effects. Beyond their ecological significance, understanding resource use in *Podocnemis* is important because these turtles are harvested for food and are the focus of community-based management initiatives in the region (Oliveira et al. 2024). Characterizing trophic niche variation can therefore help inform management strategies that account for differences among species and life stages.

Here, we evaluated ontogenetic and spatial variation in the isotopic niches of two Amazonian River turtles, *Podocnemis expansa* and *P. sextuberculata*, in the Middle Juruá River floodplain. First, we tested whether isotopic signatures and niche overlap changed across ontogenetic stages and whether these trajectories differed between species. Based on documented size-related dietary changes in Amazonian freshwater turtles, we expected isotopic niche structure to vary with ontogeny, but not necessarily in the same way in both species. Second, using *P. expansa*, the species represented in both sampled oxbow lakes, we tested whether isotopic niche structure differed between lakes. Because these floodplain

habitats are seasonally connected, we expected substantial overlap in consumer isotopic niches, while explicitly evaluating whether local primary-producers isotope signatures differed between sites. Together, these analyses assess whether ontogenetic trophic trajectories are species-specific and whether they remain consistent across seasonally connected floodplain habitats, providing a basis for understanding life-stage-specific resource use in two ecologically and socially important Amazonian turtles. By examining trophic similarity across species and life stages, our study also provides insights into potential functional overlap between these ecologically and socially important turtles.

Materials and methods

Study area

The study was conducted in the Middle Juruá River region, Amazonas, Brazil, near the municipality of Carauari, (Fig. 1). The landscape comprises a mosaic of seasonally flooded forests, unflooded *terra firme* forests, river channels, and floodplain lakes embedded within a broader system of Indigenous lands and sustainable-use protected areas, including the Middle Juruá Extractive Reserve and the Uacari Sustainable Development Reserve. Regional hydrology is strongly seasonal, with high-water conditions generally occurring during the first half of the year and lower water levels from approximately August to November (Hawes and Peres 2016). As the Juruá River rises, floodplain forests and lakes become hydrologically connected; during the low-water period, many oxbow lakes become partially or completely isolated from the main channel. This seasonal connectivity structures the availability and movement of aquatic and terrestrial resources used by freshwater turtles.

Studied species

The Amazonian giant river turtle, *Podocnemis expansa*, is a widespread species, found across the Amazon, Essequibo, and Orinoco River basins (Pearse et al. 2006). Known to have a large range, *P. expansa* can move up to 65–121 km and up to 405 km downstream from nesting beaches (Hinderaker 2021) and reaches sexual maturity, on average, at 10–12 years of age, with a weight of 10–14 kg and a carapace length of 45–51 cm in females (Mogollones et al. 2010; Andrade 2012). Lifespan is typically estimated to be 50–80 years, with adult size reached after 17–25 years (Chinsamy and Valenzuela 2008; Mogollones et al. 2010; Andrade 2012). As a broad forager, *P. expansa* diet includes mainly fruits and seeds but also stems, leaves, various insects, crustaceans, sponges, fish, and even small reptiles (Teran et al. 1995; Garcez et al. 2020; Castro et al. 2022). After feeding in flooded forests, it returns to the main rivers to nest (Hinderaker 2021). The six-tuberculed Amazonian River turtle *Podocnemis sextuberculata* is one of the smaller species within its genus and occurs in different water types of the Amazon River Basin (Fachín-Terán et al. 2003). It occurs with higher abundance in white water rivers and the lower stretch of clear water tributaries, such as Tapajós, Xingu, and Trombetas (up to the middle Trombetas), and rarely in black water rivers as the Andirá and Negro rivers (Rueda-Almonacid et al. 2007; Ferrara et al. 2017; Andrade et al. 2022). The species migrates between feeding and nesting areas, with records of

a linear home range between 16.5 and 44.5 km (Fachín-Terán et al. 2003) and movements of 60 km using waterways in the Trombetas River basin, and average displacement of 21.7 ± 16.6 km (8 to 45 km) on the Juruá river (Andrade 2012). Although some diet variation is expected according to their location (Eisemberg et al. 2017), *P. sextuberculata* is a known herbivore that ingests large amounts of Poaceae, fruits and seeds, with the latter reducing in importance for its diet as the species grows (Garcez et al. 2020). Nonetheless, animal matter has already been reported as an important item in its diet (Teran et al. 1995; Garcez et al. 2020; Oliveira et al. 2020). Based on such divergent results regarding its diet composition, *P. sextuberculata* might be classified as omnivorous (Rueda-Almonacid et al. 2007), which is supported by the morphology of the gastrointestinal tract (Magalhães et al. 2014).

Extinction risk assessment by the Chico Mendes Institute for Biodiversity Conservation (ICMBio)/Ministry of Environment (MMA) classifies *P. expansa* as 'Least Concern' (LC) (Ferrara et al. 2026), the six-tuberculed Amazonian River turtle *P. sextuberculata* as 'Endangered' (EN) (Silva et al. 2026).

Samples collection

Samplings were conducted along the Middle Juruá River in three oxbow lakes: 'Jiburi', 'Marimari', and Marari Lake (hereafter Jiburi, Marimari, and Marari, respectively), near Carauari during the period of receding river levels in June 2025. Captured turtles were temporarily maintained in a protected area on the boat deck during processing and released after sampling. Individuals of *Podocnemis expansa* and *P. sextuberculata* were measured (curved carapace length - mm) sexed when possible and weighted to the nearest g possible using a 50kg capacity digital scale. Tissue samples for SIA were extracted from the interdigital membrane of each turtle and frozen until laboratory processing. We used the number of visible annuli on the left pectoral plate was used to estimate age and characterize turtles' life stage (Spencer 2002). Because annulus counts can become less reliable with increasing age and wear, these values are treated throughout as estimated age rather than exact chronological age (Spencer 2002). Individuals were sampled during the activities of the Pé-de-Pincha Program, a community-based turtle conservation and management initiative coordinated by the Federal University of Amazonas (UFAM). Primary producers known to contribute to the diet of Amazonian River turtles were collected alongside turtle specimens to estimate their trophic position.

Stable isotope analysis

For stable isotope analysis (SIA) we selected individuals distributed into three ontogenetic classes (estimated ages 3–6, 7–12, and 13–19 years). In the laboratory, tissue samples were oven-dried at 60°C for 24 hours, ground to a fine powder for isotopic analyses. SIA were performed with an Isotope Ratio Mass Spectrometer (IRMS, ThermoFisher) coupled to an elemental analyser (EA Flash 2000 Delta V Advantage), at the *Centro Integrado de Análises* at the Federal University of Rio Grande (CIA-FURG). The analytical precision was ± 0.1‰ for $\delta^{13}C$ and ± 0.2‰ for $\delta^{15}N$ (based on triplicate samples taken every

fifth sample). Certified standards (Protein OAS/114859; elemental microanalysis) were used to determine the accuracy of the elemental and isotopic compositions. The mean recovery values were always ≥ 95% of the certified value. Stable isotope ratios are expressed in delta (δ) notation as per mil (‰) deviations from the international calibration standards.

Additionally, to estimate the relationship between isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) and growth, we ran four different linear models for each $\delta^{13}C$ and $\delta^{15}N$. The models were i) *age model*: $\delta^{13}C$ / $\delta^{15}N$ ~ age*spp; ii) *size model*: $\delta^{13}C$ / $\delta^{15}N$ ~ shell length * spp; iii) *both model*: $\delta^{13}C$ / $\delta^{15}N$ ~ age + shell length + spp; and *full model*: $\delta^{13}C$ / $\delta^{15}N$ ~ (age + shell length) * spp.

Data analysis

We first fitted a von Bertalanffy growth function (VBGF) to *P. expansa* to describe the relationship between estimated age and body size using the FSA package v.0.10.1 (Ogle et al. 2021). We did not fit a VBGF for *P. sextuberculata* because no individuals younger than seven estimated years were sampled and the total sample size was small. To check for differences in the isotopic signatures among species and ontogenetic classes (hypothesis 1) and between lakes (hypothesis 2), levels of $\delta^{13}C$, $\delta^{15}N$ and C:N ratio were compared separately among species using Kruskal-Wallis's rank sum test, followed by Dunn's multiple comparisons test when feasible using base R functions. Ontogenetic classes were used to visualize changes in isotopic niche structure, whereas shell length was retained as a continuous proxy of ontogenetic development in regression analyses. Multivariate Bayesian ellipse-based model which measures the isotopic niche through the calculated area of the ellipse (samples size corrected standard ellipse area – SEAc; 95% C.I., SIBER package v.2.1.10) (Jackson et al. 2011) was used to evaluate the isotopic composition of sampled turtles. For testing the hypothesis 2, we selected only *P. expansa* due to its representativity between the lakes regarding samples size. For both hypotheses we calculated niche overlap, which is calculated as a proportion of the non-overlapping area of the given two ellipses, using SIBER package (Jackson et al. 2011). Spatial comparisons were restricted to *P. expansa* because it was the only species represented adequately in both lakes.

To evaluate continuous ontogenetic trends, we fitted four candidate linear models separately for $\delta^{13}C$ and $\delta^{15}N$ using the base R lm() function: (1) isotope ~ estimated age × species; (2) isotope ~ shell length × species; (3) isotope ~ estimated age + shell length + species; and (4) isotope ~ (estimated age + shell length) × species. Model selection was based Akaike Information Criterion (AIC) calculated with the 'performance' package v.0.17.1 (Lüdecke et al. 2021). Species-specific slopes and their 95% confidence intervals, including for the reference-level species, were estimated using the avg_slopes() function in the 'marginaleffects' package v.0.32.0 (Arel-Bundock et al. 2024). Effects were considered supported when the 95% confidence interval did not overlap zero. We also estimated trophic position (TP) using the *one-baseline model* function from the 'tRophicPosition' package v.0.8.0 (Quezada-Romegialli et al. 2018). Because species-specific trophic discrimination factors are unavailable for *Podocnemis* skin, we used published skin discrimination factors for the green turtle *Chelonia mydas* (Tomaszewicz et al. 2017). The

use of appropriate TDFs allows a more accurate estimation of TPs (Skinner et al. 2022). TP is a link between $\delta^{15}N$ enrichment per trophic level and the trophic position of the primary producers. All analyses were conducted in R environment v.4.6.1 (R Core Team 2026).

Results

A total of 137 individuals of Amazonian River turtles were sampled (Table 1). *Podocnemis expansa* was substantially larger than *P. sextuberculata*, with a mean shell length (SL) of 449.3 ± 153.7 mm compared with 201.3 ± 28.2 mm for *P. sextuberculata.* Mean body mass also differed between species, averaging 13.1 ± 8.67 in *P. expansa* and 1.5 ± 2.1 kg in *P. sextuberculata*.

For the von Bertalanffy growth model, only females of *P. expansa* were selected once size and growth are known to vary for this species between sexes. The model converged successfully with an asymptotic length ($L\infty$) of 655.8mm (Figure S1), consistent with the maximum body size for *P. expansa*. The estimated growth coefficient ($K = 0.174$ year^{-1}) suggests a relatively slow approach to asymptotic size, as expected for long-lived chelonians. The estimated t_0 value (1.65 years) should, however, be interpreted cautiously because individuals younger than three estimated years were poorly represented, parameters describing the earliest portion of the growth trajectory should be interpreted cautiously. The positive relationship between estimated age and shell length nevertheless supported the use of body size as a continuous proxy of ontogenetic development in the isotope models.

Table 1
Sampled of both Amazonian River turtles *Podocnemis expansa* and *Podocnemis sextuberculata*. Acronyms: N – sample size, Min – minimum, Max – maximum, SL – shell length (mm) and W – weight (kg).

Species	N	Mean SL	Min SL	Max SL	Mean W	Min W	Max W
Podocnemis expansa							
3–6	33	227.1	137	450	1.932	0.358	10.58
7–12	53	501.1	290	650	14.700	3.064	45.32
13–19	36	576.6	510	647	20.878	15.000	28.46
Podocnemis sextuberculata							
7–12	10	194.5	180	239	1.637	0.650	8.60
13–19	5	214.8	185	277	1.317	0.677	2.95

How do isotopic niches vary across ontogeny?

To test for the ontogenetic changes in the isotopic niches across both species, 41 individuals were selected for isotopic analysis: 26 *Podocnemis expansa* and 15 *P. sextuberculata* (Table 2). The two

species differed in nitrogen signatures ($\delta^{15}N$; Kruskal-Wallis X^2 = 22.18, df = 1, p-value < 0.001) but not for carbon and ($\delta^{13}C$; Kruskal-Wallis X^2 = 2.136, df = 1, p-value = 0.144). Mean isotopic signatures of *P. expansa* were − 26.8 ± 0.3‰ $\delta^{13}C$ and 7.5 ± 0.8‰ $\delta^{15}N$, while for *P. sextuberculata* the signatures were − 27.2 ± 1.2‰ $\delta^{13}C$ and 9.5 ± 0.8‰ $\delta^{15}N$. As well as the $\delta^{15}N$ signatures, the trophic position (TP) of *P. sextuberculata* was higher than the that of *P. expansa* (1.346 vs 1.301, respectively). Among ontogenetic classes, only difference for $\delta^{13}C$ between the ontogenetic classes of *P. sextuberculata* was found (7–12 vs. 13–19; Kruskal-Wallis X^2 = 4.335, df = 1, p-value = 0.037). TP estimates were similar among age classes for *P. expansa* (3–6: 1.057; 7–12: 1.024; 13–19: 1.032; Figure S2).

Table 2

Sample size (N), mean shell length (SL), $\delta^{13}C$ and $\delta^{15}N$ (± standard deviation) for the specimens selected for stable isotope analysis comparing ontogenetic stages (age classes: 3–6, 7–12 and 13–19 years old) of both Amazonian River turtles *Podocnemis expansa* and *Podocnemis sextuberculata*.

Species	**N**	**Mean SL**	**$\delta^{15}N$**	**$\delta^{13}C$**
Podocnemis expansa				
3–6	8	224.0 ± 32.1	7.30 ± 0.81	-26.85 ± 0.25
7–12	12	409.6 ± 92.2	7.52 ± 0.78	-26.81 ± 0.31
13–19	6	576.8 ± 25.3	7.81 ± 0.63	-26.88 ± 0.31
Podocnemis sextuberculata				
7–12	10	194.5 ± 18.7	9.44 ± 0.80	-26.79 ± 1.18
13–19	5	214.8 ± 35.4	9.71 ± 0.74	-28.06 ± 0.76

Descriptive carbon and nitrogen ranges (CR and NR, respectively) varied among species and age classes (Table 3). In *P. expansa*, CR was largest in the intermediate class (7 to 12 years old), whereas NR declined across classes. For *P. sextuberculata* both CR and NR decreased from 7–12 to 13–19 classes. Because these range metrics are sensitive to sample size, we interpret them as descriptive complements to the ellipse-based niche estimates rather than as primary tests of niche breadth.

Table 3
Range of carbon (CR) and nitrogen (NR) signatures variation among species and age classes for *Podocnemis expansa* and *P. sextuberculata*.

Species	Age classes		
	3–6	**7–12**	**13–19**
Podocnemis expansa			
CR	0.688	1.25	0.885
NR	2.78	2.63	2.14
Podocnemis sextuberculata			
CR	–	3.92	1.90
NR	–	2.31	1.79

Ellipse-based isotopic niche differed in its ontogenetic pattern between species (Figs. 2 and S3). In *P. expansa*, SEAc increased slightly from the youngest to the oldest sampled class (Table S1) and pairwise overlap was consistently high: 57.1% between the 3–6 and 7–12 classes, 60.4% between the 3–6 and 13–19 classes, and 70.8% between the 7–12 and 13–19 classes. In *P. sextuberculata*, the older class had a smaller SEAc than the 7–12 class and overlap between the two sampled classes was 49.1%. Thus, *P. sextuberculata* showed greater ontogenetic differentiation in isotopic space than *P. expansa*, although inference is constrained by the smaller sample size and the absence of the youngest class for *P. sextuberculata*.

Model comparison identified shell length and species as the most informative predictors of isotopic variation (Table S3). For $\delta^{13}C$, the best-supported model included a shell length × species interaction ($t = -3.473$, $p = 0.0013$), indicating that the relationship between body size and $\delta^{13}C$ differed between species (Fig. 3). The shell-length slope for the reference species *P. expansa* did not differ from zero ($t = 0.361$, $p = 0.720$), whereas the species-specific relationship for *P. sextuberculata* differed significantly from that of *P. expansa* ($t = 3.115$, $p = 0.0035$). The overall model explained a modest proportion of variation (adjusted $R^2 = 0.228$; $F_{3,37} = 4.94$, $p = 0.0055$). For $\delta^{15}N$, species identity was strongly supported ($t = 3.192$, $p = 0.0029$), whereas shell length ($t = 1.144$, $p = 0.260$) and the shell length × species interaction ($t = 1.837$, $p = 0.074$) were not. The $\delta^{15}N$ model explained 61.5% of the variance (adjusted $R^2 = 0.615$; $F_{3,37} = 22.31$, $p < 0.001$), largely reflecting the difference between species.

Do isotopic niches differ between lakes?

Spatial comparisons were restricted to *P. expansa* (n = 19), raw consumer isotope values did not differ between Jiburi and Marimari for $\delta^{15}N$ (Kruskal-Wallis $\chi^2 = 0.267$, df = 1, $p = 0.870$) or $\delta^{13}C$ ($\chi^2 = 0.960$, df = 1, $p = 0.327$). Mean values at Jiburi were − 26.9 ± 0.37‰ $\delta^{13}C$ and 7.69 ± 0.98‰ $\delta^{15}N$, compared with −

26.7 ± 0.29‰ $\delta^{13}C$ and 7.66 ± 0.72‰ $\delta^{15}N$ at Marimari. Relative trophic-position estimates were similarly close (1.036 at Jiburi and 1.019 at Marimari).

The *P. expansa* ellipse was larger at Jiburi (SEAc = 1.194‰²) than at Marimari (SEAc = 0.732‰²; Figs. 4 and S4). Carbon and nitrogen ranges were also somewhat wider at Jiburi (CR = 1.25‰; NR = 2.63‰) than at Marimari (CR = 0.86‰; NR = 2.34‰). The two ellipses overlapped by 55%. The posterior probability that the Jiburi ellipse was larger than the Marimari ellipse was 0.872, indicating a tendency toward greater isotopic niche width at Jiburi but limited evidence for a strong difference between the two sampled lakes.

In contrast to the similar raw isotope values of *P. expansa*, primary producers strongly differed between lakes for $\delta^{15}N$ ($\delta^{15}N$; Kruskal-Wallis $X^2 = 21.774$, df = 1, *p*-value < 0.001), but not for carbon ($\delta^{13}C$; Kruskal-Wallis $X^2 = 0.228$, df = 1, *p*-value = 0.633). Mean $\delta^{15}N$ signature of primary producers from Jiburi was 6.57 ± 1.52‰ and 11.4 ± 1.49‰ from Marimari, while $\delta^{13}C$ was − 25.1 ± 7.94‰ at Jiburi and − 25.1 ± 8.81‰ at Marimari (Fig. 4). C3 Poaceae were the most $\delta^{13}C$-enriched sources in both lakes, while the other primary producers exhibited the typical C4 signatures, ~ 30.0‰. The pronounced $\delta^{15}N$ baseline difference indicates that direct spatial comparisons of consumer $\delta^{15}N$ should be interpreted cautiously unless local baseline variation is explicitly accounted for.

Discussion

Our study shows that ontogenetic trophic change in Amazonian freshwater turtles is not a uniform consequence of growth, but a species-specific process embedded within a spatially heterogeneous floodplain. *Podocnemis expansa* maintained a broadly overlapping isotopic niche across the sampled ontogenetic range, whereas *P. sextuberculata* showed stronger differentiation with body size, particularly along the carbon-isotope axis. The two species also differed consistently in $\delta^{15}N$, indicating distinct isotopic positions despite occupying the same river-floodplain system. At the spatial scale, *P. expansa* showed substantial isotopic overlap between the two sampled oxbow lakes even though local primary producers differed markedly in $\delta^{15}N$. Together, these findings indicate that trophic ecology in *Podocnemis* emerges from the interaction among species identity, ontogenetic stage, and the spatial and temporal structure of floodplain resource landscapes.

Species-specific ontogenetic trophic trajectories

Ontogenetic shifts in resource use are commonly associated with changes in body size, morphology, energetic requirements, digestive capacity, mobility, and habitat access (Zhao et al. 2014; Nakazawa 2015). In predominantly herbivorous vertebrates, early life stages may rely relatively more on protein-rich or easily digestible resources, whereas increasing digestive capacity can support greater use of plant material later in development (Day et al. 2011; German et al. 2014). Freshwater turtles likewise show size- and age-related variation in diet, although the timing and magnitude of these changes differ among

species and populations (Ramirez et al. 2015; Eisemberg et al. 2017; Tomaszewicz et al. 2017). Our results reinforce this variability by showing that two congeners exposed to the same floodplain environment can follow contrasting ontogenetic isotopic trajectories.

For *P. expansa*, the substantial overlap among ontogenetic classes and the absence of detectable size-related changes in $\delta^{13}C$ or $\delta^{15}N$ indicate relative stability in assimilated resource pathways from juvenile to young-adult stages. This should not be interpreted as evidence of an invariant diet. Stable isotopes integrate assimilated resources over time and may remain similar even when particular food items change, provided those resources derive from isotopically comparable basal pathways (Newsome et al. 2007). Previous dietary studies describe *P. expansa* as predominantly herbivorous but able to consume a broad range of fruits, seeds, leaves, invertebrates, and occasional vertebrate prey (Teran et al. 1995; Cunha et al. 2020). Dietary turnover can therefore occur within a relatively stable isotopic framework. This distinction is important because stomach-content and stable-isotope approaches describe complementary dimensions of trophic ecology: the former is a snapshot of the recently ingested items, whereas the latter integrates assimilated resource pathways over longer periods (Newsome et al. 2007; McClellan et al. 2010; Medeiros et al. 2015). Because our sample did not include old adults and only partially represented the earliest life stages, a later or earlier trophic shift cannot be excluded, and the inference should remain restricted to the ontogenetic range sampled here (Chinsamy and Valenzuela 2008).

By contrast, *P. sextuberculata* showed lower isotopic niche overlap between the two sampled classes and a size-related change in $\delta^{13}C$ without a comparable shift in $\delta^{15}N$. This pattern is consistent with previous evidence of ontogenetic dietary variation in the species, including changes in the relative importance of seeds and other plant resources as individuals grow (Fachín-Terán 1999; Eisemberg et al. 2017; Dias et al. 2026). The stronger response in $\delta^{13}C$ than in $\delta^{15}N$ suggests that ontogenetic change may involve a shift among basal carbon pathways or habitat-linked resource pools rather than a major change in trophic position. Growth could alter access to particular feeding habitats, substrates, or resource types without necessarily moving individuals upward or downward in the food web. This interpretation is also consistent with evidence of dietary flexibility in *P. sextuberculata* and with morphological studies indicating variation in digestive traits within Podocnemididae (Teran et al. 1995; Rueda-Almonacid et al. 2007; Magalhães et al. 2014). However, because only two ontogenetic classes were represented and the older class was small, the result is best interpreted as stronger ontogenetic differentiation in isotopic niche rather than as evidence of complete trophic partitioning.

Interspecific differentiation in assimilated resource use

The two species also occupied distinct positions in isotopic space, with *P. sextuberculata* consistently showing higher $\delta^{15}N$ values than *P. expansa*. Previous dietary studies provide a plausible ecological context for this contrast, as *P. sextuberculata* can consume proportionally more animal material than some congeners, whereas *P. expansa* often relies heavily on fruits, seeds, and other plant resources (Teran et al. 1995; Cunha et al. 2020). Previous comparisons among *Podocnemis* species have also

shown substantial but incomplete dietary and isotopic overlaps, indicating that closely related turtles can share broad resource categories while maintaining distinct trophic positions or resource-use patterns (Lara et al. 2012; Cunha et al. 2020). Nevertheless, $\delta^{15}N$ differences cannot be translated directly into fixed trophic-level differences because consumer signatures also depend on baseline variation, physiology, habitat use, and tissue-specific isotope discrimination (Newsome et al. 2007; Skinner et al. 2022). This caution is particularly important here because trophic-position estimates relied on discrimination factors derived from green sea turtle *Chelonia mydas* rather than *Podocnemis* (Tomaszewicz et al. 2017). The most robust inference is therefore that the two species differ in assimilated resource pathways and that these pathways respond differently to ontogeny. Such differentiation may contribute to reduced overlap among species and life stages, but our data does not directly test competition or coexistence mechanisms.

Spatial isotopic variation across a dynamic floodplain

The spatial comparison adds a complementary dimension to these ontogenetic and interspecific patterns. *Podocnemis expansa* showed similar raw $\delta^{13}C$ and $\delta^{15}N$ values and substantial isotopic niche overlap between Jiburi and Marimari, yet primary producers differed by almost 5‰ in mean $\delta^{15}N$. This mismatch demonstrates that apparently similar consumer niches can occur against strongly heterogeneous isotopic baselines. Because consumer isotope values inherit variation from basal resources, spatial comparisons cannot be interpreted independently of the isotopic environment in which consumers are embedded (Newsome et al. 2007). Several mechanisms could explain this apparent decoupling. The sampled producers may not fully represent the resources assimilated by turtles, since *Podocnemis* can be selective among plant taxa even within broad dietary categories (Teran et al. 1995; Cunha et al. 2020). In addition, turtle tissues integrate diet over longer temporal windows than many primary producers, so consumer signatures may retain information acquired before local baselines diverged. Finally, *P. expansa* is capable of substantial movements among feeding and nesting habitats (Mogollones et al. 2010; Hinderaker 2021), meaning that the isotopic composition of its tissues may integrate resources across a spatial domain larger than the lake in which an individual was captured.

These mechanisms are especially plausible in the Middle Juruá, where oxbow lakes reconnect with river channels and seasonally flooded forests during high water and become progressively isolated as water levels recede (Hinderaker 2021; Jardine et al. 2025). Seasonal hydrological connectivity may therefore buffer local trophic divergence by allowing turtles to access shared resource pools or by preserving isotopic signals acquired before isolation. Although our two-lake comparison cannot test this mechanism directly, it generates a clear hypothesis: isotopic divergence among turtle populations should increase with the duration or strength of hydrological isolation, particularly where basal isotope values also diverge. The pronounced difference in producer $\delta^{15}N$ should therefore be viewed not only as a methodological complication, but also as evidence that apparently similar floodplain lakes can differ substantially in the isotopic structure of their basal food webs. Testing this hypothesis will require

replicated sampling across a broader gradient of connectivity and repeated baseline measurements through the hydrological cycle.

Ecological and conservation implications

The contrasting ontogenetic trajectories observed here have direct implications for understanding and managing Amazonian freshwater turtles. Conservation of *Podocnemis* has historically emphasized nesting beaches, reproductive females, eggs, and harvest regulation, yet demographic recovery also depends on the habitats and resources used throughout development. If *P. sextuberculata* shifts among basal resource pathways as it grows, different life stages may depend on different combinations of feeding habitats or resource types. Conversely, the relative isotopic stability of *P. expansa* may reflect sustained access to a broad and seasonally connected resource base rather than dependence on a single habitat. In both cases, the relevant unit of conservation may extend beyond discrete nesting or feeding sites to the broader floodplain mosaic that maintains access to resources through the annual hydrological cycle. This is particularly important for species that remain ecologically and socially important and have long histories of exploitation throughout the Amazon basin (Fachín-Terán et al. 2003; Eisemberg et al. 2015; Oliveira et al. 2024; Dias et al. 2026).

Our results also have a methodological implication for trophic monitoring. Spatial comparisons based on consumer isotope values alone may obscure substantial heterogeneity in local food-web baselines, while apparent differences among populations may reflect environmental isotope variation rather than changes in resource use. Stable-isotope studies of mobile freshwater consumers should therefore incorporate spatially and temporally replicated baselines whenever possible and, ideally, integrate isotope data with direct diet information and movement ecology. More broadly, our findings support a view of Amazonian turtle conservation centred on ontogenetic resource landscapes: the connected set of habitats and resource pathways that support individuals as they grow. Under this perspective, species identity, developmental stage, and floodplain connectivity jointly define the trophic opportunities available to turtles, and conserving populations requires maintaining not only reproductive sites but also the hydrological and ecological processes that sustain those opportunities through time.

Declarations

Competing interests:

The authors declare no competing interests.

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Author Contribution

GCCF: conceptualization, methodology, data curation, formal analysis, writing - original draft, review and editing; GEM: investigation, writing - review and editing; LMMA: investigation, writing - review and editing; LJB: writing - review and editing; CDR: writing - review and editing; LJB: writing - review and editing; JAMD, RDM and EBS: Investigation, data curation, writing - review and editing, PCMA: Project administration, writing - review and editing; HCMC: Investigation, Project administration, conceptualization, writing - review and editing. JVC-S: Project administration, funding acquisition, writing - review and editing RGS: conceptualization, methodology, investigation, writing - review and editing, Project administration, funding acquisition, supervision.

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Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

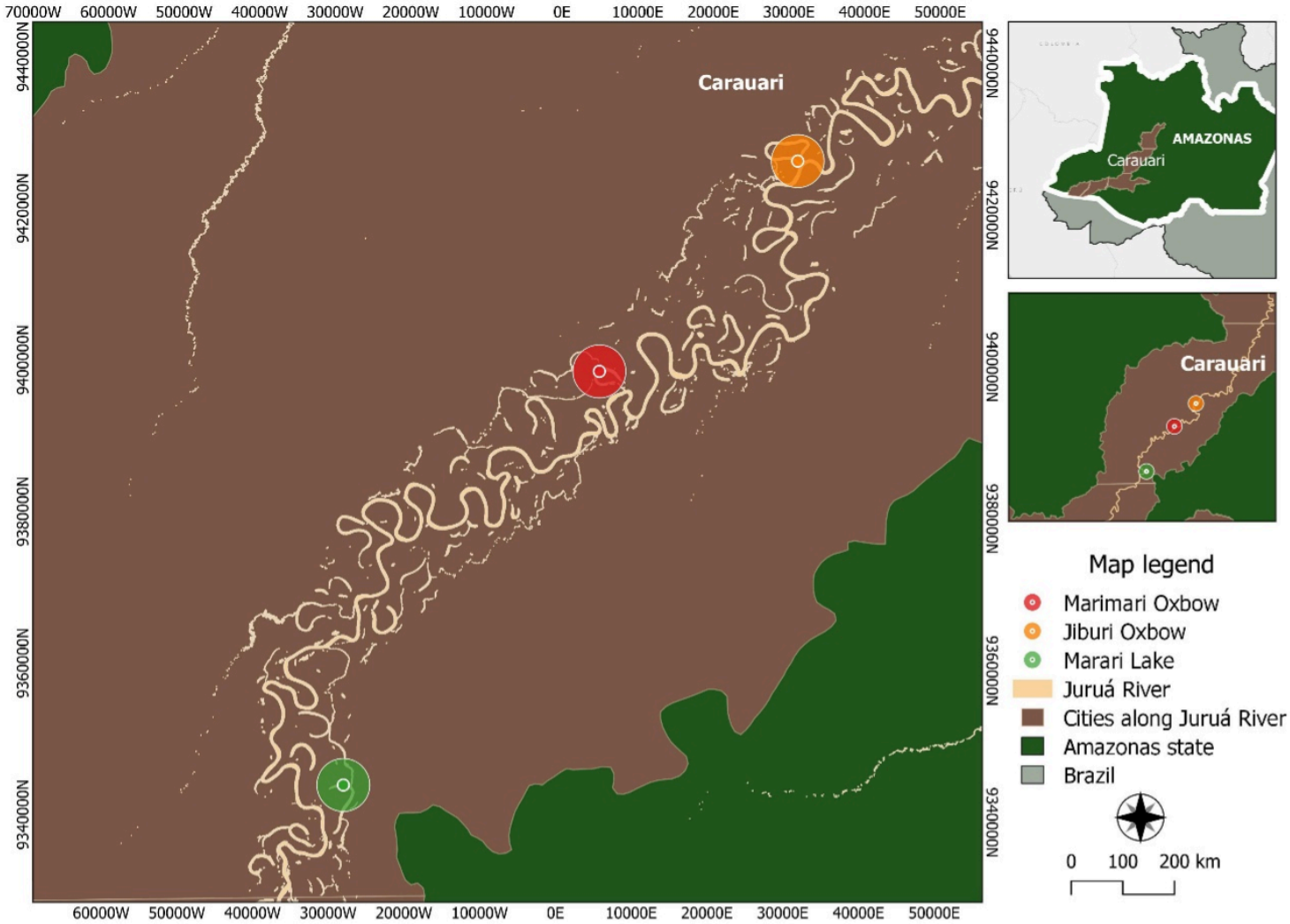


Figure 1

The Middle Juruá region, highlighting both sampling areas, the oxbow lakes ‘Jiburi’ (orange circle) and ‘Marimari’ (red circle), and the ‘Marari Lake’ (green circle), in the surrounding area of the city of Carauari, in the state of Amazonas.

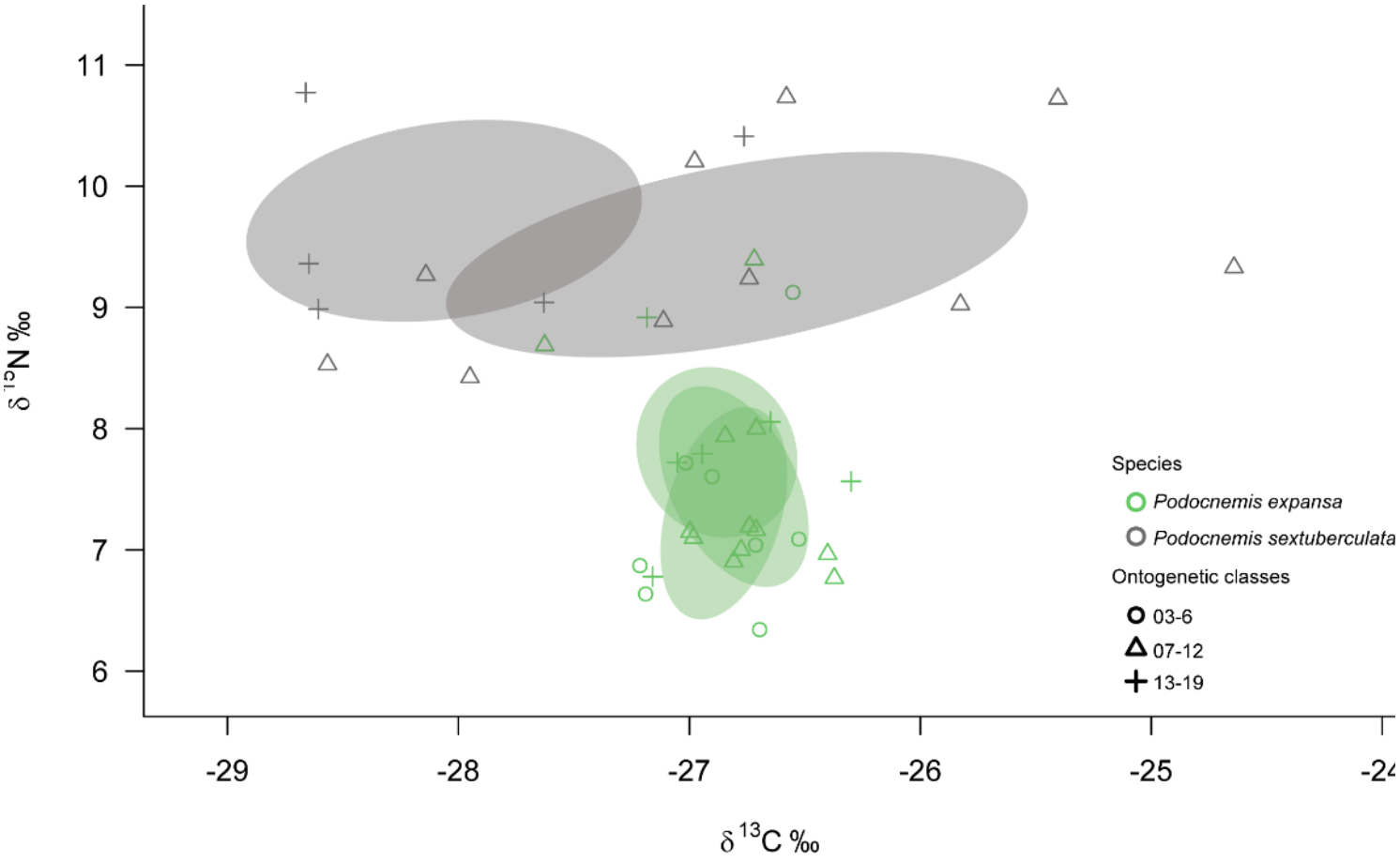


Figure 2

Ontogenetic isotopic niche (standard ellipse areas – SEAc $‰^2$; 40% C.I.) for Amazonian turtle species *Podocnemis expansa* and *P. sextuberculata*. Colors depict species and symbols are ontogenetic classes.

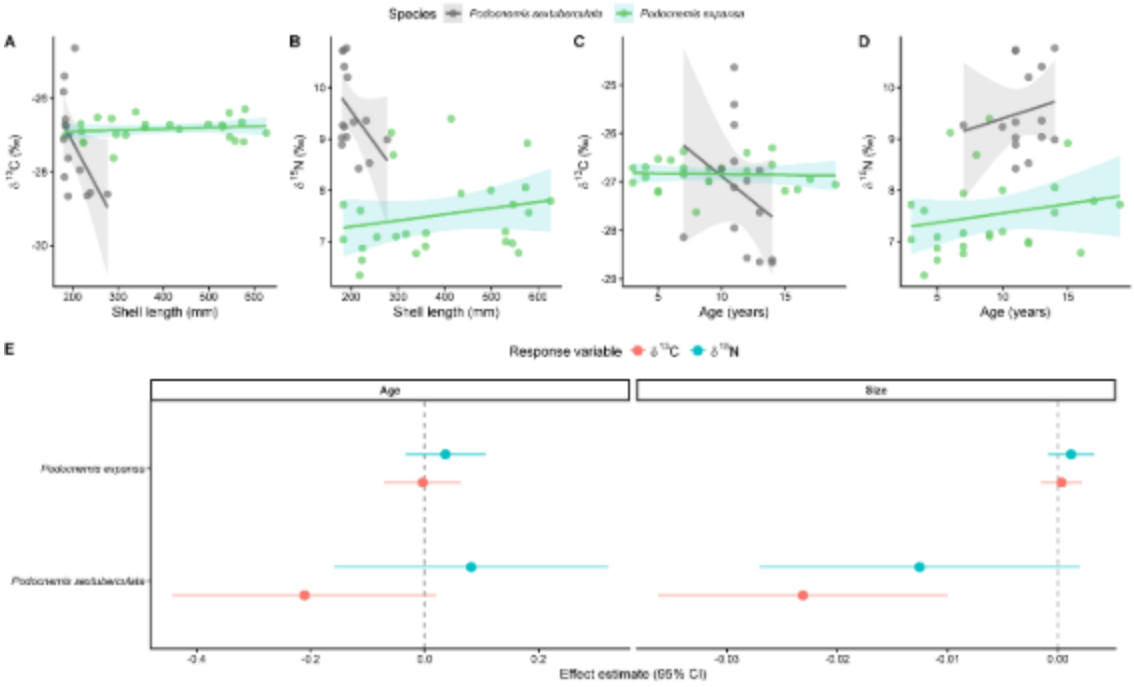


Figure 3

Relationships between $\delta^{13}C$ and $\delta^{15}N$ and shell length and age in *Podocnemis expansa* and *Podocnemis sextuberculata*. (A–D) (A–D) Scatterplots show isotope values as functions of shell length (A, B) and estimated age (C, D), with fitted linear regression lines and 95% confidence intervals for each species. (E) Forest plots show estimated species-specific slopes and 95% confidence intervals for the effects of estimated age and shell length on $\delta^{13}C$ and $\delta^{15}N$. Dashed lines indicate a null slope.

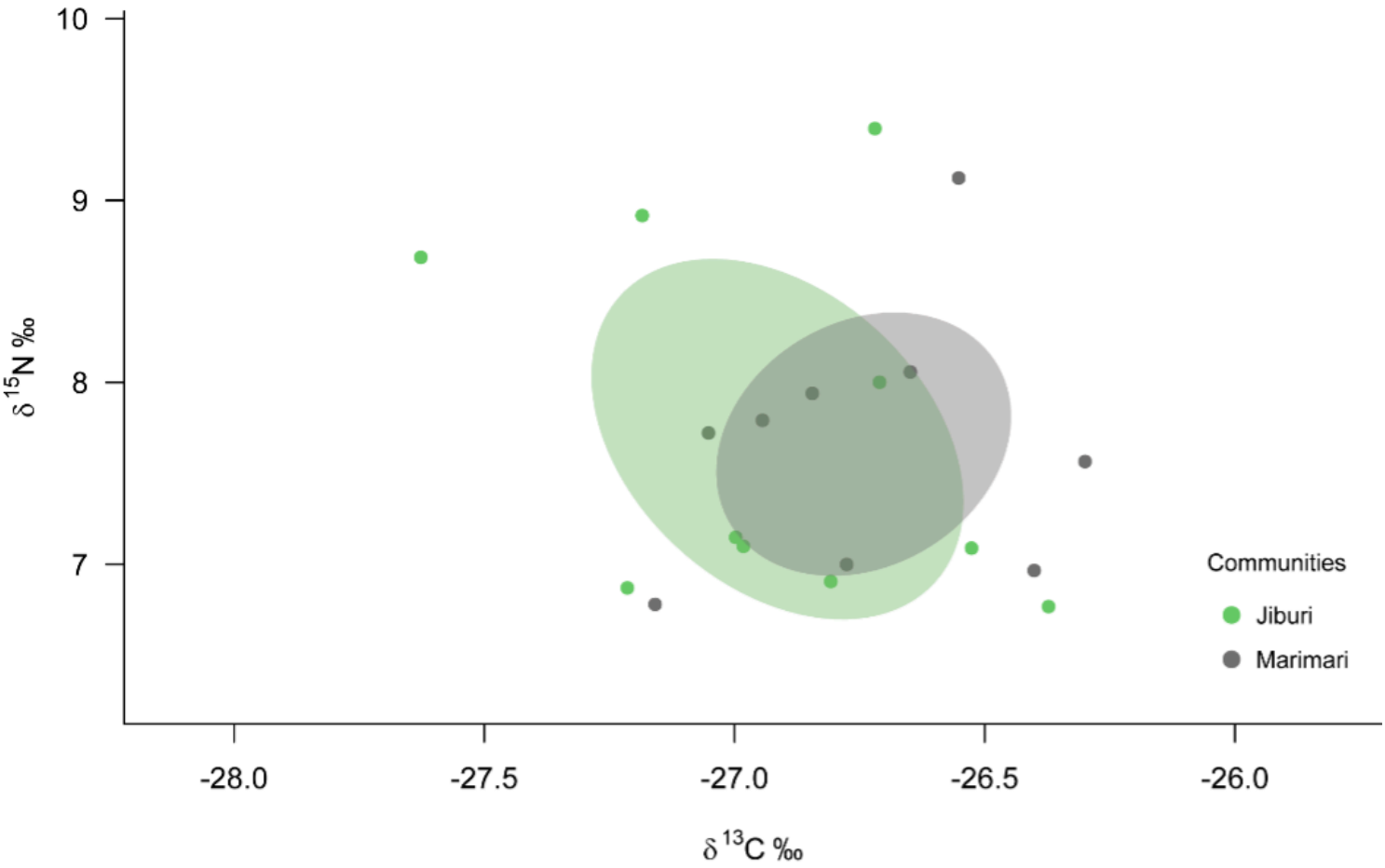


Figure 4

Isotopic niche (standard ellipse areas – SEAc $‰^2$; 40% C.I.) for the Giant Amazonian turtle *Podocnemis expansa* in the two sampled oxbow lakes: Sacado do Jiburi and Sacado do Marimari.

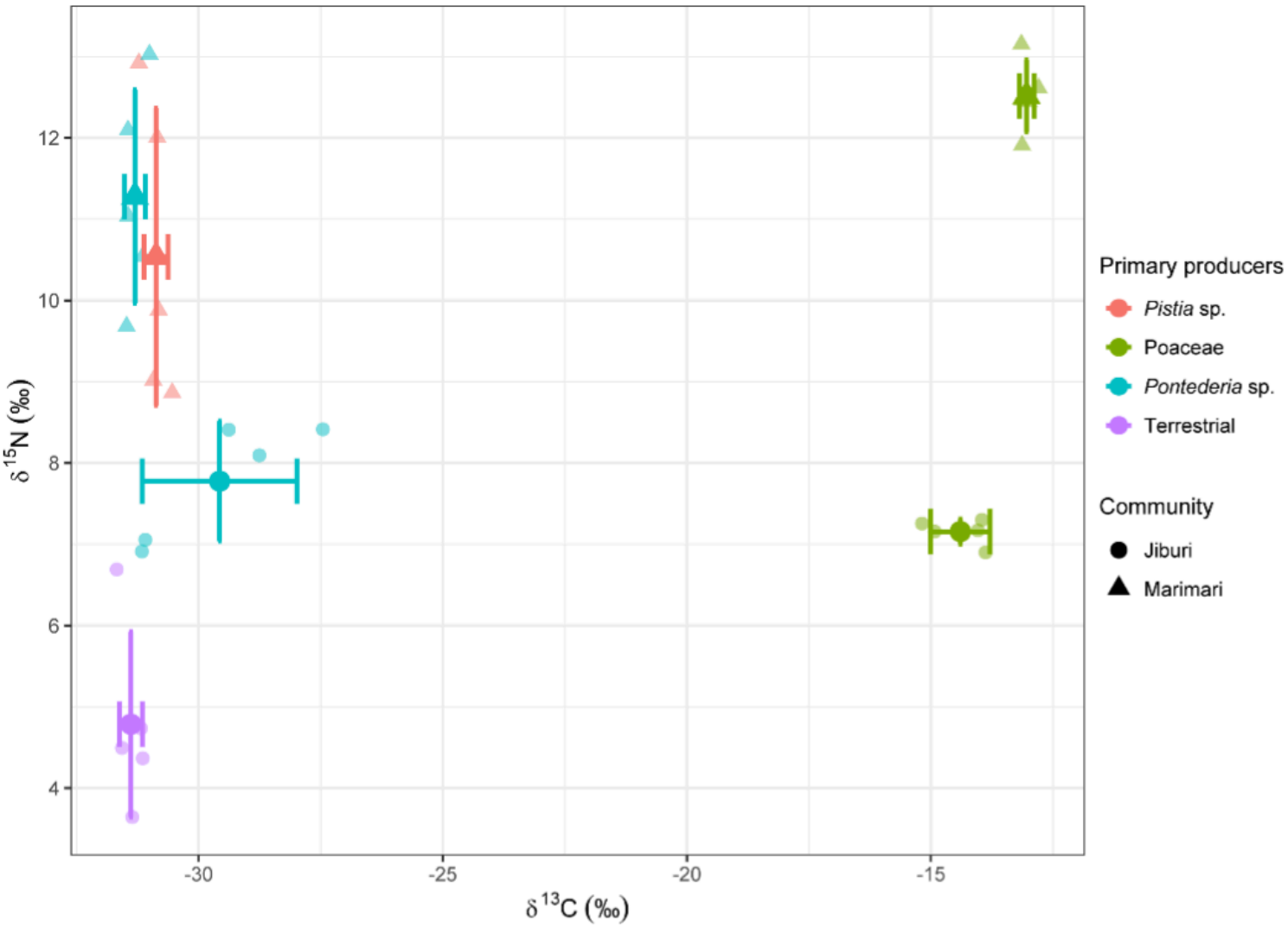


Figure 5

Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$, ‰) of primary producers sampled oxbow lakes Jiburi (circles) and Marimari (triangles). Colors depict the different primary producer groups (*Pistia* sp., Poaceae, *Pontederia* sp., and Terrestrial vegetation). Points represent individual samples, and error bars denote the mean (± SD) for each group within each lake.

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