

Opportunistic Top Predators Partition Food Resources in a Tropical Freshwater Ecosystem

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Summary

1. The structure of food webs may be strongly influenced by the distribution of top predators in space and time. The Amazon Biome is the only region in the world where four alligatorid species are known to occur in sympatry, and they attain high densities in some regions. As top predators with a diverse range of prey species occupying different trophic levels, their impact upon food webs should be substantial, but the degree to which crocodilians differ in their food sources, and potentially avoid competitive exclusion where they occur syntopically is not well understood.
2. Although most crocodilians are considered generalist opportunistic predators that feed on any source of protein available in the environment, Amazonian crocodilians show broad differences in the proportions of prey items they consume. It is believed that these differences may in part reflect habitat use, but it is unknown to what extent they represent interspecific differences in prey preferences or are a direct function of habitat selection.
3. Stable carbon isotope data ($\delta^{13}\text{C}$) of crocodilians and their potential prey were used to assess differences in reliance on terrestrial versus aquatic resources. These data were then placed in a spatial context using classified maps that reflect habitat types (headwater streams, mid-order flooded-forest streams and *várzea* floodplains) to elucidate whether dietary differences are explained by habitat selection or are more likely a reflection of prey preferences.
4. We found evidence for differences in types of basal resources supporting these crocodilians. Mean $\delta^{13}\text{C}$ values were highest in *Paleosuchus trigonatus*

(Schneider's dwarf caiman, $-25.7 \pm 1.2\text{‰}$), intermediate in *Caiman crocodilus* (spectacled caiman, $-27.4 \pm 1.2\text{‰}$) and *Paleosuchus palpebrosus* (Cuvier's dwarf caiman, $-27.7 \pm 1.1\text{‰}$) and lowest in *Melanosuchus niger* (black caiman, $-29.9 \pm 1.3\text{‰}$).

5. A progressive decrease in $\delta^{13}\text{C}$ values of crocodylian tissues occurred from headwaters to floodplains, which most likely reflects a progressive increase in autochthonous over allochthonous inputs in lower reaches of streams. The shift from terrestrial to aquatic resources sustaining these sympatric predators mirrors their spatial distribution along this ecotone. However, after taking into account the habitat in which pairs of syntopic individuals of distinct species occurred, significant differences in $\delta^{13}\text{C}$ values suggest that *P. trigonatus* and *P. palpebrosus* have different prey bases. Thus, despite being opportunistic predators, our results show that differences in crocodylians diet likely result from prey preferences and not only from habitat selection. These findings suggest that some species of crocodylians may be less generalist than traditionally thought and their influence on terrestrial or aquatic food webs might be species-specific.

Introduction

The diversity of coexisting species within ecological communities is partly determined by the ways in which they partition available resources (Finke & Snyder 2008). Coexisting species must differ in their ecological requirements for a limiting shared resource by at least some minimal amount to avoid competitive exclusion (Pianka 1974). One way in which different organisms directly interact with one another is through interspecific territorial interactions (Pulliam 2000). This implies that stronger competitors might displace others from the most suitable areas. The Amazon Biome is the only region known to sustain four alligatorid species living in sympatry. Given the high abundances of sympatric crocodylians (up to 450 individuals/km of shoreline) in some parts of the Amazon basin (Da Silveira 2002), it is likely that resource partitioning contributes to their coexistence.

Most crocodylians are considered generalist opportunistic predators that take advantage of any available source of animal protein (Pooley 1989). Amazonian crocodylians partition space, with each species occurring most frequently in specific habitats such as headwaters, flooded-forest streams or floodplain lakes (Magnusson 1985); thus, it is expected that their diets will vary depending on the availability of different prey in each habitat type. However, the extent to which habitat selection influences food habits of Amazonian crocodylians is unknown (Magnusson, da Silva & Lima 1987). Furthermore, all four species occur in syntopy in some waterbodies in the Amazon basin (Marioni et al. 2013). Within the same habitat type, prey partitioning might be a mechanism facilitating coexistence.

Crocodylians in general experience ontogenetic diet shifts starting from terrestrial and aquatic invertebrates when young, to more protein-rich diets in terms of

biomass, composed mostly of fish and terrestrial vertebrates as they grow (Ross 1998; Radloff, Hobson & Leslie 2012). Amazonian crocodylians (Alligatoridae) show this ontogenetic variation, but exhibit interspecific differences in diet as adults. Adult *Paleosuchus palpebrosus*, *Caiman crocodylus* and *Melanosuchus niger* attain up to 1.0, 1.4 and 2.5m snout-vent length (SVL), respectively (Magnusson & Campos 2010a; Thorbjarnarson 2010; Velasco et al. 2010). These species are common in open-canopy waterbodies and floodplains and have diets mostly composed of fish (Magnusson et al. 1987; Da Silveira & Magnusson 1999). In contrast, adults of *Paleosuchus trigonatus*, which are most common in closed-canopy headwater streams and can attain over 1.0m of SVL (Magnusson & Campos 2010b), consume many terrestrial vertebrates, but few fish (Magnusson et al. 1987).

Historically, researchers have used ‘snap-shot’ techniques such as stomach-content analysis to examine resource-use patterns of crocodylians (Webb, Manolis & Buckworth 1982; Magnusson et al. 1987). However, characterization of time-integrated resource-use patterns requires repetitive observations from the same individual.

Over the past few decades, stable isotope analysis (SIA) has become an important tool, able to overcome sampling limitations because it is based on the principle that tissues of consumers reflect isotopic compositions of their diet in a predictable way (DeNiro & Epstein 1978). Stable carbon isotope ratios ($^{13}\text{C}:^{12}\text{C}$; $\delta^{13}\text{C}$) in aquatic plants depend on source isotopic values of inorganic C and aquatic CO_2 , among other factors (Keeley & Sandquist 1992; Finlay, Power & Cabana 1999; Finlay 2004) and may be differentiated from terrestrial plant resources which vary substantially depending on photosynthetic pathways. Furthermore, $\delta^{13}\text{C}$ values change little with trophic transfers (DeNiro & Epstein 1978; Peterson & Fry 1987; Post 2002). Thus,

when source $\delta^{13}\text{C}$ values are different, isotopic composition of predators and their prey allows the use of mixing models to estimate the proportional contributions of different resources to consumer diets (Phillips et al. 2014).

In aquatic systems, the use of isotopic approaches has been integrated with spatial analyses to allow characterization of dietary patterns by consumers in different habitat types (Jardine et al. 2012; Villamarín et al. 2016). In the Amazon basin, remote-sensing images have been increasingly used to answer ecological questions over large geographical scales (Melack et al. 2004; Villamarín et al. 2011). L-band synthetic aperture radar (SAR) imagery has been particularly useful due to the capacity to detect water under canopy cover. Thus, SAR has been used to estimate the extent of wetlands and generate accurate classification maps of vegetation types and flooding states throughout the Amazon basin (Rosenqvist et al. 2002; Hess et al. 2003, 2012, 2015). This allows quantification of available habitat types for crocodilians.

Here, we explore dietary patterns in four species of crocodilians across a wide area of central Amazonia, which encompasses an ecotone including the main habitat types where crocodilians occur. Findings from this study may contribute to refine our understanding about crocodilian diet and flux of energy in food webs by estimating the proportions of aquatic versus terrestrial resources that sustain these predators. Furthermore, our results may transform the way that people think about these opportunistic predators by providing evidence suggesting that species divergences in diet result from prey preferences and not only from habitat selection. Therefore, we used $\delta^{13}\text{C}$ values measured in crocodilian tissues and their prey, and placed them in a spatial context using maps that reflect habitat types to answer the following questions:

- 1) To what extent do Amazonian crocodilians rely on terrestrial or aquatic resources?;

2) How do these proportions differ among the four species?; and 3) To what extent are differences in reliance on terrestrial versus aquatic resources a function of habitat selection or prey preferences?

Methods

Study region

This study was conducted in lotic waterbodies in the Central Amazon region (Fig. 1) and comprised three different hydrological sampling scales. The first scale covered first- to third-order pristine closed-canopy streams with headwaters that originate in the forests of the interfluvium between the Purus and Madeira Rivers (Fig. 1B). Stream order follows Strahler's modification of Horton's scale (Petts 1994). In this region, streams are affected by local rainfall rather than the hydrological regimes of the main rivers and most of these streams dry out completely during some months (June-October, F. Villamarín, Pers. obs.). Most headwater streams in the Amazon basin are nutrient poor (Furch & Junk 1980; Furch 1986), and their "black" waters are very poor in electrolytes, and low in pH and electrical conductivity. They support few submerged aquatic macrophytes and algal growth because of their low-light conditions (Junk et al. 2011) and are net heterotrophic as evidenced by low dissolved oxygen (see Table S1 in Supporting Information for detailed physico-chemical information).

We sampled 250m-stretches from 55 pristine headwater streams clustered in ten sampling modules. These clusters were distributed along an approximately 600 km transect throughout the interfluvial region of the Purus and Madeira Rivers (Fig. 1B). This region is intersected by the Br-319 highway, a partially unpaved road that connects

the cities of Manaus and Porto Velho and allows sampling of the otherwise inaccessible network of headwater streams. The sampling clusters are part of a research-module network of the Research Program in Biodiversity (PPBio, <http://ppbio.inpa.gov.br/sitios/br319>).

The second hydrological sampling scale was comprised of third- to fifth-order flooded-forest streams and ria lakes within four sub-basins, which originate within the Purus-Madeira interfluvium, and flow into the Purus River (Fig. 1D). These wetlands are subject to predictable monomodal pulses of inundation (Junk et al. 2011; Jardine et al. 2015), with flood amplitudes that are greatest near the confluence with nutrient-rich “white” waters of large rivers and decline rapidly upstream (Junk et al. 2011). Ria lakes may be temporarily influenced by sediment-laden waters during high-water periods, but are filled by black waters when river levels are low (Junk et al. 2011).

The third hydrological sampling scale of this study covered the western margin of the Purus River, where large extensions of white-water (sediment-laden) floodplains, locally known as “*várzeas*” extend for dozens of kilometers within the limits of the Piagaçu-Purus Sustainable Development Reserve (PP-SDR) (Fig. 1C). *Várzea* floodplains receive water, sediments, and biological material from large parent rivers originating in the Andes and are subjected to long-lasting, monomodal and predictable flood pulses with high amplitudes (Junk et al. 2011). These are the most species-rich wetland forests in the World (Wittmann et al. 2006); they have mean flood periods of around 230 days per year (Junk et al. 2011) and have rates of net primary productivity of up to 33 Mg ha⁻¹ yr⁻¹ (Megagram = 10⁶ g; Schöngart, Wittmann & Worbes 2010). Five waterbodies in *várzea* floodplains were sampled during crocodylian-monitoring activities carried out by the Crocodylian Conservation Program of the Piagaçu Institute.

Food web sampling

Primary producers were collected at each study site to characterize isotope values at the base of the food web. Biofilm samples were obtained via toothbrush scrapes of submerged vegetation surfaces, such as leaves and twigs. Samples were placed in small ziplock bags with distilled water. In the field camp, the contents of the bags were transferred into capped cryogenic vials and stored in liquid nitrogen. Samples of stream water were collected and filtered in the field on glass-fiber filters (47-mm diameter, 0.6 μ m pore size). These filtered samples represent fine particulate organic matter (FPOM) in suspension as no phytoplankton growth was expected in these headwater streams. No submerged aquatic plants were found. Leaf-litter samples were collected from the stream margins, rinsed with distilled water and placed in ziplock bags. In most cases, these samples were collected from outside the water column, as many of the streams were dry when sampled.

Potential crocodylian prey groups, such as terrestrial and aquatic invertebrates, were captured according to their availability. Terrestrial invertebrates, such as coleopterans and ants, were captured by hand. Aquatic invertebrates and fish were captured using dipnets, in a 50m-stretch of each stream. Small fish (< 50 mm Standard Length) were stored whole and a small piece of white dorsal muscle was collected from larger fish (> 50 mm SL). Claw samples from terrestrial vertebrates, such as agouti (*Dasyprocta sp.*) and paca (*Cuniculus sp.*), were obtained opportunistically from subsistence hunters in the area. While some samples of invertebrates and fish were preserved in ethanol for identification, all isotope samples collected from all trophic levels were kept frozen in liquid nitrogen for approximately one month before their return to the laboratory.

Crocodylians were captured using fyke nets in headwater streams and steel snares at night in other water bodies. After measuring (snout-vent length, SVL), sexing and weighing the animals, a piece of claw and a small piece of dorsal tail muscle underlying the scutes was removed and rinsed with distilled water to avoid contaminating the sample with blood. Claw tissue was used for isotopic mixing models as this was the tissue with the highest number of collected samples. However, in the case of *M. niger*, only one sample of claw tissue was available, the remaining were muscle-tissue samples. Thus, linear regressions were performed using muscle and claw tissues from the other three species to correct the values of muscle tissue in *M. niger* ($\delta^{13}\text{C}_{\text{Claw}} = -3.09 + 0.86 * \delta^{13}\text{C}_{\text{Muscle}}$; $r^2 = 0.63$; $p < 0.001$; $df = 61$).

SIA Laboratory processing

All samples were kept frozen at -20°C in the laboratory. Biofilm samples were sieved using a $300\mu\text{m}$ mesh to remove larger detrital material. The biofilm was then subsampled into a bulk fraction and a second sub-sample that was centrifuged using LUDOX®-TM50 colloidal silica following Hamilton, Sippel & Bunn (2005).

All samples were dried in an oven at 60°C for 24 to 48 h before grinding and homogenizing with a mortar and pestle. Samples were combusted in a EuroEA 3000 (EuroVector, Italy) or Europa GSL (Sercon Ltd, Crewe, UK) elemental analyzer and the resulting CO_2 and N_2 gases were chromatographically separated and fed into an IsoPrime (Micromass, UK) or Hydra 20–22 (Sercon Ltd, Crewe UK) isotope-ratio mass spectrometer. This measures the ratio of heavy and light isotopes in a sample relative to a standard. Isotope ratios (δ) are expressed in parts per mil (‰), defined as δ (‰) = $(R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$, where R_{sample} and R_{standard} are the isotope ratios of the sample

and standard, respectively. Isotopic standards used were referenced to PeeDee Belemnite (PDB) for carbon, and atmospheric air for nitrogen.

Although both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained for all samples included in this study, we used only $\delta^{13}\text{C}$ in the mixing model analyses due to uncertainty in $\delta^{15}\text{N}$ fractionation values and the limited differences in $\delta^{15}\text{N}$ values between our aquatic and terrestrial endmembers.

Statistical analysis

We assessed differences in isotopic composition between primary sources using a one-way Analysis of Variance (ANOVA). Before performing ANOVA tests, we tested if our data met the assumptions of homogeneity of variances using Levene's test. When the assumptions were not met, we used Kruskal-Wallis non-parametric analysis of variance. Pairwise differences among primary sources were assessed using a Tukey HSD post-hoc test. Pairwise differences between centrifuged and bulk biofilm samples were assessed using a Paired t-test. To estimate differences in $\delta^{13}\text{C}$ values of centrifuged biofilm samples as a function of habitat type, we used a Kruskal-Wallis test.

Differences in crocodylian isotopic composition as a function of taxon, habitat type, snout-vent length (SVL) and sex were assessed using an ANCOVA test with multiple factors in which the only continuous variable was SVL.

We performed a T-test to assess differences in $\delta^{13}\text{C}$ values between aquatic and terrestrial endmembers sustaining each crocodylian species. A one-way ANOVA was performed to assess differences in aquatic and terrestrial endmember isotopic composition as a function of crocodylian species. Differences in $\delta^{13}\text{C}$ values of fish,

which was the only aquatic prey group with available isotopic data from all the habitat types, were assessed using a Kruskal-Wallis test.

Endmember isotopic composition for mixing models

Isotopic mixing models using Bayesian frameworks (e.g., MixSIAR, SIAR) allow users to incorporate variation in source isotope values and trophic-discrimination factors as well as prior information, such as stomach-content data, thereby reducing uncertainty in mixing-model predictions (Moore & Semmens 2008; Semmens et al. 2009; Ward, Semmens & Schindler 2010; Francis et al. 2011; Parnell et al. 2013; Stock & Semmens 2013). Unbalanced sample sizes of different prey organisms may lead to miscalculation of their relative contribution to endmember mean $\delta^{13}\text{C}$ values. For example, low-biomass prey that are easy to capture may be over represented in the sample, while larger, more energy-rich prey that are only opportunistically sampled may be under represented. Therefore, isotope values of prey were aggregated into one of two major categories, either terrestrial or aquatic. We then used previous diet studies to calculate $\delta^{13}\text{C}$ weighted means and standard deviation using the proportion of recovered prey mass (Pérez 1992), per number of prey individuals per crocodylian size class (Magnusson et al. 1987) as weighting factors in the calculation. Crocodylians were grouped into six size classes: <20cm, 20.1 to 30cm, 30.1 to 40cm, 40.1 to 50cm, 50.1 to 60cm, and >60cm SVL, and the weighted prey mean (g/crocodylian/size class) based on the number of individuals per size class in our sample, was calculated for each of the four species. All $\delta^{13}\text{C}$ values of these prey came from our sample set with the exception of those for *várzea* fish, which were obtained from Forsberg et al. (1993).

Calculations of endmember isotopic composition were assessed for each crocodylian species separately. Fish was the only aquatic group with available samples

in all three habitat types and also the one with the most variation on biomass contribution to crocodilian diets. Therefore, *várzea* fish data were used to estimate isotopic composition of aquatic endmembers for *M. niger*, a combination of *várzea*- and headwater-fish data were used for *C. crocodilus* and *P. palpebrosus*, and headwater-fish data were used for *P. trigonatus*. Terrestrial endmember samples were available only from headwater habitats and we used these values for all crocodilian species. Endmember $\delta^{13}\text{C}$ mean and SD were used to run a one-isotope, two-source model in MixSIAR (Stock & Semmens 2013).

Model parameterization

The MixSIAR mixing-model parameterization included three chains, a chain length of 100,000, burn-in interval of 50,000, and thin-by interval of 50. The trophic discrimination factor used was 1.2 ± 0.1 ‰ (Marques et al. 2014). Results are reported as medians with 95% Bayesian Credible Intervals (95% BCI) (Table 1).

Model diagnostics

The Bayesian procedures within the MixSIAR framework include statistical diagnostic tests to assess MCMC convergence. The Gelman-Rubin test (Gelman & Rubin 1992; Brooks & Gelman 1998) is based on analyzing multiple simulated MCMC chains by comparing the variance within each chain to the variance between chains. Large deviation between these variances indicates non-convergence and the ratio will be near 1 at convergence. The Geweke test (Geweke 1991) is a two-sided z-test comparing the mean of the first part of the chain with the mean of the second part. At convergence, these means should be the same, and large absolute z-scores indicate that the result should be rejected.

Diet overlap

To compare the posterior estimates of source contributions among crocodylian diets, pairwise Bhattachayya Coefficients (BC; Bhattachayya 1943), defined as an approximate measurement of the amount of overlap between two statistical samples, were calculated. This coefficient will be 0 if there is no overlap and can reach 1 when the samples are completely overlapping (Bond & Diamond 2011).

Spatial analysis

To further assess occupation of the different aquatic-habitat types (headwaters, flooded-forest streams and *várzea* floodplains; see study area) and how habitat use influenced diet, the extent of non-flooded forest surrounding each sampled individual was assessed. A larger proportional area of non-flooded forests around individuals indicated that aquatic habitats became smaller towards the headwaters. A classified-image map of wetland extent, vegetation type, and dual-season flooding state of the entire lowland Amazon basin was used (Hess et al. 2015). The classified image was derived from the Global Rain Forest Mapping Project (GRFM) Amazon mosaics (Siqueira et al. 1999; Rosenqvist et al. 2002) acquired during October-November 1995 and May-June 1996 (see Hess et al., 2015 for details of classification procedures). From this map, spatial analysis R packages *sp* and *raster* (Pebesma & Bivand 2005; Hijmans & van Etten 2014) were used to calculate the proportion of non-flooded forest present in a 1km-radius around each of the captured crocodylians. Multiple-regression models were then used to estimate the influence of the proportion of non-flooded forest and crocodylian body length (SVL) on $\delta^{13}\text{C}$ values. Finally, assuming that adult Amazonian crocodylians, specially *Paleosuchus* spp., have small home ranges (Magnusson & Lima 1991), pairs of individuals of different species captured within a

maximum distance of 200 m of each other were compared using paired t-tests on $\delta^{13}\text{C}$ values to determine if they had similar prey bases. All statistical analyses and graphics were run using R software (R Development Core Team 2016).

Results

At the first hydrological scale, a total of 55 first- to third-order headwater streams were sampled. Within these headwater sites, 30 *P. trigonatus*, eight *P. palpebrosus* and six *C. crocodilus* individuals were captured. Further downstream, in the second hydrological scale, four sub-basins comprising third to fifth-order flooded-forest streams and ria lakes that flow into the Purus River were sampled, and 15 *P. trigonatus* individuals, 28 *P. palpebrosus* individuals and six *C. crocodilus* individuals were captured. On the opposite margin of the river, in *várzea* floodplains, one *P. palpebrosus* individual, four *C. crocodilus* individuals and nine *M. niger* individuals were captured. Mean \pm SD $\delta^{13}\text{C}$ values measured in crocodilians were highest in *P. trigonatus* ($-25.7 \pm 1.2\text{‰}$), intermediate in *C. crocodilus* and *P. palpebrosus* ($-27.4 \pm 1.51\text{‰}$; $-27.7 \pm 1.07\text{‰}$, respectively) and lowest in *M. niger* ($-29.9 \pm 1.3\text{‰}$; Fig. 2). Although not used in mixing models and other analyses, mean $\delta^{15}\text{N}$ values in crocodilians varied from 7.1 to 8.2‰, while prey items ranged from 2.5‰ in Formicidae to 10.1‰ in Erythrinid fish. The range of variation in snout-vent length (SVL) was 23.8 - 99.2 cm in *P. trigonatus*; 17.4 - 96.4 cm in *P. palpebrosus*; 30.3 - 97.8 cm in *C. crocodilus*; and 56.5 - 105.5 cm in *M. niger*.

Mean \pm SD $\delta^{13}\text{C}$ values measured in primary producers were lowest in C3 leaf litter ($-33.1 \pm 1.6\text{‰}$), intermediate in bulk biofilm ($-31.5 \pm 1.4\text{‰}$) and highest in

suspended FPOM ($-29.5 \pm 0.8\%$). These three sources were statistically different (ANOVA: $F_{2,75} = 13.52$; $p < 0.001$), but their distributions overlapped considerably. Pairwise differences among all sources were significant according to a Tukey HSD post-hoc test ($p < 0.027$ in all cases). Bulk biofilm samples showed no statistical differences from centrifuged samples ($-31.5 \pm 2.7\%$) (Student's t-test: $t = -0.11$, $df = 78.8$, $p = 0.915$). Furthermore, no statistical differences were found in centrifuged biofilm samples collected in headwater, mid-order flooded-forest streams and *várzea* floodplains (Kruskal Wallis $\chi^2 = 3.3$, $df = 2$, $p = 0.19$).

We found a significant effect of taxon (ANOVA $F_{3,98} = 43.4$; $p < 0.001$) and habitat type ($F_{2,98} = 10.8$; $p < 0.001$), but not of snout-vent length ($F_{1,98} = 1.3$; $p = 0.262$), nor sex ($F_{2,98} = 1.3$; $p = 0.280$), on $\delta^{13}\text{C}$ values of all species together. However, when we analyzed each species separately, multiple-regression models ($\delta^{13}\text{C} = -29.8 + 0.02_{\text{SVL}} + 3.18_{\text{NFF}}$; $F_{2,42} = 12.5$, $R^2 = 0.37$, $p < 0.001$) indicated that variation in *P. trigonatus* $\delta^{13}\text{C}$ values was predicted by both body length (SVL; $p < 0.001$) and the proportion of non-flooded forest (NFF; $p < 0.001$). This relationship was different for *P. palpebrosus* ($\delta^{13}\text{C} = -30.01 + 0.008_{\text{SVL}} + 2.75_{\text{NFF}}$; $F_{2,31} = 13.57$; $R^2 = 0.47$; $p < 0.001$) where the proportion of non-flooded forest had a significant effect ($p < 0.001$) on $\delta^{13}\text{C}$ values, but body length did not ($p = 0.204$). In contrast, $\delta^{13}\text{C}$ values in *C. crocodilus* ($\delta^{13}\text{C} = -24.3 - 0.06_{\text{SVL}} + 0.84_{\text{NFF}}$; $F_{2,28} = 8.4$; $R^2 = 0.38$; $p = 0.001$) varied as a function of body length ($p = 0.011$), but not the proportion of non-flooded forest ($p = 0.434$). In *M. niger*, the multiple regression including both body length and the proportion of non-flooded forest was not statistically significant ($F_{1,7} = 0.49$, $R^2 = 0.06$, $p = 0.505$), but the low sample size precludes confidence in this result.

Aquatic and terrestrial prey endmembers sustaining all four crocodilian species were significantly different in $\delta^{13}\text{C}$ values (t-test: $t > 14$; $df > 108$; $p < 0.001$ in all cases, see Tables S2 and S3). Despite leaf litter having lower $\delta^{13}\text{C}$ than biofilm, terrestrial prey were enriched in ^{13}C relative to aquatic prey.

Fish and terrestrial vertebrates represented the bulk of prey mass found in previous stomach-content studies and endmember values were more similar to the isotopic composition of these prey (Table S1). Terrestrial endmember $\delta^{13}\text{C}$ values did not differ among species (ANOVA: $F_{3,396} = 0.2$; $p = 0.89$), whereas aquatic endmembers composing *M. niger* diet were more depleted in ^{13}C than those of the other three crocodilians ($F_{3,396} = 29.2$; $p < 0.001$, Table S1).

Fish was the only group of aquatic prey for which $\delta^{13}\text{C}$ data were available from all three habitat types. The $\delta^{13}\text{C}$ values of fish from headwater, mid-order streams and *várzea* floodplains were significantly different according to a Kruskal-Wallis test ($\chi^2 = 21.16$, $df = 2$, $p < 0.001$).

MixSIAR models converged satisfactorily. Out of 13 variables, the Gelman-Rubin diagnostic yielded only one value > 1.05 . For the Geweke diagnostic, only two variables were outside ± 1.96 in one chain. For all individuals, independent of species, terrestrial resources made a predicted median proportional contribution of 36%, against 64% from aquatic inputs. However, these proportional contributions differed among species. *P. trigonatus* had the highest estimated median proportional contribution from terrestrial resources (58%), as opposed to the other species in which terrestrial inputs progressively decreased. *C. crocodilus*, *P. palpebrosus* and *M. niger* had 34, 30, and 21%, respectively (Fig. 3 and Table 1). Overall, Bhattachayya's coefficients were near 0.5 for all species pairs (Table 2), suggesting approximately 50% overlap of diet. Of all

species pairs, *C. crocodilus* and *P. palpebrosus* showed the highest diet overlap (BC = 0.55) and *P. trigonatus* and *M. niger* had the lowest overlap (BC = 0.51) (Table 2).

Individuals of *P. trigonatus* were captured together with *P. palpebrosus* at 15 locations and with individuals of *C. crocodilus* at four locations, but not with individuals of *M. niger*. *Paleosuchus palpebrosus* individuals were captured sharing space with *C. crocodilus* in nine locations but only in one location with *M. niger*. *Caiman crocodilus* and *M. niger* were captured together in seven locations. Values of $\delta^{13}\text{C}$ of syntopic individuals of different species were significantly different for the congeners *P. trigonatus* and *P. palpebrosus* (Paired t-test: $t = 4.12$, $df = 14$, $p = 0.001$, Fig. 4), but not for other species pairs: *P. trigonatus* and *C. crocodilus* ($t = -1.19$, $df = 3$, $p = 0.319$); *P. palpebrosus* and *C. crocodilus* ($t = -1.31$, $df = 8$, $p = 0.228$); *C. crocodilus* and *M. niger* ($t = -0.86$, $df = 6$, $p = 0.422$).

Discussion

Combining stable isotope and spatial analyses, we found evidence of differences in resources supporting Amazonian crocodylians in an ecotone comprising headwater streams, mid-order flooded-forest streams and *várzea* floodplains. Mean $\delta^{13}\text{C}$ values were highest in *P. trigonatus* from headwaters, intermediate in *C. crocodilus* and *P. palpebrosus* in flooded-forest streams and lowest in *M. niger* in *várzea* floodplains. The progressive decrease in $\delta^{13}\text{C}$ values of crocodylians occurred from headwaters to floodplains. This reflects an increasing downstream reliance on aquatic over terrestrial resources and mirrors the way these sympatric predators are distributed along this ecotone. However, when taking into account the influence of habitat type by analysing pairs of syntopic individuals of different species, significant differences in $\delta^{13}\text{C}$ values

suggest that *P. trigonatus* and *P. palpebrosus* have different prey bases when in syntopy, so species differences probably result from prey preferences in addition to habitat selection.

Most crocodylians are considered generalist, opportunistic predators (Pooley 1989) that take advantage of any available source of ingestible animal protein of adequate size. Amazonian crocodylians partition space, each species occurring most frequently in specific habitats (Magnusson 1985), so it is expected that their diets will vary depending on the availability of different prey in each habitat type (Magnusson et al. 1987).

Paleosuchus trigonatus and the African dwarf crocodile, *Osteolaemus tetraspis*, are the only extant crocodylians known to thrive in headwater streams under closed-canopy forests (Magnusson 1985). In the streams we studied, terrestrial resources represented almost 60% of carbon inputs contributing to *P. trigonatus* tissues. This is expected for a species that lives in headwater streams where large terrestrial prey are readily available. These prey may provide greater sources of organic matter in terms of biomass than crustaceans and small fish (which commonly grow to less than 25mm standard length). The primary carbon sources sustaining the terrestrial vertebrates are most likely derived from forest trees (C3 sources). Vertebrates comprised more than 99% of the biomass of terrestrial endmembers in the diet of *P. trigonatus* in this study. Most carbon inputs probably originate from tree fruits and seeds, as they represent the main food sources for forest-floor herbivores, such as species of *Dasyprocta* and *Cuniculus* (Dubost & Henry 2006). Non-photosynthetic parts of trees, such as reproductive and woody-stem parts, usually show higher $\delta^{13}\text{C}$ values than leaves (Medina & Minchin 1980; Martinelli et al. 1998; Blumenthal et al. 2015). Furthermore,

^{13}C -depleted samples of leaf litter may be caused by uptake of respired CO_2 in the forest understory (Medina & Minchin 1980). These factors may explain why our C3 leaf-litter $\delta^{13}\text{C}$ values were around 8‰ lower than those of terrestrial prey. Fruits and flowers had mean $\delta^{13}\text{C}$ values of $-26.5 \pm 1.6\text{‰}$ in a closed-canopy tropical African forest (Blumenthal et al. 2015). Although we do not have estimates of fruit $\delta^{13}\text{C}$ values from our study area, the values reported by Blumenthal et al. (2015) match well with those of keratin tissue from *Cuniculus* and *Dasyprocta* in our study.

Headwater streams receive significant carbon inputs from litter fall from C3 trees, with litter fall rates of $>10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ occurring in lowland tropical regions (Naiman, Decamps & McClain 2010). Allochthonous resources, whether from trees or other sources, enter streams as coarse particulate organic matter (CPOM) that degrades to fine particulate organic matter (FPOM) and accumulates on underwater surfaces. When deposited, FPOM particles mix with live algae, algal detritus and detritus of terrestrial or aquatic vascular plant origin (Hamilton et al. 2005). This conglomerate of allochthonous and autochthonous matter, known as biofilm, is common in streams and could represent a second pathway by which terrestrial carbon reaches crocodilians via consumption of small fish that feed on biofilm and detritus. However, as the potential contribution of endmembers was weighted by the estimated volume consumed, and the large *várzea*-fish would not eat biofilm from streams, this had little effect on estimates of primary sources contributing to crocodilian diets.

Although low in biomass, periphyton within the biofilm most likely represents the only source of autochthonous inputs in the shaded environments of forest streams, as no phytoplankton growth is expected. In these conditions, contributions of microalgae and allochthonous resources are often difficult to distinguish using stable isotopes

as both resources often overlap in $\delta^{13}\text{C}$ values in headwater streams (France 1995; Finlay 2004; Jardine, Kidd & Cunjak 2009). This occurs as the result of isotopic overlap and the contamination of the autochthonous samples with allochthonous detritus (Jardine et al. 2009). The first problem is difficult to deal with, but the latter can potentially be overcome by centrifuging biofilm samples with colloidal silica and physically separating micro-algae from detritus (see Hamilton et al., 2005). In this study, even after centrifuging biofilm in colloidal silica, we found no significant differences in $\delta^{13}\text{C}$ values between bulk and centrifuged samples, with few exceptions. Since bulk biofilm samples consist mostly of allochthonous FPOM, little micro-algae was present in our samples, a reflection of what is expected in unproductive closed-canopy streams (Fisher & Likens 1973).

When there is relatively poor distinction of isotopic compositions between sources, other information can be used to parameterize MixSIAR models (Moore & Semmens 2008; Soto et al. 2016). We were able to estimate the relative importance of carbon inputs from aquatic versus terrestrial resources in the isotopic composition of caiman tissues by using prior information of the relative mass contributions of prey to define endmember $\delta^{13}\text{C}$ means and SD. *Caiman crocodilus* and *P. palpebrosus* are often found occupying mid-order stream channels and flooded-forest habitats in syntopy. Some *P. trigonatus* may also be found sharing the same habitats. More autochthonous primary production is expected in the lower reaches than in the headwaters as stream channels widen progressively and the quantity of light reaching streams increases (Naiman et al. 1987). Although not quantified in this study, if this is the case in these streams, the increasing amounts of autochthonous carbon entering the food web are expected to be progressively incorporated in higher trophic levels, such as fish and crocodylians. Furthermore, fish size increases downstream as the waters become deeper

(Schlosser 1982; Harvey & Stewart 1991). Crocodilian species living in the mid-reaches of these streams apparently benefit more from such prey than from terrestrial vertebrates. Consequently, isotopic inputs from aquatic resources are greater for both *P. palpebrosus* and *C. crocodilus* than for *P. trigonatus*. On the other hand, low algal production in headwater streams may cause aquatic consumers, such as invertebrates and fish, to rely mainly on terrestrial carbon. This means that even the small percentage of aquatic prey found in the diet of headwater crocodilians is probably sustained by terrestrial carbon (but see Brito et al. 2006; Lau, Leung & Dudgeon 2009; Neres-Lima et al. 2016).

Further downstream, *várzea* floodplains are extremely productive habitats (Junk et al. 1989; Schöngart et al. 2010), and it is there that *M. niger* reaches its highest densities (Da Silveira 2002). In these floodplains, *M. niger* and *C. crocodilus* occur syntopically, sharing foraging areas (Marioni et al. 2008) and partitioning nesting sites (Villamarín et al. 2011). Considerable amounts of fish in the diet of adult *M. niger* are responsible for their high reliance on aquatic resources. Floodplain fish included in this study are ^{13}C -depleted ($\delta^{13}\text{C}$ mean \pm SD = $-33.9 \pm 1.2\text{‰}$), as they are supported by carbon from phytoplankton (Forsberg et al. 1993). Phytoplankton mean $\delta^{13}\text{C}$ values in central Amazon *várzea* floodplains are low, varying between -40‰ and -30‰ (Araujo-Lima et al. 1986; Forsberg et al. 1993; Caraballo, Forsberg & Leite 2014; Mortillaro et al. 2015).

Significant differences in $\delta^{13}\text{C}$ values of caiman tissues suggest different proportions of terrestrial or aquatic resources sustaining these species. However, differences in diets may be a reflection of spatial distributions of these sympatric species (Magnusson et al. 1987; this study). Bhattachayya's coefficients derived from

posterior distributions of MixSIAR models showed overall overlaps in carbon inputs of around 50% among pairs of Amazonian crocodylian species. However, since the mixing models did not explicitly take into account spatial distributions, this is not by itself strong evidence of syntopic resource partitioning.

When taking into account habitat by selecting pairs of individuals of different species occurring syntopically, we found significant differences in $\delta^{13}\text{C}$ between *P. trigonatus* and *P. palpebrosus*. This suggests partitioning of prey resources between these closely related species that is not caused simply by habitat selection. Evidently, even in locations where aquatic prey are more readily available, *P. trigonatus* exploits more terrestrial prey than *P. palpebrosus*. This might be facilitated by its terrestrial habits, as it is commonly found inside terrestrial retreats up to 90 m from streams (Magnusson & Lima 1991). Morphological adaptations may be related to higher efficiency in consuming certain groups of prey. Analysis of skull shape shows divergences between the two species of *Paleosuchus* within morphometric space. In fact, *P. palpebrosus* is closer to *M. niger* and *C. crocodilus* than to its congener, *P. trigonatus*, within skull morphospace (Pierce, Angielczyk & Rayfield 2008). This observation is in agreement with our findings on interspecific isotopic patterns which mirror the spatial distribution of Amazonian crocodylians. However, the interpretations of Pierce et al. (2008), suggesting higher ingestion of fish and terrestrial prey by long and broad-snouted crocodylians, respectively, are not supported by our data set. In fact, Amazonian crocodylians show the opposite pattern: *P. trigonatus* with a long narrow skull seems to be more adapted for preying on medium-sized terrestrial animals, while *P. palpebrosus* with a broader skull is evidently ingesting more fish, as do the other two species. Magnusson (2015) suggested that skull shape is more related to the difficulties caused by dense vegetation than by the type of prey. These contrasting sources of

evidence suggest that the relationship between morphological adaptations and food habits is complex and further studies that include morphological and dietary analysis, taking into account habitat characteristics, are needed in order to make broad generalizations.

In this study, we found interspecific differences in the proportions of terrestrial and aquatic carbon inputs sustaining Amazon crocodilians. This advances understanding of the ways that energy flows between aquatic and terrestrial food webs in these habitats. Our results suggest that despite being considered opportunistic generalist predators, Amazon crocodilians have diet divergences resulting not only from habitat selection but also from prey preferences. Thus, these species show some degree of specialization that may contribute to avoiding competitive exclusion in these waterbodies. Furthermore, reliance on different carbon resources varies in some species also as a function of body length (e.g. Davis et al. 2012; this study). Thus, ontogenetic shifts in reliance on aquatic or terrestrial carbon resources might be related to the way that individuals of different sizes are distributed in space. Since differences in body length can limit competition, intraspecific differences in isotopic composition of crocodilians might be as important as interspecific differences, a subject that deserves further investigation.

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Tables

Table 1. Median estimates of aquatic and terrestrial proportional contributions in Amazonian crocodilian diets derived from MixSIAR mixing models. 95% Bayesian Credible Intervals (BCI) are shown in parentheses.

Species	% Terrestrial Median (95% BCI)	% Aquatic Median (95% BCI)
<i>P. trigonatus</i>	58 (47 - 68)	42 (33 - 54)
<i>P. palpebrosus</i>	30 (17 - 41)	70 (59 - 83)
<i>C. crocodilus</i>	34 (14 - 48)	66 (52 - 86)
<i>M. niger</i>	21 (2 - 35)	79 (65 - 98)

Table 2. Pairwise comparisons of median Bhattacharyya coefficients estimating overlap in dietary source proportions in four Amazonian crocodilian species. Lower (LCL) and upper (UCL) 50% confidence limits are given in parentheses.

	<i>M. niger</i> Median (LCL-UCL)	<i>P. palpebrosus</i> Median (LCL-UCL)	<i>P. trigonatus</i> Median (LCL-UCL)
<i>C. crocodilus</i>	0.54 (0.31-0.78)	0.55 (0.37-0.74)	0.54 (0.5-0.59)
<i>M. niger</i>		0.54 (0.29-0.80)	0.51 (0.39-0.63)
<i>P. palpebrosus</i>			0.54 (0.47-0.60)

Supporting Information

Table S1. Physico-chemical characteristics of sampled waterbodies.

Table S2. Prior information on contributions of prey items composing Amazonian crocodilian diets for endmember isotopic groupings

Table S3. Mean $\delta^{13}\text{C}$ values of available prey used to estimate aquatic and terrestrial endmember isotopic composition.

Figure legends

Fig. 1. Study region. A) Northern South America showing the Amazon Basin in gray. B) Purus - Madeira interfluve region showing the three hydrological scales of this study surrounded by dashed lines. Numbers within the largest dash-lined region correspond to the 55 headwater streams studied. C) Detail of the *várzea* floodplains region. D) Detail of the region of mid-order flooded-forest streams and ria lakes. Symbols represent the four crocodilian species (*P. trigonatus* = o, *P. palpebrosus* = □, *C. crocodilus* = ◇, *M. niger* = △). Grayscale colors in B, C and D represent water (black), non-flooded forests (dark grey) and floodplains (light grey).

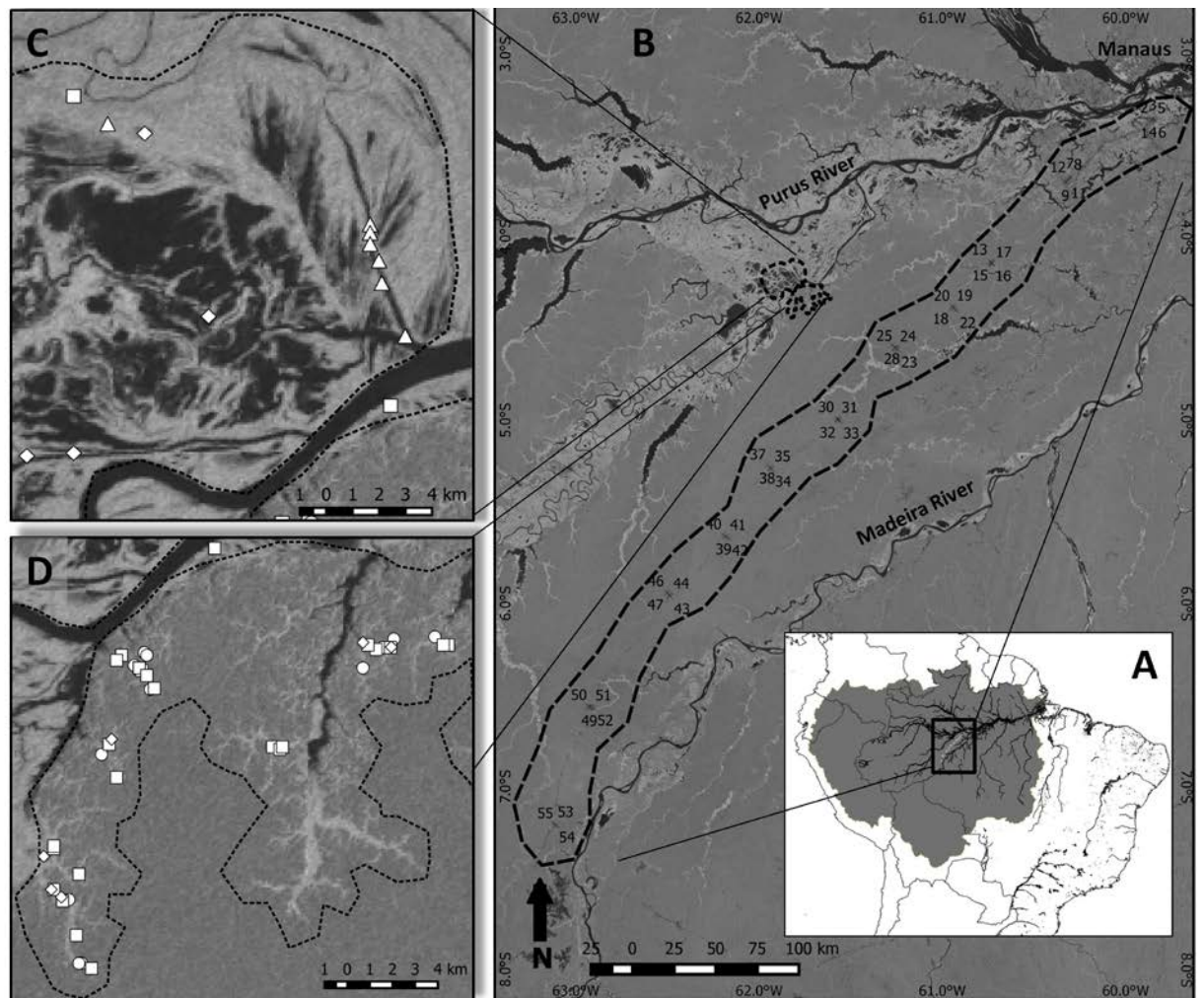


Fig. 2. Isospace of crocodilians and endmembers. Graphic representation of isotopic composition of the four caiman species (A-D), aquatic (E) and terrestrial (F) endmembers. The size of endmember symbols is proportional to their relative biomass contribution to crocodilian diets.

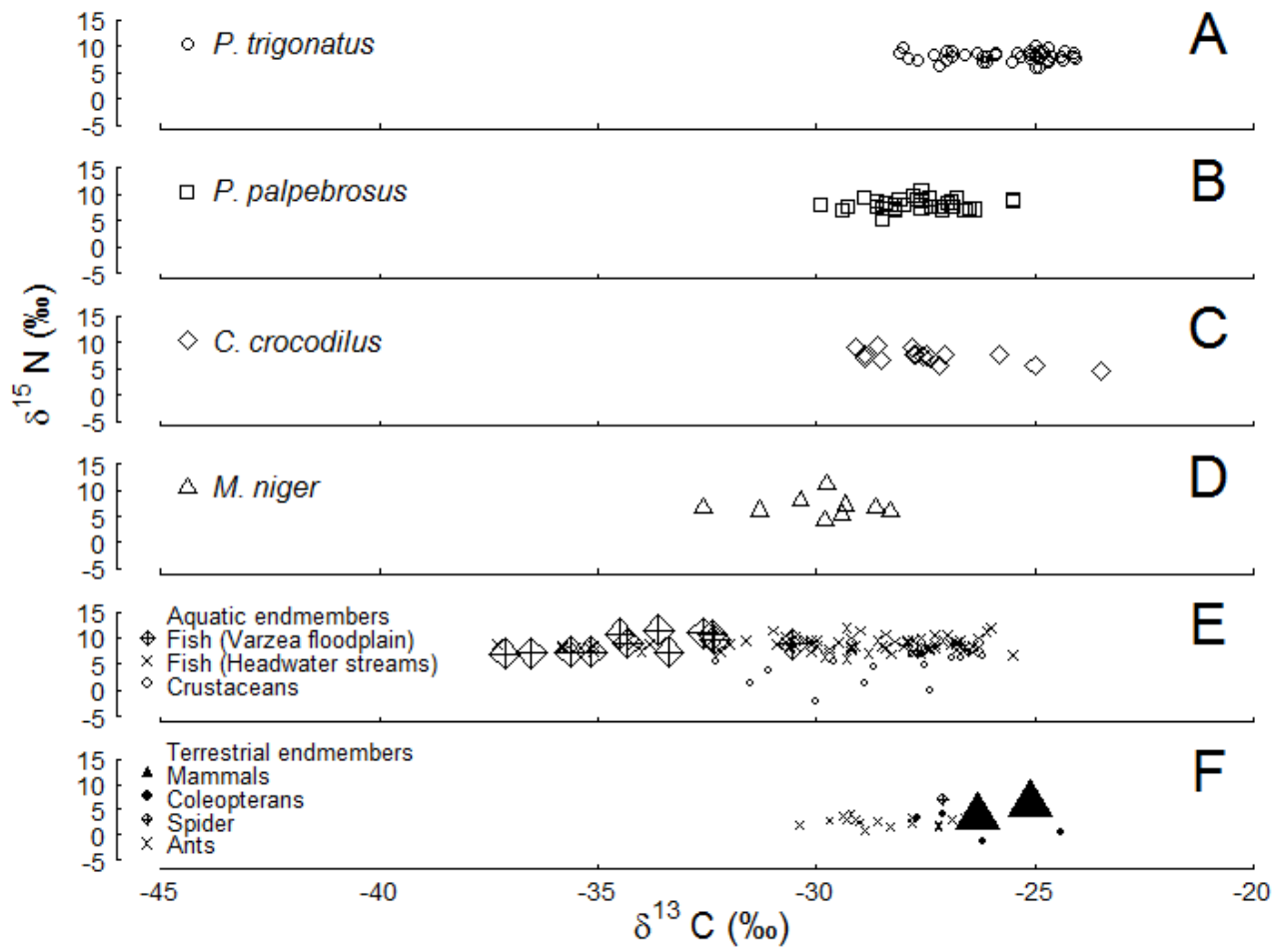


Fig. 3. Posterior distributions produced by the MixSIAR simulations. Terrestrial and aquatic resources are represented in dark and light grey, respectively, for *P. trigonatus* (A), *P. palpebrosus* (B), *C. crocodilus* (C), and *M. niger* (D).

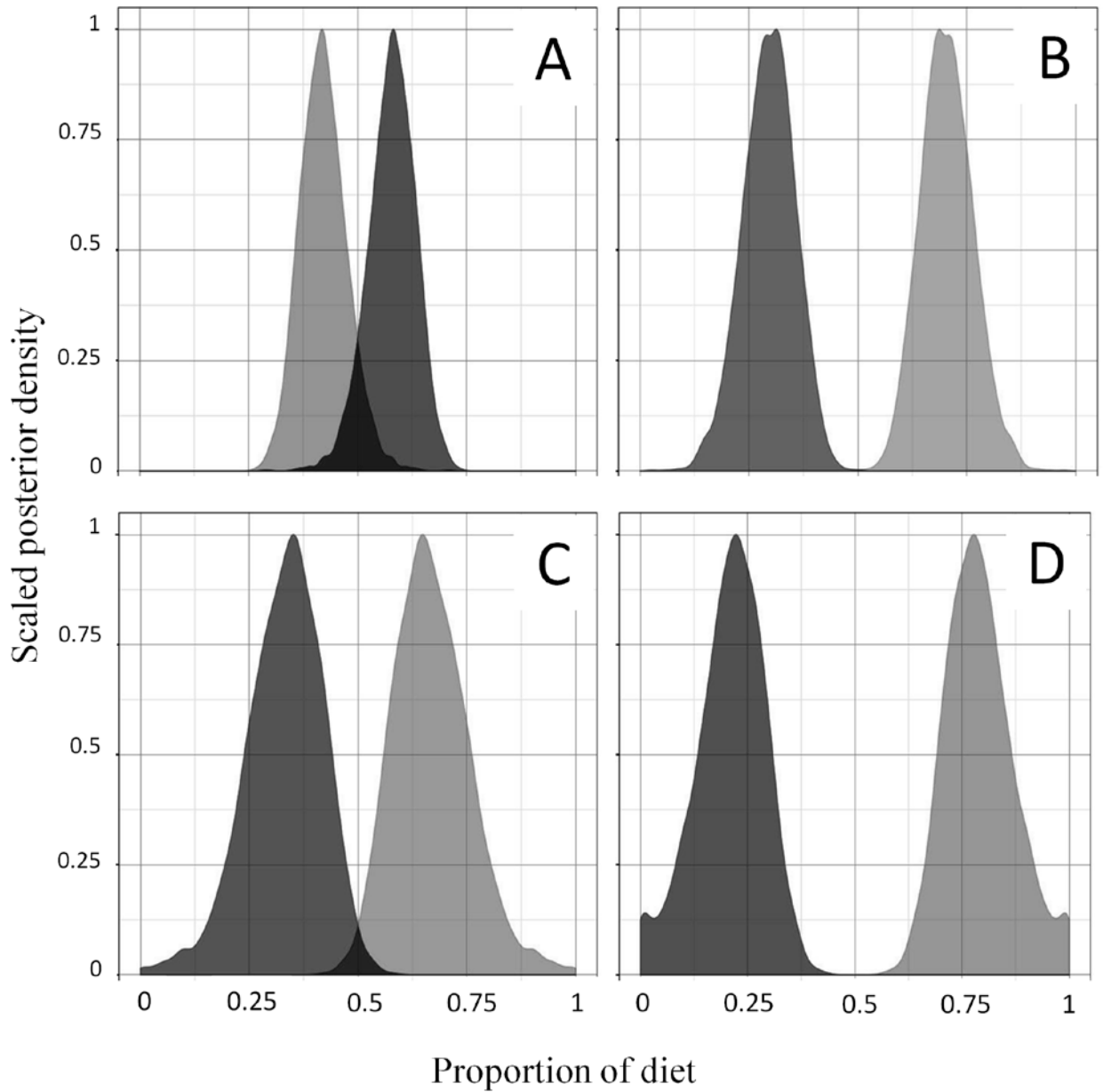


Fig. 4. Interspecific isotopic comparisons. Pairwise comparisons of $\delta^{13}\text{C}$ values between individuals of *Paleosuchus trigonatus* (●) and *P. palpebrosus* (□) in fifteen sites where they were captured syntopically.

