



Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia

Efeitos da alteração da paisagem e uso da terra no nicho trófico e índice corporal de populações de *Caiman crocodilus* na planície de inundação da Bacia do Médio Rio Araguaia

André Costa Pereira

Brasília - DF
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Tese de Doutorado apresentada ao Programa de Pós-Graduação *stricto sensu* em Ecologia da Universidade de Brasília como parte dos requisitos para obtenção do título de Doutor em Ecologia.

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RESUMO

Modificações da paisagem através da conversão e fragmentação de habitat afetam a persistência da biodiversidade em planícies de inundação devido às alterações nas condições ambientais, de recursos e dinâmica populacional (ocupação, movimento, distribuição) na paisagem. Esses efeitos negativos podem ser observados através da condição populacional de saúde e mudanças de nicho trófico. Avaliamos os impactos das modificações da paisagem sobre a biodiversidade da planície de inundação do rio Araguaia usando o predador *Caiman crocodilus* (Crocodylia, Alligatoridae) como espécie indicadora. Modelamos parâmetros de nicho trófico dos jacarés (estimados pela análise de isótopos estáveis) e índice de condição corporal (SMI) com características da paisagem, contabilizando a variabilidade do habitat, sexo e ontogenia. Ademais, verificamos diferenças em produtores primários entre corpos hídricos de áreas naturais e antropogênicas usando a análise isotópica de carbono em aminoácidos essenciais. Diferenças no uso de recursos para sexo e ontogenia sugerem uma partição de nicho. A dinâmica sazonal e conectividade na planície de inundação propiciam que habitats partilhem recursos usados pelos jacarés. A cobertura de pastagem afetou positivamente a largura de nicho, com altos valores distribuídos em regiões agrícolas. Fontes basais das teias alimentares diferiram entre habitats naturais (lagos e rios) e antropogênicos (canais e açudes), com carbono agrícola suportando em parte teias alimentares em áreas agrícolas. Jacarés apresentaram melhores condições corporais em habitats antropogênicos, indicando melhores características para forrageamento. Áreas agrícolas relacionadas à produção de arroz irrigado são matrizes de alta qualidade para a persistência de jacarés. Nosso estudo sugere que políticas ambientais, de conservação e manejo da terra devem considerar características da paisagem e condições do habitat para que a biodiversidade perdure em paisagens modificadas, inclusive mitigando impactos agrícolas negativos. Corpos hídricos antropogênicos e áreas agrícolas podem conciliar objetivos orientados à sociedade e biodiversidade, fornecendo serviços ecossistêmicos e habitats para espécies tolerantes às modificações da paisagem.

Palavras-chaves: entrada de carbono agrícola; conectividade; fragmentação; variação de nicho intraespecífico; configuração e composição da paisagem; habitats seminaturais.

ABSTRACT

Landscape modifications from habitat conversion and fragmentation affect biodiversity's persistence in floodplains due to alterations in the environmental conditions, resource diversity, and population dynamics (occupation, movement, distribution) across landscape. These negative effects can be observed through populations' health conditions and trophic niche shifts. We assessed impacts of landscape modifications upon biodiversity in the middle Araguaia River floodplain using the top predator *Caiman crocodilus* (Crocodylia, Alligatoridae) as indicator species. We modeled the parameters of caiman trophic niche (estimated by stable isotope analysis) and body condition index (SMI) with the landscape features, accounting with habitat, sex, and ontogeny variability. Furthermore, we verify differences in primary producers between waterbodies from natural and anthropogenic areas using carbon isotope analysis of essential amino acids. Differences in the resource use for sex and ontogeny suggest a niche partitioning. Seasonal dynamics and connectivity in the floodplain allow habitats to share resources used by caimans. Pasture coverage affected positively the caiman niche width, with high values distributed in agricultural region. Basal sources of food webs differed between natural (lakes and rivers) and anthropogenic habitats (ditches and man-made ponds), with agricultural carbon supporting in part food webs in agricultural areas. Caimans showed better body conditions in anthropogenic than in natural habitats, indicating better features for foraging. Agricultural areas related to irrigated rice yields are a high-quality matrix for caiman persistence. Our study suggests that environmental policies, conservation planning, and land use management should consider landscape features and habitat condition for wetland biodiversity endures in human-modified landscapes, besides mitigating negative agricultural impacts. Anthropogenic wetlands and agricultural areas can conciliate human-oriented and biodiversity-oriented purposes, providing ecosystem services and habitats for some species tolerant to landscape modifications.

Keywords: agricultural carbon input; connectivity; fragmentation; intraspecific niche variation; landscape configuration and composition; semi-natural habitats.

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INTRODUÇÃO GERAL

Estima-se a distribuição mundial de áreas alagáveis (wetlands) entre 7 milhões km² (Whigham 2009) e 12.8 milhões km² (Millennium Ecosystem Assessment 2005; Zedler & Kercher 2005). No Brasil, as áreas alagáveis representam aproximadamente 20% do território nacional, distribuídas principalmente pelo Pantanal e bacia dos rios Amazonas, Araguaia, Guaporé, Mamoré e Mortes (Junk et al. 2014). Áreas alagáveis possuem alta funcionalidade e complexidade ecológica que proporcionam bens e serviços ecossistêmicos vitais para a sociedade (Hails 1997; Baron et al. 2002; Millennium Ecosystem Assessment 2005; Maltby 2009). A alta biodiversidade associada também exerce papel fundamental na estabilidade, resistência e resiliência deste ecossistema (Scheffer et al. 2001; Hooper et al. 2005; Rooney et al. 2006; Duffy et al. 2007). No entanto, a exploração exacerbada dos serviços ecológicos tem fragilizado e prejudicado a integridade, estrutura e funcionalidade das áreas alagáveis por alterações geomorfológicas e hidrológicas (perda de área, uso da terra, represamento, diques, drenagem), faunísticas (caça e pesca, extinção e invasão de espécies exóticas), contaminadoras (eutrofização e agroquímicos) e climáticas (Baron et al. 2002; Brinson & Malvárez 2002; Maltby 2009).

A conversão de áreas alagáveis para atividades agropecuárias tem profundos efeitos sobre a biodiversidade e processos ecológicos devido à perda e fragmentação de habitat e alteração da matriz (Fischer & Lindenmayer 2007; Haddad et al. 2015). Mudanças na composição e configuração da paisagem podem afetar como as espécies usam, exploram e acessam habitats e alimentos, consequentemente influenciando sua persistência (Bennett et al. 2006; Villard et al. 2007; Liao et al. 2017). A configuração, o tamanho e a qualidade do habitat são determinantes na dinâmica de ocupação, distribuição e extinção local de populações (Fahrig 2003; Ewers & Didham 2006). Como consequência, há alterações nas interações tróficas, integridade da teia alimentar e vias de fluxo de energia na cadeia trófica aquática (Hillebrand & Shurin 2005; Duffy et al. 2007; Cardinale et al. 2012). Assim, o conceito de nicho trófico baseado nas dimensões de recursos e habitats (Chase & Leibold 2003) fornece bases teóricas para investigações e compreensão das mudanças e adaptações da dieta e ocupação de habitats das espécies para persistir em áreas antropogênicas sob constante modificações da paisagem.

Em ambientes alterados, a disponibilidade e diversidade de recursos é reduzida (Tschardtke et al. 2012). Conforme a disponibilidade de recursos e requisitos nutricionais das

espécies, tais ambientes condicionam recursos não saudáveis, de baixo ganho energético e conteúdo nutricional, repercutindo na condição corporal individual e populacional (Lane et al. 2014; Smyth et al. 2014; Gallego-Carmona et al. 2016). Portanto, uma rápida avaliação da saúde dos indivíduos pode revelar estressores ambientais ou antropogênicos operando em pequenas escalas espaciais antes que toda a população decline (Janin et al. 2011; Ellis et al. 2012). Através do uso de índices de condição corporal – que indicam o estado energético, saúde ou condição fisiológica e nutricional (Peig & Green 2009, 2010), estudos ecológicos e de conservação têm demonstrado efeitos negativos de algumas ameaças ambientais e antropogênicas, incluindo perda e perturbação no habitat, pesticidas (revisado em Stevenson & Woods, 2006) ou efeitos positivos de ações de restauração e práticas de gestão hídrica (Fujisaki et al., 2009; Mazzotti et al., 2009). Em ambientes e paisagens alteradas surge a oportunidade de avaliar os mecanismos pelos quais os atributos da paisagem conduzem indivíduos e populações a condições saudáveis adequadas, identificando aqueles que melhor mitigam os impactos antrópicos e, portanto, potencial para contribuir para as práticas de conservação e manejo.

Em planícies de inundação, os crocodilianos são predadores de topo e importantes atores na funcionalidade de ecossistemas aquáticos e terrestres quanto ao funcionamento, integridade e estabilidade de teias alimentares (Mazzotti et al. 2009; Rosenblatt et al. 2013; Somaweera et al. 2020). São capazes de utilizar habitats e paisagens em larga extensão, com exploração dos diversos recursos disponíveis devido a comportamentos distintos provocados por fatores ontogenéticos e sexuais (Barão-Nobrega et al. 2016; Thorbjarnarson 1993). Além disso, alguns crocodilianos demonstram adaptabilidade ecológica e resiliência para persistir em paisagens agrícolas, como açudes, canais de irrigação, barragens e represas (Borteiro et al. 2008; Marques et al. 2016). Presumidamente, modificações na configuração e composição da paisagem podem afetar os crocodilianos através de efeitos *bottom-up* e com severas consequências para cadeia alimentar e funcionamento ecossistêmico quando perdidos (Estes et al. 2011; Ripple et al. 2014). Portanto, são organismos modelo para detectar e investigar os efeitos da modificação da paisagem e perturbação antropogênica na cadeia alimentar, bem como avaliar o papel da variação de características intraespecíficas na dinâmica trófica.

Diante do exposto, este estudo visa avaliar os efeitos da alteração da paisagem e uso da terra sobre a largura do nicho e condição corporal de *Caiman crocodilus* (Crocodylia, Alligatoridae). *Caiman crocodilus* (jacarétinga) é uma espécie indicadora da biodiversidade na bacia do médio rio Araguaia, Tocantins, útil como organismo modelo para detectar e monitorar impactos ambientais devido à alta detectabilidade, movimentos sazonais e

ontogenéticos em uma variedade de habitats terrestres e aquáticos, inclusive naturais e antropogênicos. Esta tese está estruturada em três capítulos:

Capítulo 1 – Aborda-se os efeitos da variação intraespecífica quanto aos atributos de sexo, ontogenia e uso do habitat sobre as dimensões do nicho trófico (largura e posição) de *C. crocodilus*, em uma paisagem agrícola sob uma abordagem temporal utilizando-se da técnica de análise de isótopos estáveis de carbono e nitrogênio. Este capítulo foi submetido e seguiu as normas da revista *PLOS ONE* (Qualis A1 em Biodiversidade).

Capítulo 2 – Investiga-se os efeitos das modificações da paisagem sobre teias alimentares na planície de inundação do rio Araguaia, utilizando *C. crocodilus* como organismo modelo deste estudo e espécie indicadora para a biodiversidade da região. Ao longo de diferentes paisagens sob diferentes tipos de uso da terra na planície de inundação do Araguaia, avaliou as mudanças na composição e configuração da paisagem sobre os parâmetros de nicho trófico (posição e largura) de *C. crocodilus* em uma abordagem espacialmente explícita. Este capítulo seguiu as normas da revista *Journal of Applied Ecology*.

Capítulo 3 – Avalia-se os efeitos das modificações da paisagem sobre a condição corporal de *C. crocodilus* ao longo de diferentes paisagens sob diferentes tipos de uso da terra na planície de inundação do Araguaia, buscando as características da paisagem que possibilitam populações viáveis e maximizam sua persistência. Este capítulo seguiu as normas da revista *Freshwater Biology*.

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CAPÍTULO 1. SOURCES OF INTRASPECIFIC VARIATION IN THE ISOTOPIC NICHE OF *CAIMAN CROCODILUS* (REPTILIA, ALLIGATORIDAE) IN AN AGRICULTURAL LANDSCAPE

ABSTRACT

Intraspecific variation is a driver of the resource use of species, with ecological implications for the structure and stability of food webs. Habitat use varies according to traits of sex and body size, conducting to variations in resource exploitation and niche parameters of populations. However, human disturbance can impact communities and food webs that reflects in trophic niche changes due to alterations in the resource diversity and availability. Using stable isotopes analysis, we assessed the effects of sex, ontogeny, and habitat use on the trophic niche of *Caiman crocodilus* in an agricultural landscape of Central Brazil. Moreover, we used different body tissues to evaluate temporal variations in the trophic niche. Females had a larger niche width than males, although sexes had high niche overlaps, indicating that they share a greater part of resources. We observed ontogenetic trophic shifts: trophic level increases with snout-vent length (SVL), while basal source differs with SVL but was dependent on sex. Such patterns suggest partitioning of food resources through a sexual body-sized organization that could reduce intraspecific competition. Caiman niche width indicated differences in the use of food resources between habitats, but this was not related to habitat origins (natural or anthropogenic origins). High niche redundancy apparently results from movements across interconnected habitats. Despite the strong wet-dry seasonality in the floodplain, we found no temporal variation in the trophic niche. Our results suggest that *Caiman crocodilus* is a dietary generalist but an isotopic specialist, which results from the mutual effect of diet and diet-tissue discrimination factors. Since that anthropogenic habitats

can increase the susceptibility of caiman populations to harmful impacts, intraspecific variation should be the concern of decision-makers and stakeholders for sustainable management and conservation actions.

Keywords: anthropogenic habitats; niche width; niche overlap; sexual niche variation; temporal invariability; isotopic specialist

INTRODUCTION

Intraspecific variation has significant ecological effects on populations, communities, and ecosystems, mainly acting as the raw ingredient of natural selection (when heritable) and a factor that promotes coexistence [1, 2]. Despite receiving diminished attention at the turn of the century, interest in intraspecific variation has resurged, and it is regarded as important as interspecific variation in studies of community assembly and dynamics [3]. Through ecological and evolutionary processes, intraspecific trait variation influences population dynamics, community assembly, and ecosystem functioning. For instance, intraspecific trait variation affects predator-prey interactions, both at the individual and population levels, which in turn can modify the structure and stability of food webs [4-7]. Through phenotypic plasticity and contemporary evolution, human activity is a powerful driver of change in species traits, implying dramatic and harmful ecological effects [8, 9]. Therefore, understanding intraspecific variation is crucial to predicting population processes and dynamics in the face of changing environments and to promoting successful management and conservation of species.

Intraspecific variation is evident in the sexual and body size/age traits of species [10, 11]. By reducing intraspecific competition, such variation can drive habitat segregation and coexistence [12, 13]. Body size is a structural-functional regulator of food webs, trophic

interactions, and other ecological processes [13, 14]. Ontogenetic shifts in metabolic rates and energetic requirements with increasing body size can generate functionally separate groups with distinct ecological niches due to changes in resource use and foraging areas [15]. Hence, niche width and trophic level can be positively related to body size due to a strong predator-prey size relationship in size-structured food webs [16]. In the same way, sexual differences in predation-risk, dimorphism, physiological requirements, forage selection, and activity budgets can drive differences in resource and habitat use, causing sexual segregation [12, 17-20].

Trophic ecology has gained recent impetus by developments in stable isotope analysis (SIA). The quantification of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes, incorporated through the diet in body tissues across the lifespan of an organism, enables insights on diet composition and trophic relationships through the calculation of an isotopic niche in multivariate δ -space [21]. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vary spatially and temporally in food webs, enabling inferences on the basal energy source via $\delta^{13}\text{C}$ and on the trophic level via $\delta^{15}\text{N}$ [22, 23]. Thus, SIA can inform on various aspects of an animal's trophic ecology, including dietary and habitat use, trophic specialization, movement patterns, trophic coupling, and anthropogenic impact on the food web [24-27]. For these applications, SIA enables characterizing and quantifying niche properties, such as evenness and packing, width or area, position or trophic length, resource diversity, degree of overlap, dietary variation, and niche path trajectories [25, 28-32]. Moreover, tissues with different turnover rates from the same individuals allow resource use analyses at multiple temporal and spatial scales [33, 34]. For instance, metabolically active tissues (e.g., plasma, liver) convey short-term dietary information, while inert tissues (e.g., scute, claw, hair) incorporate long-term evidence. Therefore, intraspecific variation in body size and sex traits can be investigated, quantified, and revealed by SIA.

Isotopic niche parameters can inform about spatiotemporal patterns of niche shift, acting as predictors of intraspecific trait development and species responses to habitat alteration [35-38]. In disturbed habitats, the low resource availability alters the foraging behavior of species, causing either niche expansion and high niche overlap [39, 40], or collapse with a reduction of niche width and trophic level [27, 41]. The potential increase of competition causes extirpation of sensitive species, affecting community structure and the food web [42]. Further, human-induced trait changes can alter processes (migration, movement, maturation, and habitat selection) that reflect on individual fitness and population persistence and also trigger non-natural eco-evolutionary dynamics, including phenotypic plasticity and contemporary evolution [9]. The magnitude of the anthropogenic impacts on the food web can become even more severe when they fall on a top predator species through trophic cascades [43, 44].

Crocodylians are top predators and play a crucial role in maintaining the structure and functioning of food webs in diverse ecosystems, where the strength and dynamics of trophic relations are regulated by their intraspecific traits variation [45, 46]. They have an ontogenetic dietary shift: while hatchlings feed primarily on aquatic or terrestrial invertebrate prey, adults feed largely on large vertebrates and fish [47, 48]. As female crocodylians build terrestrial nests and tend to stay at or near the nest through incubation, there are often diet differences between nesting females vs. non-nesting females and males [49, 50].

Crocodylians take advantage of man-made or disturbed waterbodies, demonstrating some ecological adaptability and resilience to persist in agricultural landscapes [51, 52]. Therefore, they are model organisms for detecting and investigating the effects of human disturbance upon the food web and assessing the role of intraspecific trait variation on trophic dynamics. Here, using stable isotopes of carbon and nitrogen from different tissues, we investigate the effects of sex, ontogeny, and habitat use on the trophic niche of *Caiman*

crocodilus in a human-modified landscape at the Formoso River floodplain, central Brazil. We predicted (i) differences in niche width and position between tissues due to different turnover rates and changes in food resources induced by the seasonal dynamics of the floodplain; (ii) differences in niche position between natural (e.g. river and lake) and anthropogenic habitats (e.g. ditch and man-made ponds) due to the influence of agricultural nutrient input, but similarity in niche width and high overlap within habitats of the same origin; (iii) differences in niche width between the sexes because of differences in their foraging behavior, but high overlap in niche position due to larger prey items shared between them; and (iv) ontogenetic niche shift regarding $\delta^{15}\text{N}$ values (trophic level) and $\delta^{13}\text{C}$ values (basal source).

MATERIALS AND METHODS

Ethics statement

We conducted this study under permit SISBIO #13324-6, issued by Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais – IBAMA. All tissues were collected using non-lethal sampling techniques following standard protocols [53-55].

Study area

The study area is located at Praia Alta farm in the municipality of Lagoa da Confusão (Lat. 10°44'0.94"S; Long. 49°51'23.66"W), Tocantins, Brazil. The city is the most significant rice producer in the state, with 43,600 ha of irrigated rice funded by international and state programs to expand the infrastructure of irrigation projects [56]. The agricultural activity follows the hydrologic regime, with rice being cultivated in the rainy season (October to April) and soybean or other crops in the dry season (May to September) [57].

Lagoa da Confusão is in the Formoso River basin, a sub-basin of the middle Araguaia River basin, in the Cerrado–Amazonia ecotone [58]. The vegetation consists of alluvial and

semi-deciduous forests and floodplain grasslands [59]. In the wet season, the flood pulse interconnects most water bodies, including abandoned channels and oxbow lakes, which can span about 90,000 km², reach 8 m at some places, and last for up to 5 months [59]. The climate is Aw in the Köppen climate classification; the mean annual temperature is 26°C, the mean annual precipitation is 1,700 mm, and the air relative humidity is 40% in the dry season and 90% in the wet season [59-61].

Sampling

We sampled caimans in four habitats in July 2016: (i) river – the Formoso River, a tributary of the Javaés River, ca. 70 m wide and 5 m deep; (ii) lake – the Retiro Lake, covering ca. 5 ha, surrounded with riparian vegetation, and used for cattle watering; (iii) pond – a muddy water reservoir (0.3 ha, 1 m deep) for cattle watering, surrounded by pastures and with aquatic macrophytes; (iv) ditch – irrigation channels for agriculture (3 m wide, ca. 1.5 m deep). We captured 42 caimans in nocturnal spotlight surveys with the aid of locking cable snares or by hand [62, 63]. The number of captures was independent of animal size in all study habitats. We physically restrained the mouth and limbs of captured animals with ropes and adhesive tape and brought them to a field lab [63]. Within 24 h, from each captured caiman, we recorded the snout-vent length (SVL), body mass, and sex by cloacal examination and palpation of the penis [64]; collected tissue samples for SIA (below); placed a permanent and individual mark by notching tail scutes as a standardized numerical code; and released the animal at the same place of capture [65].

Stable isotope analyses

From each captured caiman, we collected samples of the claw (5 mm), tail scute (1 cm²), tail muscle (2 cm²), and blood (3 ml) [53-55]. We collected blood from the dorsal

cervical sinus using a 4 ml BD Vacutainer[®] blood collection kit with lithium heparin additive. Within four hours, we used a centrifuge (OMEGA Mod. 1 Labor Import[®]) to separate samples into red blood cells (RBC) and plasma components at 3,000 rpm for 60 s. We kept all tissue samples at -80°C in a cryogenic liquid nitrogen container. Back to the university, we washed claw, scute, and muscle samples with a 2:1 ratio chloroform: methanol solvent to extract lipids [66], dried them at 50°C to constant mass, and ground to a fine powder. We freeze-dried plasma and RBC samples for 24 h, weighed about 1-2 mg of each sample, and stored in 3 x 5 mm tin capsules.

The carbon and nitrogen isotope ratios were determined by combustion using an elemental analyzer (Carlo Erba, CHN-1100) coupled to a Thermo Finnigan Delta Plus mass spectrometer at the Laboratory of Isotope Ecology of the Centro de Energia Nuclear na Agricultura (CENA/Universidade de São Paulo), Piracicaba, SP, Brazil. The results were expressed in delta notation (δ), in parts per thousand (‰), based on internationally recognized standards. We used the following equation: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) = $(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1.000$), where R_{sample} and R_{standard} represent the heavy/light isotope molar ratio of the sample and standard, respectively. The standard used for carbon analysis was Vienna Pee Dee Belemnite (Vienna PDB; $^{13}\text{C}:^{12}\text{C}$ ratio = 0.01118), and the standard used for nitrogen analysis was atmospheric air ($^{15}\text{N}:^{14}\text{N}$ ratio = 0.0036765). Internal standards (tropical soil and sugarcane leaves) are routinely interspersed with target samples during analysis runs. The long-term analytical error for the internal standards is 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Most samples had C:N ratio values within acceptable limits in plasma [mean (SD): 3.4 (0.2)], RBC [3.0 (0.2)], muscle [3.4 (1.9)], claw [3.0 (0.1)], and scute [2.7 (0.1)] [66]. However, 17 muscle samples had a C:N ratio above 4.0, indicating a high lipid content with a likely effect on $\delta^{13}\text{C}$ values [66, 67]. To solve the problem, we decided to impute the $\delta^{13}\text{C}$

values of these samples [68]. We did not consider using lipid correction equations because such equations are species- and tissue-specific, focusing mainly on fishes [67].

Statistical analyses

We treated the missing values (the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for plasma and RBC samples of one individual; $n = 4$) and $\delta^{13}\text{C}$ values for muscle samples with a C:N ratio > 4 ($n = 17$), representing 0.1% of all data, through imputation using the R package MISSFOREST [69]. Imputation is a viable solution where missing data can introduce bias and lead to incorrect conclusions due to masking biological patterns [68]. The MISSFOREST is among the best imputation approaches for animal trait data [68, 69]. It is a non-parametric method that relies on Random Forest algorithms [70], and thus, a machine learning technique that handles in an iterative imputation scheme by training a Random Forest on observed values, predicting the missing values, and then proceeding iteratively [69]. Its performance is assessed using the normalized root mean squared error (NRMSE), where an excellent performance leads to a value close to 0 [69]. In our case, the NRMSE was 0.023%.

Then, we initially calculated summary statistics of the *C. crocodilus* dataset, expressing values as mean (standard deviation). We assessed between-habitat differences in the SVL of caimans using a one-way ANOVA, followed by a Tukey posthoc test, and between sexes using a non-parametric ranked t -test, i.e., a Mann-Whitney test. We used a significance level of 5% in hypothesis testing.

To assess the effects of tissue, SVL, habitat, and sex on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, we used a Bayesian model averaging approach [71, 72]. In this analysis, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were response variables (analysis for each one), while tissue, SVL, habitat, sex, and all possible interactions among them were the predictors. We implemented the Bayesian model averaging with R package BMS [73] using 10^6 iterations, 10^5 burn-ins, the birth-death model-sampler,

BRIC Zellner’s g-prior, uniform model size prior, retention of 1,000 best models, and default settings for the other parameters. In the modeling, the SVL was standardized around the mean with one standard deviation. Necessary to Bayesian model averaging, we numerically codified and ordered the categorical predictors: sex (1 – female; 2 – male); habitat (1 – river; 2 – lake; 3 – pond; 4 – ditch); and tissues according to incorporation time (1 – plasma; 2 – muscle; 3 – RBC; 4 – claw; 5 – scute; [74]).

We assessed models with the posterior model probability correlation (*Corr.PMP*), which indicates convergence, and the shrinkage coefficient as a Bayesian “goodness-of-fit” indicator [73]. We identified the most important predictors through the posterior inclusion probability (PIP), which is the sum of PMP for all models including the predictor. We also performed a diagnostic of the standardized coefficients posterior means (*PostMean*) and posterior standard deviation (*PostSD*). The posterior mean gives the intensity and direction of the relationship between predictor and response, while the posterior standard deviation reflects the strength of the dispersion of the predictor. Commonly, higher PIP values reflect in higher *PostMean* and *PostSD*.

Next, we assessed differences in resource use and niche width between tissues, habitats, and sexes through the standard ellipse and estimated Bayesian standard ellipse area metrics (SEA_B ; in $\%o^2$) using the R package SIBER [28]. In the analysis, we considered SEA_B as a niche width measure and the standard ellipse as the niche position occupied in the bidimensional isotopic space. We estimated the SEA_B through a Markov chain Monte Carlo simulation with 10^4 iterations, 10^3 burn-ins, and two chains [28].

To compare niche width between groups (e.g., tissue vs. tissue, habitat vs. habitat, or male vs. female), we performed pairwise tests using SEA_B values drew in the simulations for each group, inferring the certainty of difference through the probability that one group was larger (reference group) than another: $SEA_{groupA} > SEA_{groupB}$ [28]. Thus, the probability of

difference can range from 0.5 (equal probabilities or smaller certainty) to 1.00 (higher certainty). Furthermore, we assessed diet similarity between groups by niche overlap [28, 39], calculated through the area of overlap between two fitted ellipses based on the maximum likelihood with 95% of the data using function *maxLikOverlap*. We performed all statistical tests in R version 3.6.1 [75].

RESULTS

The sampled *C. crocodilus* had mean SVL of 56.22 (20.17) cm, with significant differences in SVL between habitats ($F_{3,38} = 4.072$, $P = 0.013$). Larger individuals were found in the river [69.16 (15) cm] in relation to lake [53.43 (17.2) cm], pond [48.11 (17.67) cm], and ditch [47.56 (22) cm]. The sex ratio was 1.1 female for 1 male, with no significant difference in SVL [male: 60.83 (23.41) cm, $n = 20$; female: 52.03 (16.13) cm, $n = 22$; ranked $t_{40} = -1.755$, $P = 0.08$].

The Bayesian model averaging for $\delta^{13}\text{C}$ demonstrated that SVL, sex, sex:SVL interaction, tissue, and habitat were the most important predictors with higher PIPs and standardized coefficients (Table 1, Fig 1A). Also, they were included in the top model, which concentrated 14% of the posterior model probability ($\text{Corr.PMP} = 0.99$, shrinkage = 0.99). $\delta^{13}\text{C}$ values decreased with SVL (Fig 2A). Females had higher $\delta^{13}\text{C}$ and range than males (Fig 2B). $\delta^{13}\text{C}$ values increased according to isotopic incorporation time, from smaller values in plasma to higher values in scute (Fig 2C). $\delta^{13}\text{C}$ values were smallest in the river and highest in the ditch (Fig 2D). The $\delta^{13}\text{C}$ –SVL relationship was dependent on sex, with a stronger $\delta^{13}\text{C}$ decrease in females than males with increasing SVL (Fig 2E).

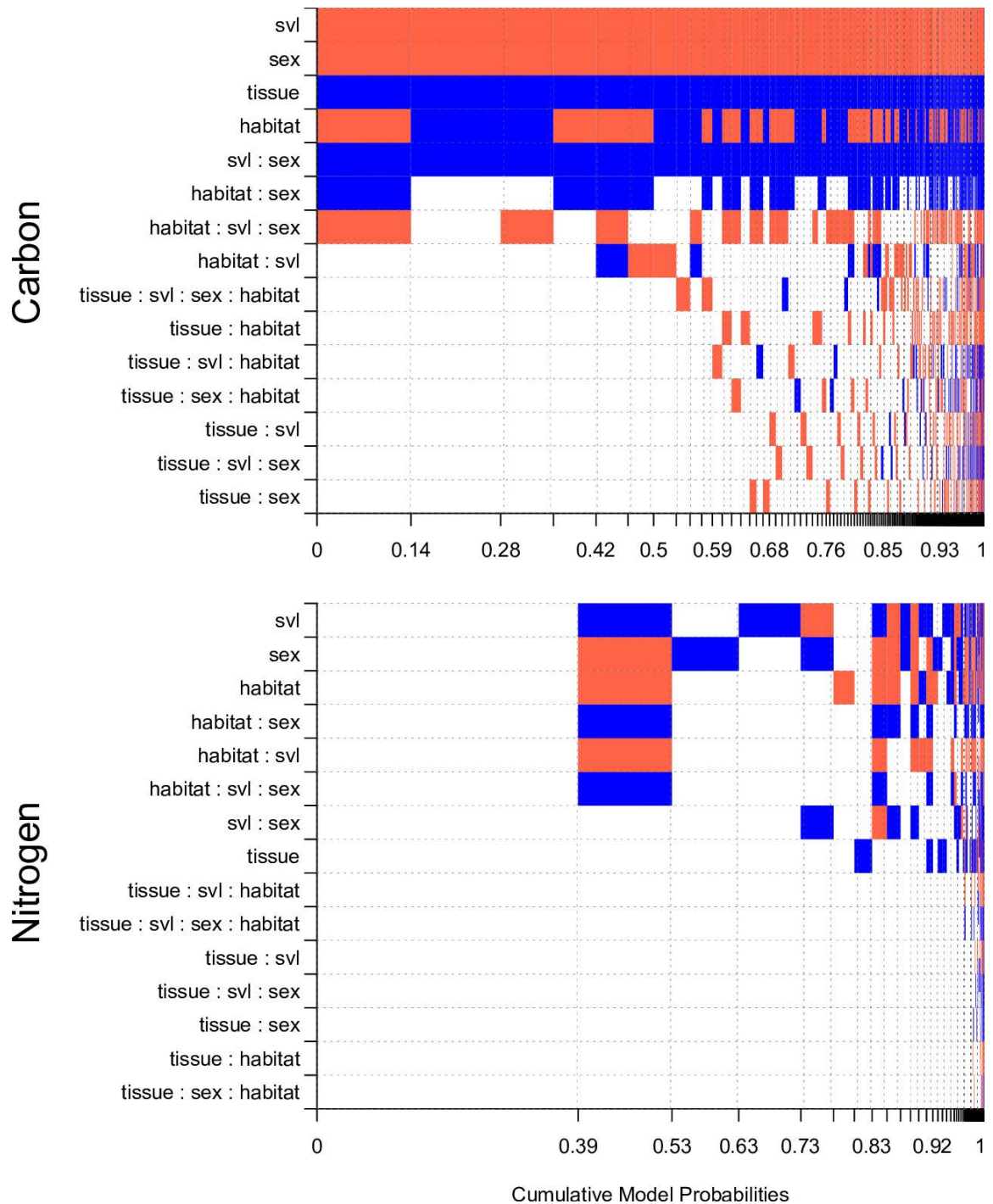


Fig 1. Bayesian model averaging of $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) values. The Y-axis contains the predictors of carbon or nitrogen stable isotopes, while the X-axis is scaled by the posterior model probabilities. Colors indicate predictor inclusion in models: positive coefficients are in blue, negative coefficients are in red, and non-inclusion is in white.

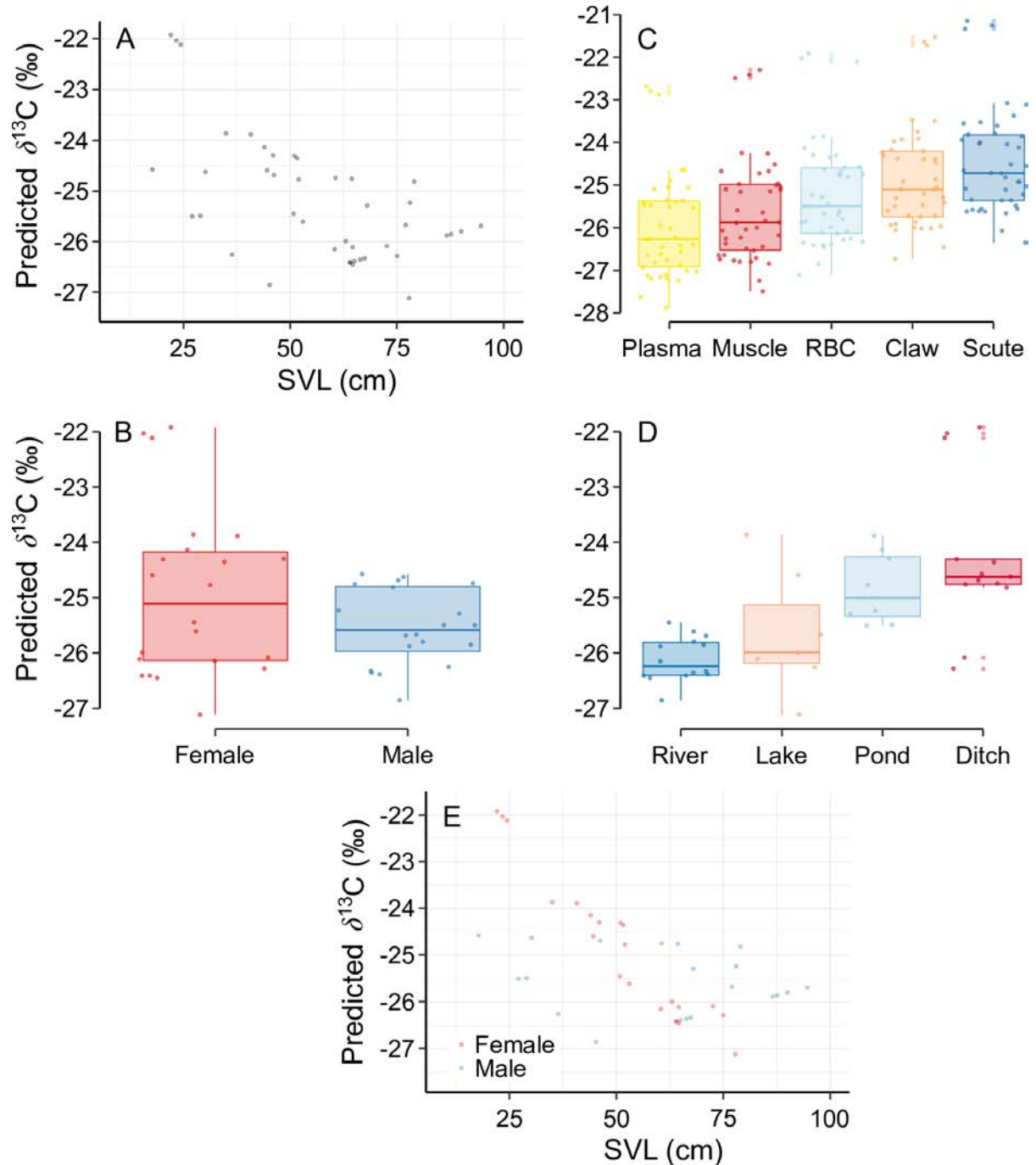


Fig 2. Most significant predictors of $\delta^{13}\text{C}$: (A) SVL, (B) sex, (C) tissue, (D) habitat, and (E) interaction between SVL and sex. Tissues are ordered according to turnover rates [74]. Except for (C), each point corresponds to the mean $\delta^{13}\text{C}$ value for all tissues of one individual. Lines indicate the BMA model fit, and their respective polygons correspond to the 95% confidence interval.

Table 1. Bayesian model averaging estimates for $\delta^{13}\text{C}$.

Predictor	PIP	<i>PostMean</i>	<i>PostSD</i>	<i>CondPosSign</i>
SVL	1.000	-3.422	1.025	0.000
Sex	1.000	-0.984	0.790	0.000
Tissue	0.999	0.403	0.127	1.000
SVL : Sex	0.999	2.034	0.621	1.000
Habitat	0.999	0.137	0.420	0.489
Habitat : Sex	0.524	0.253	0.283	1.000
Habitat : SVL : Sex	0.476	-0.111	0.184	0.001
Habitat : SVL	0.229	0.053	0.276	0.474
Tissue : SVL : Sex : Habitat	0.108	-0.002	0.010	0.227
Tissue : Habitat	0.097	-0.006	0.030	0.000
Tissue : SVL : Habitat	0.082	0.000	0.013	0.392
Tissue : Sex : Habitat	0.081	-0.001	0.014	0.408
Tissue : SVL	0.070	-0.001	0.040	0.154
Tissue : SVL : Sex	0.069	0.001	0.023	0.295
Tissue : Sex	0.068	-0.004	0.046	0.042

PIP: posterior inclusion probabilities, i.e., the sum of posterior model probabilities for all models wherein a predictor was included; *PostMean*: coefficients averaged over all models; *PostSD*: coefficients' posterior standard deviations; *CondPosSign*: posterior probability of a positive coefficient expected value conditional on inclusion.

For the $\delta^{15}\text{N}$, the Bayesian model averaging analysis indicated that the predictors did not have a good percentage of inclusion in the best models, resulting in the null model as the top model, which corresponded to 39% of the posterior model probability (*Corr.PMP* = 0.94, shrinkage = 0.99, Fig 1B). The most important predictors were sex and SVL, with higher PIPs and standardized coefficients (Table 2). Both predictors were in the second-best model, explaining only 14% of the posterior model probability. Although SVL had a negative coefficient, it was positive in 63% of the models (see *CondPosSign* in Table 2), demonstrating an overall positive relationship with $\delta^{15}\text{N}$ (Fig 3A). For sex, males had higher $\delta^{15}\text{N}$ values than females (Fig 3B). The remaining predictors had meager contributions to posterior model probability and smaller PIPs and standardized coefficients, indicating a small predictive power.

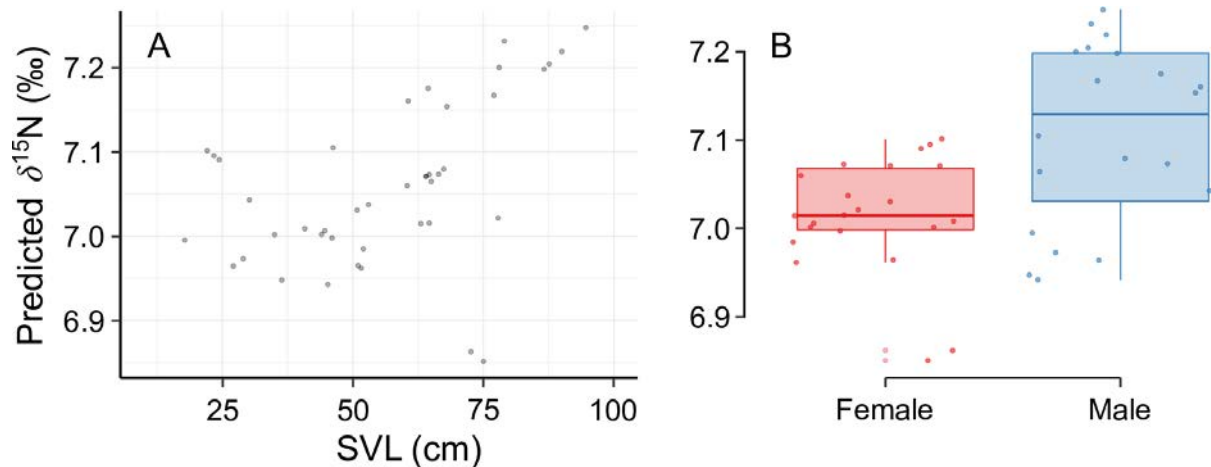


Fig 3. Most significant predictors for $\delta^{15}\text{N}$: (A) SVL, (B) sex. Each point corresponds to the mean $\delta^{15}\text{N}$ value for all tissues of one individual. The line is the BMA model fit, and its respective polygon corresponds to the 95% confidence interval.

Table 2. Bayesian model averaging estimates for $\delta^{15}\text{N}$.

Predictor	PIP	<i>PostMean</i>	<i>PostSD</i>	<i>CondPosSign</i>
SVL	0.358	-0.030	0.266	0.637
Sex	0.341	0.024	0.200	0.853
Habitat	0.157	-0.025	0.112	0.316
SVL : Sex	0.132	0.050	0.151	0.978
Tissue	0.071	0.001	0.013	0.962
Habitat : SVL	0.051	-0.013	0.070	0.000
Habitat : Sex	0.050	0.016	0.076	1.000
Habitat : SVL : Sex	0.023	0.004	0.030	0.946
Tissue : SVL	0.002	0.000	0.005	0.043
Tissue : SVL : Sex	0.002	0.000	0.003	0.996
Tissue : Sex	0.001	0.000	0.003	0.994
Tissue : SVL : Habitat	0.001	0.000	0.001	0.000
Tissue : Habitat	0.001	0.000	0.001	0.010
Tissue : Sex : Habitat	0.000	0.000	0.001	0.615
Tissue : SVL : Sex : Habitat	0.000	0.000	0.001	0.752

PIP, posterior inclusion probabilities, i.e., the sum of posterior model probabilities for all models wherein a predictor was included; *PostMean*, coefficients averaged over all models; *PostSD*, coefficients' posterior standard deviations; *CondPosSign*, posterior probability of a positive coefficient expected value conditional on inclusion.

Concerning isotopic niches, the tissues were concentrated in a specific isotopic region, with high overlap overall (Fig 4A). Muscle–scute ellipses had the smallest niche overlap (22.6‰²), while RBC–plasma had higher overlaps (35.7‰², S1 Table). Niche width varied

significantly among tissues (Fig 4D, S2 Table), with the ascending order: muscle (24.5‰²), scute (32.6‰²), claw (32.8‰²), plasma (36.2‰²), and RBC (41.6‰²).

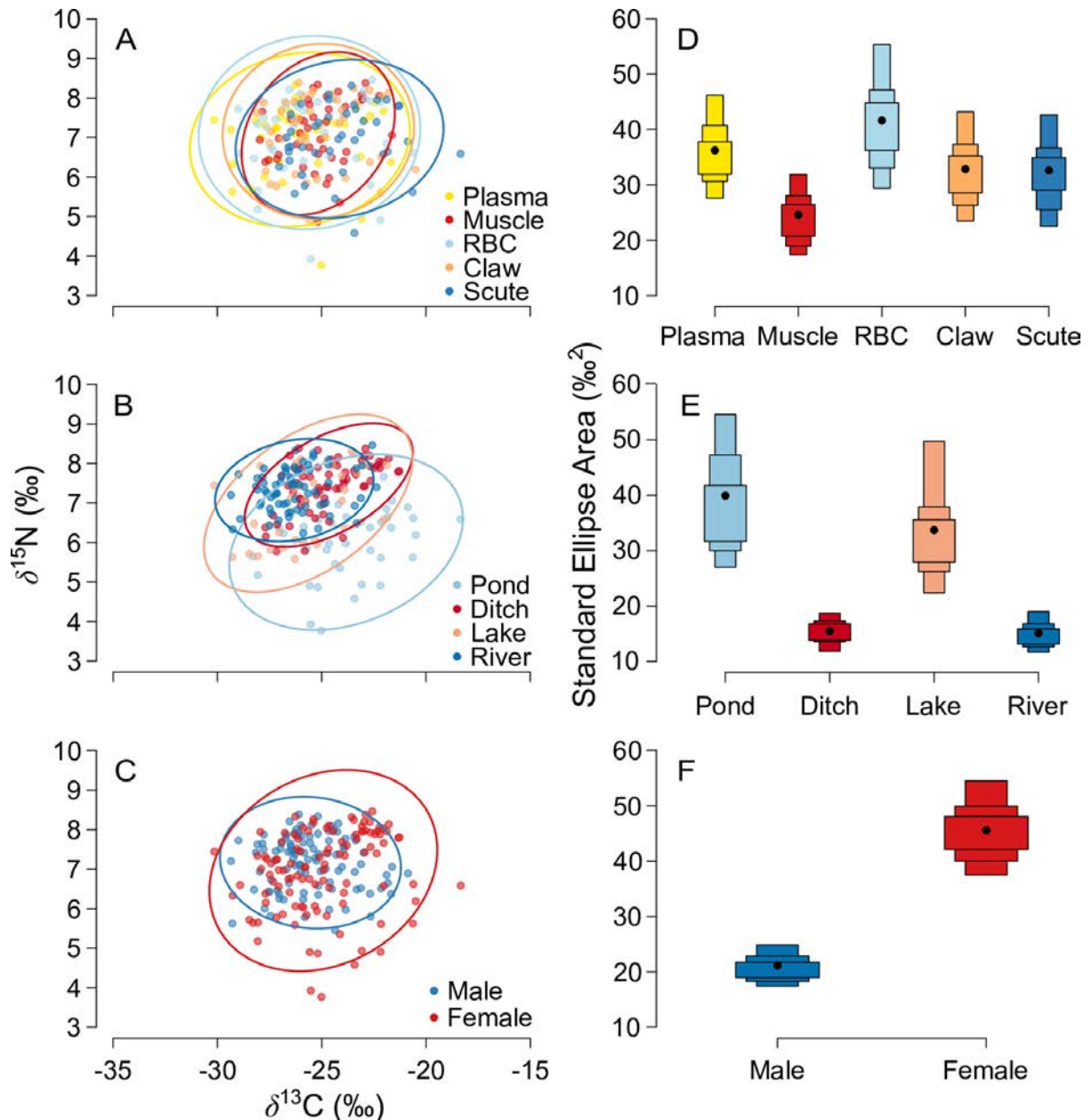


Fig 4. Isotopic niches and estimated niche width for tissues (A, D), habitats (B, E), and sexes (C, F). Scatter plots for habitats and sexes exhibit mean isotopic values of all tissues from each individual. Solid lines represent the core isotopic niche space. Black dots correspond to the mean, and boxes represent 50%, 75%, and 95% credibility intervals.

Habitats also concentrated their isotopic niches, whereas pond had a visible large niche and a short displacement in location (Fig 4B). Niche overlap area ranged from 8.9‰²

between river and pond to 19.8‰² between lake and pond (S3 Table). Overall, the pond (39.9‰²) and lake (33.7‰²) had larger niche widths compared to the river (15.0‰²) and ditch (15.4‰²) (Fig 4E, S2 Table). Patterns of niche width and overlap between habitats within tissues overall resembled patterns of the pooled tissues, except for muscle (S1 Fig).

The females' niche encompassed fully the males' niche, with overlap area of 22.8‰² (Fig 4C). There was a pronounced difference in niche width between sexes, with females having a larger niche than males (respectively, 45.5‰² and 21.1‰², Fig 4F). Overall, patterns of niche width and overlap between sexes within habitats (S2 Fig) or tissues (S3 Fig) resembled those of the pooled data.

DISCUSSION

Patterns of variation in the trophic niche of a population reveal mechanisms that reduce intraspecific competition for habitat or food resources and improve population fitness. Our study contributes with new information and perspectives on habitat and resource use of a semi-aquatic top predator population, revealing a particular dynamic in the human-modified floodplain reflected in (i) temporal invariability of the trophic niche; (ii) discrete differences in the food resource diversity among habitats; and (iii) resource partitioning driven by sexual and ontogenetic differences in the foraging behavior across trophic levels and basal sources.

Seasonal isotopic shifts are known in basal sources and consumers of the floodplains [76, 77]. These shifts are induced by trophic and nutrient dynamics associated with biotic and abiotic processes [22, 78-80], as well as by anthropic activities and land use change [36-38, 41]. In our study, *Caiman crocodilus* showed variation in $\delta^{13}\text{C}$ values, increasing throughout distinct time windows (i.e., tissues), while $\delta^{15}\text{N}$ did not differ among tissues. Hence, our results suggest that niche width differed among tissues mediated by a discrete variation in the

basal source in the floodplain food web, but not associated to shift in the trophic level to support a clear seasonal difference in resource availability and use.

Our results reflected a population of isotopic specialists and dietary generalists of a conceptual model developed by [24] (panel B of Fig 1), characterized by integrating short- and long-term isotopic information invariably and homogeneously [31]. The isotopic niche positions among tissues (i.e., niche ellipses) suggest the consumption of the same prey mixture and a constant diet throughout the tissue integration time. Diverse factors could act mutually to reproduce a population of isotopic specialists and dietary generalists. First, the isotopic variability of caiman prey could be not so high between seasons in the Formoso River floodplain to reflect in distinct isotopic niche positions among tissues. The variation of isotopic composition from the diet is assimilated and weighted to the isotopic composition of the tissues according to their proportional contribution, the base of diet contribution studies using mathematical mixing models [21, 81]. For this, we assume that available prey items were at isotopic equilibrium, that is, isotopic compositions in the tissues reflected the time-integrated average of the habitats used by *C. crocodylus* [22]. Future directions for research are in identifying the isotopic composition of different prey types and determining the contribution of each resource in the caiman diet, considering the seasonality [76, 77], and the use of complementary techniques such as stable isotopes analysis and gut content analysis [82]. The findings will help elucidate the prey types that contribute to maintaining an isotopic invariability of caiman niche during the dry and wet seasons in the floodplain.

Second, the isotopic similarity among tissues could be driven by a diet-tissue discrimination factor, i.e., a difference between the isotopic composition of a consumer tissue and its diet, expressed in $\Delta^{13}\text{C}$ (carbon) or $\Delta^{15}\text{N}$ (nitrogen) [23, 34, 81]. Discrimination factors have several sources of variation [83, 84], including differences among tissues relates to protein turnover, amino acid allocation [34, 83, 84], and even diet [83]. Crocodylians

apparently have low discrimination factors in tissues [74, 85-87]; thus, considerable between-tissue differences in $\Delta^{13}\text{C}$ or $\Delta^{15}\text{N}$ could reflect distinct ingested prey and seasonal isotopic niche according to tissue assimilation time. The uncertainties concerning the seasonal variability in prey consumption and its isotopic values, and different diet-tissue discrimination factors could interact to generate similar isotopic values among tissues [31]. Hence, the trophic niche estimates have potential similarity in the isotopic area between each tissue, overlapping among them.

Significant differences in crocodylians trophic niches are observed in cross-ecosystem studies (e.g., freshwater and marine-estuarine systems) in which prey differ clearly in diversity and isotopic composition according to primary producers and trophic levels [20, 26, 85, 88]. Alternatively, crocodylian species also exhibit clear niche segregation under sympatry [82]. Our results demonstrated high niche redundancy among habitats revealed by niche position, indicating that they supply a large part of resources from the same pool (Fig 4B, S1 Fig). Further, habitats did not differ in trophic structure ($\delta^{15}\text{N}$ values) to note a human disturbance on caiman trophic level through some anthropogenic nitrogen input, like evidence in some studies [36-38]. Otherwise, we found two distinct groups of caiman niche width resembling the pattern throughout the tissue time windows (Fig 4E), suggesting differences in food resources in the habitat scale.

The intrinsic ecological dynamic of wetland animals in the floodplain could produce differences in niche width and high niche overlap among habitats in our human-modified landscape. The dynamic in the resource diversity and availability across several different aquatic habitats and waterbodies in floodplain ecosystems, mediated by seasonal flood pulses and hydric connectivity, could influence trophic niche parameters of consumers according to their habitat use and mobility [76, 89]. Consequently, habitats could vary their suitability for caimans or sustain a complex food web with larger animals [88, 90, 91]. For example, smaller

waterbodies complement the insufficient energy of autochthonous production with an allochthonous subsidy [79, 80]. Some studies show that terrestrial food web can be more important in supporting crocodylians than aquatic food web [82, 88, 91]. Therefore, large predators may reside in an aquatic habitat but not participate in its food web [88, 90]. On the other hand, larger habitats (i.e., river and lakes) can supply resources for small ones due to higher availability and condition to sustain a complex food web [26, 90], where caimans have movement patterns across habitats in the landscape [26, 85, 92]. Hence, a population in a habitat can comprehend a combination of individuals with broad home ranges and highly mobiles among habitats (larger isotopic variability) and individuals with small home ranges or residents (lower isotopic variability), influencing on the niche width measure for that population of the habitat [88, 90, 92]. In this sense, landscape configuration and composition impose some influence on how populations use habitats and explore the resources across the landscape, dynamizing trophic relations of the food webs and affecting their trophic niche position and width [14, 40].

However, we should be alert on the food web of the habitats and caiman trophic niche regarding the possible influence of the anthropogenic disturbance. For example, we found similar results to studies in the tropical floodplains [82, 92], where the decrease in $\delta^{13}\text{C}$ values is associated to C_3 carbon from autochthonous aquatic resources [82]. Nonetheless, a C_3 carbon may come from soybean and rice crops, which have C_3 photosynthetic pathway and are the most common crops harvested in the Formoso River floodplain [57]. The occurrence of caimans in agricultural ditches can imply in the incorporation of agricultural C_3 inputs and differ from natural habitats. To investigate such effect that bulk tissue stable isotope analysis is unable, the use of compound-specific stable isotopes analysis (CSIA) can be ideal for discriminating and identifying differences in the basal source of natural and anthropogenic habitats [93, 94]. Another way, the land use cover may promote C_4 energy source in the food

web due to pasturelands in the landscape [37, 39, 77], generating larger niches and high overlaps [37, 39]. Although our results did not show that caimans incorporate C₄ energy source ($\delta^{13}\text{C} > -18\text{‰}$), populations in man-made ponds have potential susceptibility for such effect.

Additionally, we observed that ditch and river had smaller niche width. Studies that report smaller niche widths suggest a homogenization of resource, and loss of multiple energy flow pathways in the agricultural system [27, 41], which have implications to structure and stability of food webs [6, 95]. However, caimans could be coping with the cost of habitat alteration, changing the feeding strategy at the individual level to reduce intraspecific competition to persist in disturbed habitats [96, 97], developing some degree of individual specialization [1, 4], including mediated by sex [18-20]. Future studies can investigate the hypothesis of individual specialization as a mechanism for adaptation of caimans in the disturbed areas.

Sexual body-size dimorphism can trigger niche divergence and decrease intersexual competition [20, 98]. This can result from differences related to physiological requirements and cost-benefit ratios of prey, conducting in distinct resource use on the same habitat and enabling the coexistence of individuals in the population [12, 17-19]. For example, sexual niche segregation can be evident seasonally due to sex-specific seasonal foraging behavior related to reproduction [17, 19]. In *C. crocodilus*, prior conventional dietary studies reported no divergence between sexes [47, 48], but new information associated nesting strategy and reproduction period brought evidence of sexual and seasonal dietary differences [49]. Nesting females (reproductively active at SVL > 60 cm) change the diet to more terrestrial prey in reason of the nesting attendance (~3 months) compared to non-nesting females and males that stay in the waterbody and consume aquatic prey [49]. Our findings revealed through stable isotopes that the female population had a larger niche than the male population in reason of

resource exploitation varying as the habitat (S2 Fig). Although we could not infer about seasonal period and reproduction status (not possible due to ultrasonography tools and sample size restrictions), such understanding supports our results; it seems plausible that our female population could have comprehended reproductive ones that forage during the nesting activity, broadening the female niche width. Otherwise, the high overlap between sexes indicates the similarity and sharing of resources. The verification of isotopic niches for each habitat and throughout the tissue time windows provides compelling evidence of high overlaps (S2 and S3 Figs).

The ontogenetic shifts suggest a sex-related body-sized organization to reflect niche partitioning. In our study, $\delta^{15}\text{N}$ demonstrated a positive relationship with the ontogenetic shift and no statistical difference between sexes. The positive body size- $\delta^{15}\text{N}$ relationship reveals the predicted shift in trophic level [35, 88, 92, 98]; hatchlings consume prey of lower trophic levels (invertebrates in larger quantity), while adults consume more protein-rich diets composed of prey in higher trophic level, like larger vertebrates and fishes [47, 48, 98]. Additionally, we found that $\delta^{13}\text{C}$ was dependent on sex during trophic ontogenetic shifts: females had a higher negative slope than males, suggesting a distinct basal source. Considering both patterns, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, it is probable that caimans may be partitioning food resources on a microhabitat scale [35]. Such findings indicate a social organization to decrease intraspecific competition with a distinct niche shift as the ontogeny and sex. Further, agonistic behaviors can limit some groups to the access of food resources in the microhabitat level, forcing a niche partitioning [35, 92].

The intraspecific variation in caimans must be the concern of environmental decision-makers and stakeholders since that caimans use anthropogenic habitats and human-crocodilians conflicts can generate sex-related mortality – due to sexual dimorphism (males are larger than females) – with implications on the population sex-ratio and possible local

population declines. The sex-specific diets may lead to differential exposure to anthropogenic pollutants or agricultural nutrient input [12], the nesting strategy and foraging behavior of reproductive females may increase their chances of consuming terrestrial prey with agricultural origins [49, 50]. Contributions to reduce deleterious effects on a determined intraspecific trait relates to recognition by landowners that anthropogenic waterbodies could comprehend ecological purposes too, implicating in the sustainable management of water resource and land use associated to actions of waterbody restorations to enhance ecological results. For instance, actions that improve habitat conditions to several wetland species beyond caimans, such as habitat heterogeneity, diversity and connectivity, water stability, native vegetation buffer zone, non-use of agrochemicals.

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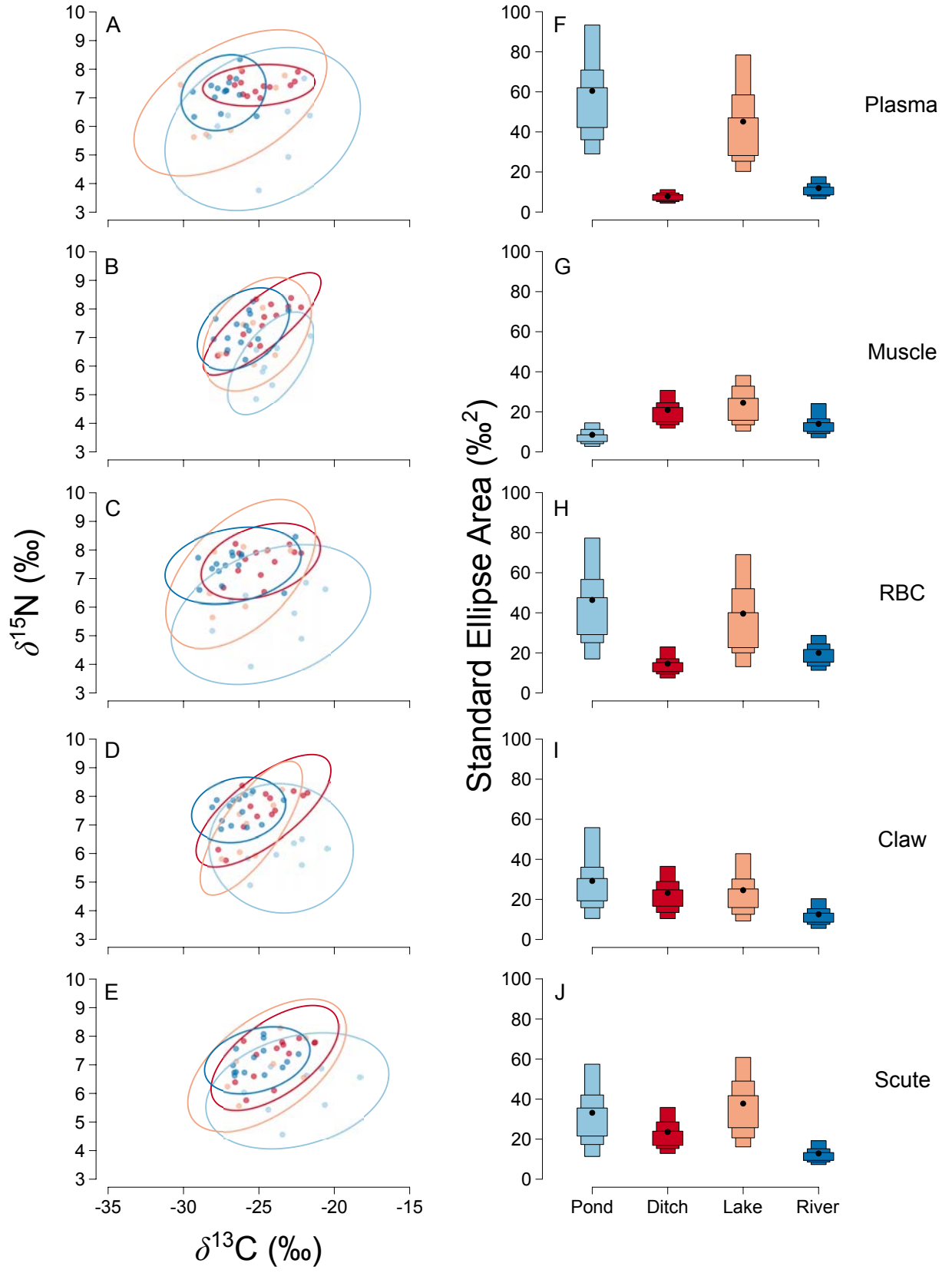
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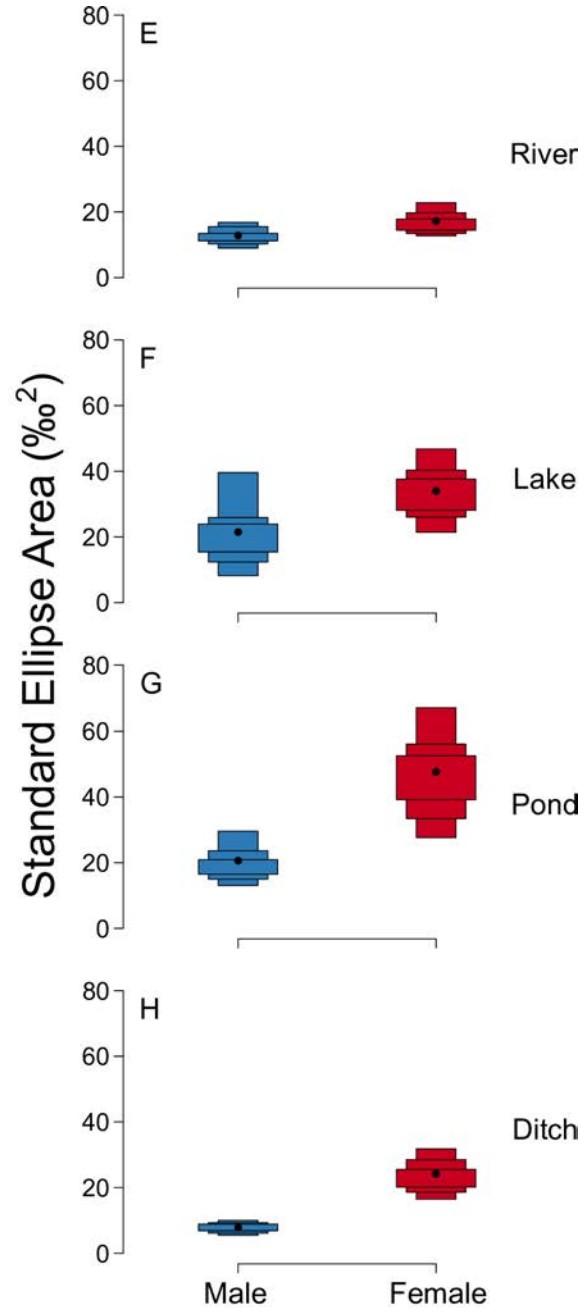
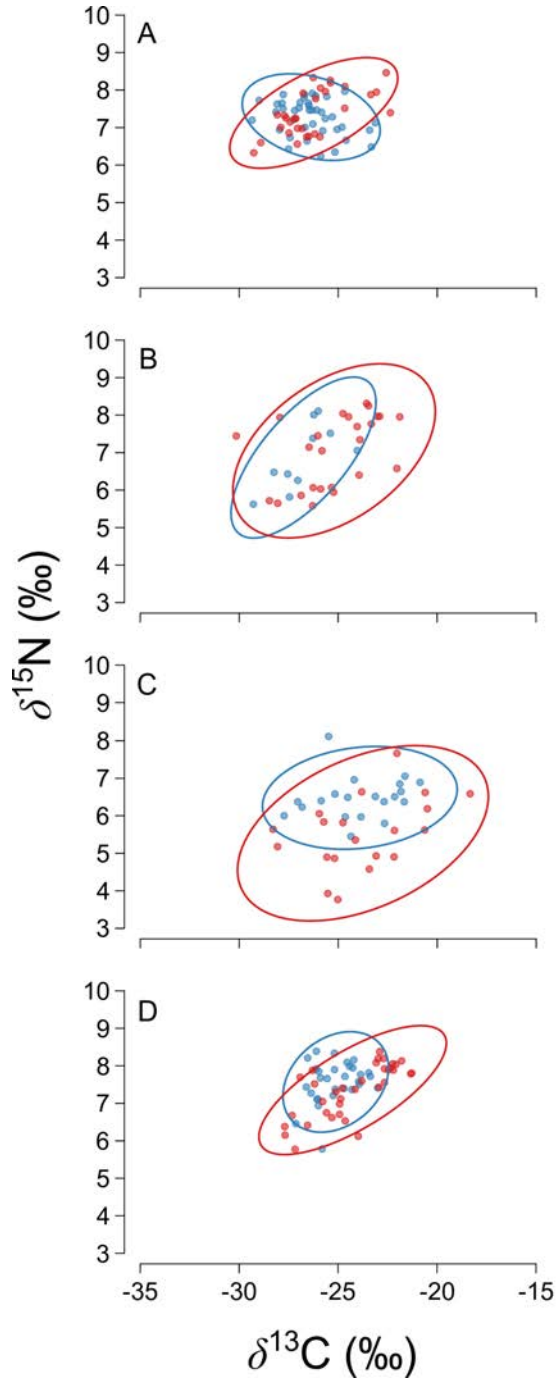
FIGURES

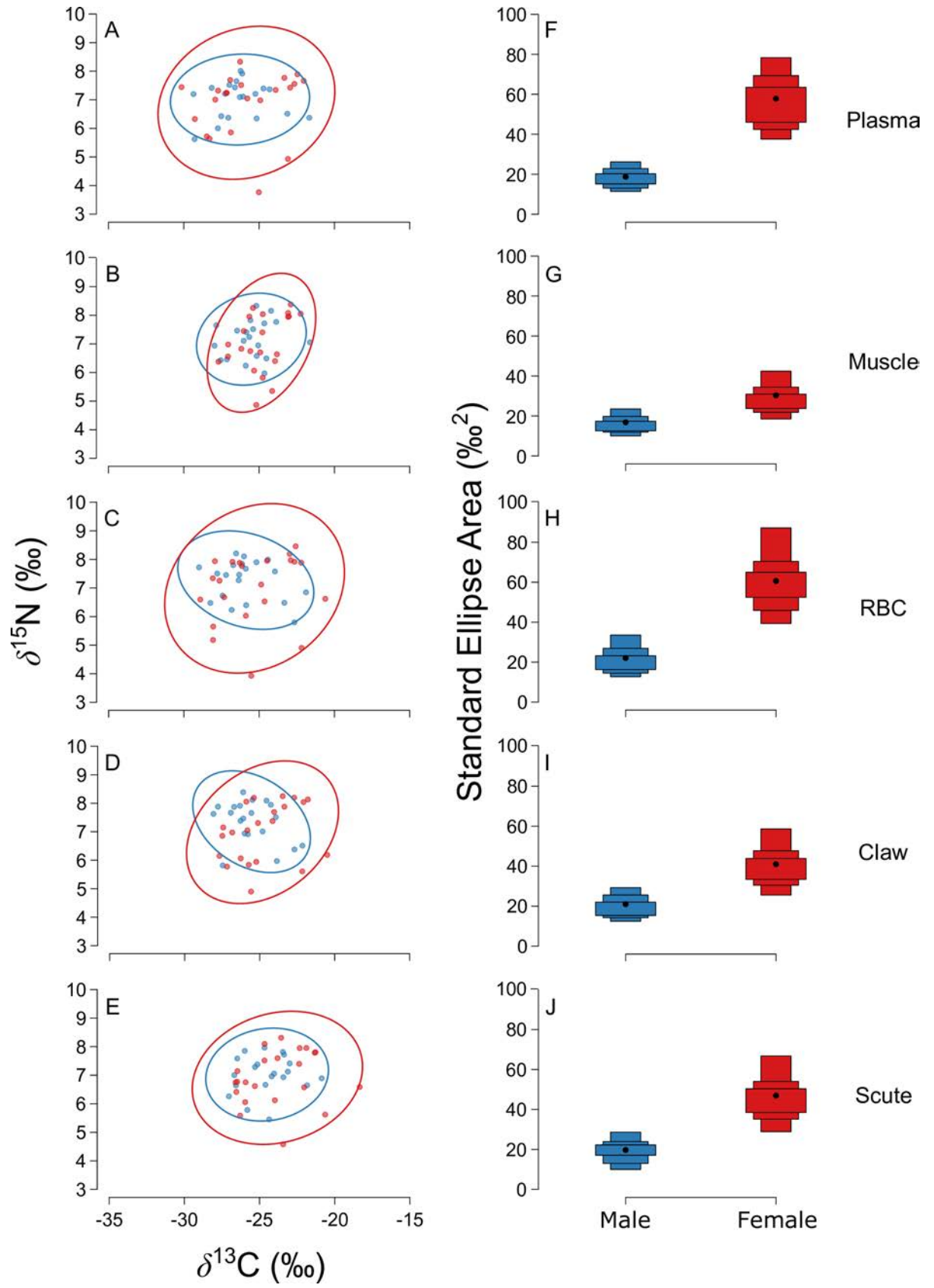
S1 Fig. Isotopic niches and estimated niche width for habitats. Habitat data for plasma (A, F), muscle (B, G), RBC (C, H), claw (D, I), and scute (E, J). Solid lines represent the core isotopic niche space. Black dots correspond to the mean and boxes represent the 50%, 75% and 95% credible intervals.

S2 Fig. Isotopic niches and estimated niche width for sexes. Sex data in the river (A, E), lake (B, F), pond (C, G), and ditch (D, H). Scatter plots had the isotopic values from all tissues. Solid lines represent the core isotopic niche space. Black dots correspond to the mean and boxes represent the 50%, 75% and 95% credible intervals.

S3 Fig. Isotopic niches and estimated niche width for sexes. Sex data for plasma (A, F), muscle (B, G), RBC (C, H), claw (D, I), and scute (E, J). Scatter plots had the isotopic values from all habitats. Solid lines represent the core isotopic niche space. Black dots correspond to the mean and boxes represent the 50%, 75% and 95% credible intervals.







TABLES

S1 Table. Niche overlap area among tissues. Values in %².

	Muscle	RBC	Claw	Scute
Plasma	23.3	35.7	30.6	26.2
Muscle	–	23.5	23.5	22.6
RBC		–	32.6	28.8
Claw			–	27.3
Scute				–

S2 Table. Probability of difference between groups for tissues and habitats. The first group was the largest group (reference for comparisons).

Tissue	
Comparison	Probability
$SEA_{RBC} > SEA_{muscle}$	1.0
$SEA_{plasma} > SEA_{muscle}$	0.97
$SEA_{scute} > SEA_{muscle}$	0.90
$SEA_{nail} > SEA_{muscle}$	0.87
$SEA_{RBC} > SEA_{scute}$	0.84
$SEA_{RBC} > SEA_{nail}$	0.82
$SEA_{plasma} > SEA_{RBC}$	0.78
$SEA_{plasma} > SEA_{nail}$	0.71
$SEA_{plasma} > SEA_{scute}$	0.68
$SEA_{nail} > SEA_{scute}$	0.55
Habitat	
$SEA_{pond} > SEA_{river}$	1.0
$SEA_{pond} > SEA_{ditch}$	1.0
$SEA_{lake} > SEA_{river}$	1.0
$SEA_{lake} > SEA_{ditch}$	1.0
$SEA_{pond} > SEA_{lake}$	0.7
$SEA_{river} > SEA_{ditch}$	0.6

S3 Table. Niche overlap area among habitats. Values in %².

	Ditch	Lake	River
Pond	11.7	19.8	8.9
Ditch	-	17.1	11.6
Lake		-	14.7
River			-

CAPÍTULO 2. SPATIALLY EXPLICIT TROPHIC NICHE AND AGRICULTURAL CARBON INPUT IN THE FOOD WEB: FINDINGS FROM A SEMI-AQUATIC TOP PREDATOR ACROSS A HUMAN-MODIFIED LANDSCAPE GRADIENT IN THE MIDDLE ARAGUAIA RIVER FLOODPLAIN, CENTRAL BRAZIL

ABSTRACT

1. Landscape modifications for agribusiness from land-use conversion and fragmentation affect trophic niche of species through changes in habitat and resource diversity in a spatial context, including for highly mobile and generalist top predators, like crocodylians in floodplains. To ignore spatial context, species traits, environmental heterogeneity, and landscape attributes to define a trophic niche for top predators can confound and make misinterpretations in the assessment of anthropogenic impacts.

2. We investigated the effects of landscape modifications upon food webs in the Araguaia floodplain, central Brazil, using the top predator and indicator species *Caiman crocodilus* (Crocodylia, Alligatoridae). We estimated trophic niche parameters (position and width) by stable isotope analysis for three tissues with different integration time, and evaluated changes in caimans niche parameters through spatial hierarchical Bayesian modeling, accounting for habitat use, intraspecific trait variation (sex and body size), and landscape attributes (composition and configuration). Additionally, we performed the carbon isotope analysis of essential amino acids to investigate differences in primary producers between waterbodies from natural and anthropogenic areas.

3. Spatial distribution of stable isotope compositions showed high values in agricultural areas while natural areas had lower values. Habitats reflected differences in the caiman isotopic niche width, but their niche positions demonstrated similar locations among them

across tissues. Remarkably, the spatial distribution of caiman niche width demonstrated that the largest agricultural irrigation project had a higher value, relied on by the effect of extensive pasture coverage areas surrounded agricultural places. Essential amino acids showed a clear distinction in basal sources between natural and anthropogenic habitats. Our findings indicated that agricultural carbon sources can support in part caiman food webs in agricultural areas.

4. *Synthesis and applications.* Realistic trophic responses of species face landscape alterations depend on intraspecific traits, habitat perception, and landscape characteristics in a spatially explicit context. The use of the landscape by species mediates the food web dynamic in fragmented landscapes. The findings that crop energy can support a top predator imply alterations of trophic control, energy flow dynamic, and long-term biodiversity persistence in human-modified landscapes. Environmental policies, conservation planning, and land use management should rely on spatial trophic dynamic information to implement future actions.

Keywords: basal energy source, compound-specific stable isotope analysis, crocodilians, essential amino acids, human disturbance, landscape configuration and composition, spatial hierarchical Bayesian modeling, trophic dynamic.

INTRODUCTION

Agribusiness has required extensive areas to increase food production, compromising natural biodiversity, and processes in the ecosystem (Phalan *et al.* 2013; Laurance, Sayer & Cassman 2014). Floodplains provide fertile soils and water for agricultural activities but suffer intense degradation and reduction that impact both terrestrial and aquatic ecosystems (Allan 2004). These debts occur in one of the wetland ecosystems with high complexity, productivity, and functionality that support unique and rich biodiversity and provide

ecosystem goods and services (Millennium Ecosystem Assessment 2005; Maltby & Baker 2009). In the middle Araguaia River floodplain in central Brazil, the rich natural communities and ecosystem processes copy with the quick native vegetation conversion and waterbody management (pumping irrigation and damming) to supply agricultural demands and development, mainly soybean and rice production and livestock (Hunke *et al.* 2014; CONAB 2015; Oliveira *et al.* 2015; Garcia *et al.* 2017; Araújo *et al.* 2019). Hence, efforts toward sustainable and good practices in land and water management have an important role on ecological integrity of floodplain ecosystems, contributing to conservation of biodiversity and ecosystem processes and reduction of anthropogenic negative impacts (Laurance, Sayer & Cassman 2014; Leal *et al.* 2020).

Biodiversity patterns and food web dynamics suffer effects of modification in multiple dimensions of landscape (extension, composition, and configuration) due to habitat loss, fragmentation, and alteration of the matrix (Fischer & Lindenmayer 2007; Haddad *et al.* 2015; Liao, Bearup & Blasius 2017b). Habitat configuration, size, and quality are determinant in the dynamic of occupation, distribution, and local extinction of populations (Fahrig 2003; Ewers & Didham 2006). Matrix quality and type also play pivotal importance for population dynamic by mediating factors such as permeability, hostility, abiotic alteration, and resource availability (Prevedello & Vieira 2009; Quesnelle, Lindsay & Fahrig 2015), though its quality varies spatially and temporally, implying in a non-homogeneous and static factor for biodiversity (Driscoll *et al.* 2013). Because matrix and habitat quality are a species-specific perception, species traits play critical importance for persistence in fragmented landscapes, such as dispersal ability, habitat specialization, trophic level, feeding behavior (Ewers & Didham 2006). Landscape simplification acts as an ecological filter and drives to biotic homogenization in terms of biodiversity abundance and richness, where restriction to habitat and resource availability favors species with ecological plasticity while sensitive and

specialist species are eliminated (Newbold *et al.* 2015; Siqueira, Lacerda & Saito 2015; Le Provost *et al.* 2020). Such changes imply in serious consequences to ecological processes (productivity, functioning, stability, resilience, and resistance) (Scheffer *et al.* 2001; Duffy *et al.* 2007; Hooper *et al.* 2012).

Nowadays, stable isotopes analysis (SIA) methodology offers an integrated analytical assessment of biochemical cycle, food webs dynamic, and trophic niche parameters for organisms, commonly through carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes incorporated in body tissues (termed as bulk tissue samples) (Crawford, McDonald & Bearhop 2008; Shipley & Matich 2020). Through consumer–resource trophic dynamic, SIA allows to trace the basal carbon source via $\delta^{13}\text{C}$ (e.g., among plants with C_3 and C_4 photosynthetic cycles) and estimate trophic level via $\delta^{15}\text{N}$ due to predictable enrichment at each trophic transfer (Gannes, del Rio & Koch 1998; Ben-David & Flaherty 2012). The isotopic trophic niche of an organism (a bidimensional δ -space) has elucidated ecological niche variation in body size and sex traits, leading to differences in resource exploitation, ecosystem or habitat use, and trophic position (Marques *et al.* 2013; Nifong, Layman & Silliman 2015). Additionally, applications of SIA reveal ecological responses to anthropogenic disturbances. For example, agricultural matrixes (pastures or croplands) alter the nutrient dynamic and proportions of natural C_3 autochthonous production and C_4 allochthonous subsidy in aquatic food webs (Martinelli *et al.* 2007; Carvalho *et al.* 2015; Bentivoglio *et al.* 2016; Parreira de Castro *et al.* 2016). Under landscape modification, top predators reveal changes in the trophic dynamic and structure, such as trophic downgrading, niche collapses, lower niche redundancy, high niche overlap, energy flow homogenization, and niche shift from feeding plasticity (Layman *et al.* 2007; Resasco *et al.* 2017; Korotkevich *et al.* 2018; Magioli *et al.* 2019; Price *et al.* 2019; Burdon, McIntosh & Harding 2020).

Many assessments of the impacts of anthropogenic disturbances in the aquatic ecosystem using SIA make inferences from categorical or disturbance gradient design using dispersal-limited top predators, like fishes (Carvalho *et al.* 2015; Price *et al.* 2019; Burdon, McIntosh & Harding 2020). Such approaches are limited for a wetland top predator highly mobile and with generalist feeding behavior, like crocodilians. Recognized as a long-lived and large-bodied animal, crocodilians can explore all waterbody habitats and have population dynamic according to landscape attributes (Ouboter & Nanhoe 1988; Somaweera *et al.* 2020), exerting ecological implications for the dynamic of terrestrial and aquatic food webs (McCann, Rasmussen & Umbanhowar 2005; Rooney, McCann & Moore 2008). Thus, landscape patterns (amount, composition, and configuration of habitats and matrix types) can provide background information of ecological processes in the floodplains associated with spatial context (Wang, Blanchet & Koper 2014; Riva & Nielsen 2020). Further, spatial extension mediates spatial heterogeneity of stable isotope ratios in the ecosystems, including under small scale and human influence (Zambrano, Valiente & Vander Zanden 2010; Doi *et al.* 2013; Merlo-Galeazzi & Zambrano 2014), with direct effect in the isotopic trophic niche (Ceia *et al.* 2014; Reddin *et al.* 2018). To ignore spatial context, isotopic variability, and landscape attributes could make misinterpretations in the analyses and hide anthropogenic disturbances upon wetland food web through the isotopic trophic niche of a top predator. In this sense, the use of hierarchical Bayesian modeling allows verifying significance of species traits, habitat, and landscape attributes involved in the variability of trophic niche from SIA, accounting at the same time for spatial patterns and representations of the studied ecological process (Lindgren & Rue 2015; Rue *et al.* 2017; Wang, Yue & Faraway 2018). The hierarchical Bayesian approach has been a powerful and extraordinary tool to assess diverse ecological processes, including anthropogenic disturbance upon biodiversity (Blangiardo & Cameletti 2015; Abreu *et al.* 2020).

However, studies using SIA from bulk tissue in top predators can have difficulties to evidence alterations in the energy flow from the basal carbon source, due to $\delta^{13}\text{C}$ has high similarity among aquatic and terrestrial primary producers (Finlay & Kendall 2008; Zaia Alves *et al.* 2017), and suffers other multiple sources of variations (Boecklen *et al.* 2011; Shipley & Matich 2020). As an alternative, the emergent and robust compound-specific stable isotope analysis (CSIA) overcomes the caveats/limitations of bulk tissue SIA to interpret and disentangle energy/nutrient flow across the aquatic food chain using amino acids. This is because primary producers in basal food web have distinct patterns in the essential amino acid $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{EAA}}$) based on metabolic pathways and primary source of carbon (Larsen *et al.* 2009; Larsen *et al.* 2013; McMahon *et al.* 2016). Essential amino acids are those that consumers cannot synthesize, having a direct route from the diet, and thus, remain with minimal isotopic alteration in tissue samples of organisms across the food chain (Whiteman *et al.* 2019). Applying CSIA, we can infer about the basal source of food web directly from consumers (Arthur *et al.* 2014; McMahon *et al.* 2015; Thorp & Bowes 2016), as well as examine potential human-induced changes (Thorp & Bowes 2016; Bowes, Thorp & Delong 2019), especially agricultural carbon input across human-modified landscapes.

Here, we combined landscape attributes, species intraspecific traits, and trophic ecology of *Caiman crocodilus* to investigate anthropogenic impacts of landscape modifications upon food webs of the Araguaia floodplain in a spatially explicit approach. *Caiman crocodilus* (spectacled caiman) is an indicator crocodylian species for Araguaia biodiversity, useful as a model organism for detecting and monitoring environmental impacts due to high detectability, seasonal and ontogenetic movements across a variety of terrestrial and aquatic habitats in the floodplain (Rosenblatt *et al.* 2013; Somaweera *et al.* 2020). Applying spatial hierarchical Bayesian modeling, we investigated (1) the effects of intraspecific traits of sex, ontogeny, and habitat use on the carbon and nitrogen stable isotopes

of *C. crocodilus*; and (2) what landscape attributes (land use composition and wetland configuration) influenced and affected trophic niche of *C. crocodilus*. Further, we performed CSIA for essential amino acids ($\delta^{13}\text{C}_{\text{EAA}}$) to evaluate and characterize differences in primary producers between waterbodies from natural areas (i.e., lake and river) and man-made waterbodies from agricultural areas (i.e., cattle ponds and irrigation ditches), verifying especially participation of crop-derived energy on *C. crocodilus* food web in the human-modified environments.

MATERIALS AND METHODS

Study area

We conducted this study in the middle Araguaia River floodplain (Figure 1). This region is in a highly dynamic and complex Cerrado–Amazonia transition zone in central Brazil, where ecotonal boundaries were recently redefined by Marques *et al.* (2019). The pronounced tropical wet-dry climate influences the flooding patterns: the discharge increases from November to April (wet season), when the flood pulse that can span about 88,000 km² of surface area at maximum flood level and interconnect several and diverse waterbodies, and decreases during June and September (dry season), when waterbodies are only 3.3% (2,930 km²) of coverage area (Irion *et al.* 2016). Most of the phytophysiognomies consist of Cerrado savannas and seasonally flooded grasslands, with smaller areas occupied by alluvial and semi-deciduous forests (Valente, Latrubesse & Ferreira 2013). The high spatial and temporal heterogeneity of the floodplain supports a rich and abundant biota, many endemic and endangered species, which are protected in several conservation units and indigenous lands, including in a RAMSAR site (n° 624) – the Bananal Island (RAMSAR 1998). These protected areas play a crucial role in limiting the fragmentation and land-use conversion

advances due to their biological and ecological purpose (Carranza *et al.* 2014; Garcia *et al.* 2017).

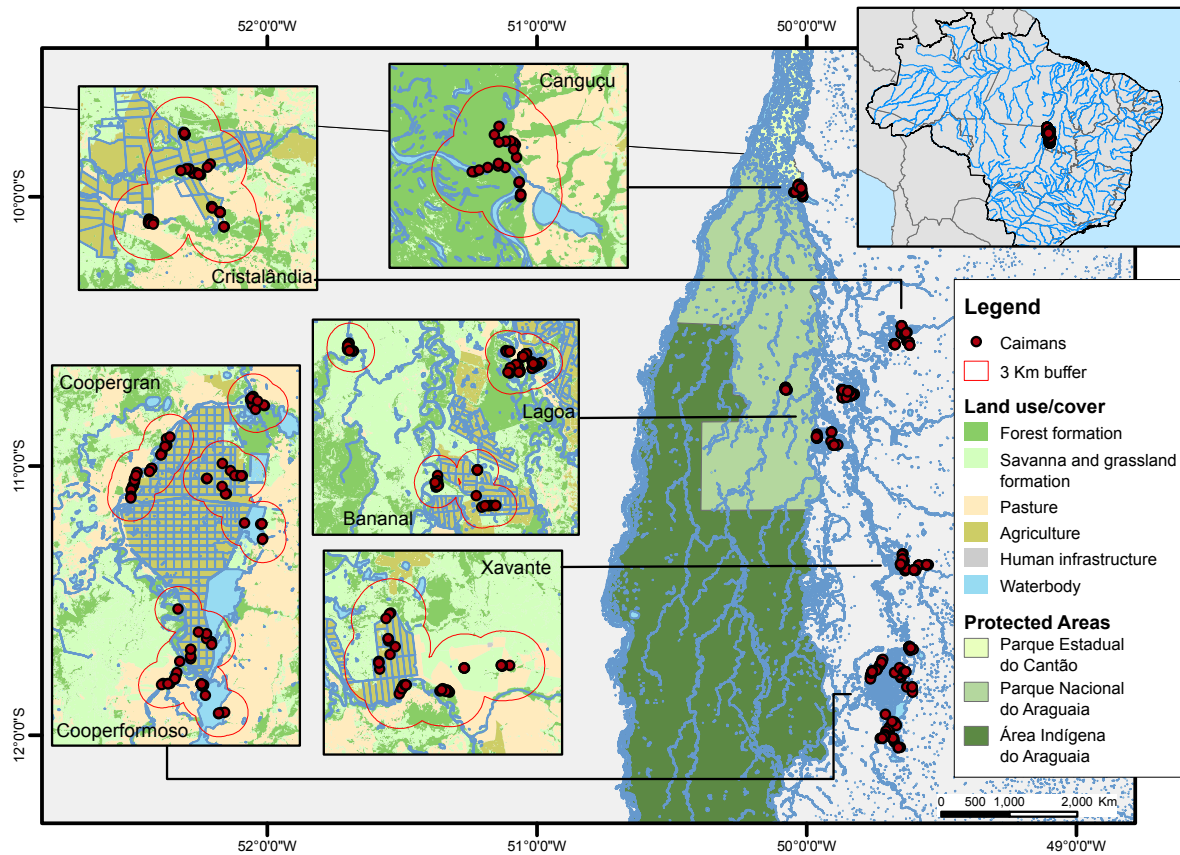


Figure 1. Location of seven sampling landscapes in the middle Araguaia River floodplain, Central Brazil. Hydrograph and protected areas in the region are depicted. Red points represent the location of captured caimans in sampling sites. The 3 km buffer indicates the maximum spatial region for data acquisition of landscape attributes.

However, the region is under sustained pressure from agricultural development funded by international and state programs due to favorable topography and hydrology that turned this region into one of the main producers of irrigated rice in Brazil (Fragoso *et al.* 2013; CONAB 2015). The production is across several irrigation projects, where crops are cultivated according to the hydrological regime, rice in wet season alternating to other crops (e.g., soybeans, beans, watermelon) in the dry season (Oliveira *et al.* 2015). During the last decades, Tocantins state expanded the cultivated area from 49,000 to 120,000 ha between 1989 and 2015, with a maximum of 160,000 ha in 2008 (Santos & Rabelo 2008; IBGE 2016).

Like in the whole Cerrado biome (Hunke *et al.* 2014; Dias *et al.* 2016), the Araguaia River Basin suffers sustained pressure from agricultural activities, with less than 50% of native vegetation remaining in the Upper Araguaia River (Ferreira *et al.* 2008; Coe *et al.* 2011), and experiencing changes in hydro-geomorphological dynamics due to water damming, pumping, sedimentation, silting, erosion, and contamination (Latrubesse *et al.* 2009; Coe *et al.* 2011; Oliveira *et al.* 2015). In the middle Araguaia River floodplain, during 1975-2013, there was a reduction of 26% of native vegetation coverage, driven mainly by expansion of pasturelands (Garcia *et al.* 2017). Nowadays, the land use pattern of Cerrado is changing slowly from extensification to intensification of agricultural activities, but pasturelands coverage remains large (Dias *et al.* 2016).

Sampling

We carried out fieldworks during the dry season of 2016 and 2018 (July to September) in seven localities in five municipalities of Tocantins State (Figure 1), labeled as Bananal, Canguçu, Cristalândia, Cooperformoso, Coopergran, Lagoa, and Xavante. We sampled caimans in natural (e.g., rivers and lakes) and artificial habitats (e.g., man-made ponds and irrigation ditches), distributed in 32 sites under distinct areas of land use and cover, including inside and outside of protected areas. To maximize spatial independence, localities were at least 20 km from each other, and sites within each locality were as apart as possible from each other. This distance is based on the migration, movement patterns, and home ranges described for *C. crocodilus* (Gorzula 1978; Ouboter & Nanhoe 1988).

We captured caimans through nocturnal spotlight surveys with the aid of locking cable snares or by hand after locating the animals by eye-reflection, following physical restraint of mouth and limbs with ropes and adhesive tape (Fitzgerald 2012; Brien & Manolis 2016). The capture effort was independent of animal size. We recorded the snout-vent length (SVL; with

a 0.1 cm precision tape), body mass (with 0.1 kg precision Pesola[®]), and sex, determined by cloacal examination and palpation of the penis (Reed & Tucker 2012). We individually marked *C. crocodilus* by notching tail scutes as a standardized numerical code and released at the same capture local after handling (Plummer & Ferner 2012).

Bulk tissue stable isotope analyses

SIA has an essential advantage compared to conventional stomach flushing, isotopic compositions provide longer-term estimates of prey incorporated into predator tissue, irrespective of the timeframe of predator sampling, condition of the stomach (empty or not), or differential prey digestibility (Crawford, McDonald & Bearhop 2008; Ben-David & Flaherty 2012). Thus, tissues with different turnover rates from the same individual allow evaluating resource use at multiple temporal and spatial scales. Metabolically active tissues (e.g., plasma, liver) integrate short-term dietary information while metabolically inert tissues (e.g., scute, claw, hair) incorporate long-term information (Gannes, del Rio & Koch 1998; Vander Zanden *et al.* 2015). In this sense, we integrated a temporal analysis in our study assessing carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes in different tissues. Presumably, the effects of human disturbance can be evidenced in *C. crocodilus* in the short-term by plasma, mid-term by muscle, and long-term by claw (Caut 2013). Moreover, the differences among tissues could reveal crop rotation whether the crops have distinct carbon and nitrogen isotopic values (e.g., C₃, versus C₄ plants) incorporated in the local food web.

We collected samples of the claw (~5 mm of fragments), tail muscle (1 g), and blood (~3 mL) of captured animals for SIA (Beaupre *et al.* 2004; Fleming & Fontenot 2015). The blood sample was obtained from the dorsal cervical sinus with a blood-collection kit using 21G × 1" needles (25 × 8 mm) coupled to a 4 mL BD Vacutainer[®] with lithium heparin anticoagulant. Within four hours, we used a centrifuge (OMEGA Mod. 1 Labor Import[®]) to

separate and collect plasma samples at 3,000 rpm for 60 s. We kept all tissue samples at -80 °C in a cryogenic liquid nitrogen container until preparation, which we washed claw and muscle samples with a 2:1 ratio chloroform:methanol solvent to extract the lipids (Post *et al.* 2007), dried them at 50 °C to a constant mass, and ground to a fine powder. For plasma tissue, we freeze-dried for 24 hours. Moreover, we also collected and prepared crop samples from agricultural areas to characterize the anthropogenic basal source in the SIA. We used seeds from Coopergran locality (rice: $n = 10$; soybean: $n = 10$), dried in an oven (60 °C for 48 h), and ground into a fine powder. Finally, we weighed about 1-2 mg for each caiman sample and 2-2.5 mg for each crop sample and placed them in 3×5 mm tin capsules for SIA.

Carbon and nitrogen stable isotopes were determined by combustion using an elemental analyzer (Carlo Erba, CHN-1100) coupled to a Thermo Finnigan Delta Plus mass spectrometer at the Laboratory of Isotope Ecology of the Centro de Energia Nuclear na Agricultura (CENA/Universidade de São Paulo), Piracicaba, SP, Brazil. The results were expressed in delta notation (δ), in parts per thousand (‰), based on the internationally recognized standard. We used the following equation: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$, where R_{sample} and R_{standard} represent the heavy/light isotope molar ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) of the sample and standard, respectively. The standard used for carbon analysis was Vienna Pee Dee Belemnite (Vienna PDB; $^{13}\text{C}/^{12}\text{C}$ ratio = 0.01118), and the standard used for nitrogen analysis was atmospheric air ($^{15}\text{N}/^{14}\text{N}$ ratio = 0.0036765). Internal standards (tropical soil and sugarcane leaves) are routinely interspersed with target samples during analysis runs. Long-term analytical errors for the internal standards are of 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Most samples had CN ratio values within acceptable limits in plasma (mean \pm SD: 3.3 ± 0.2), muscle (3.3 ± 1.9), and claw (2.9 ± 0.1) (Post *et al.* 2007). However, 17 muscle samples had a CN ratio above 4.0, indicating a high lipid content with a likely effect on $\delta^{13}\text{C}$

values (Post *et al.* 2007; Logan *et al.* 2008). To solve the problem, we decided to impute the $\delta^{13}\text{C}$ values of these samples (Penone *et al.* 2014). We did not consider using lipid correction equations because such equations are species- and tissue-specific, focusing mainly on fishes (Logan *et al.* 2008).

Essential amino acid $\delta^{13}\text{C}$ analysis ($\delta^{13}\text{C}_{\text{EAA}}$)

We selected 40 individuals to analyze essential amino acids ($\delta^{13}\text{C}_{\text{EAA}}$) using muscle samples. They came from natural and anthropogenic habitats of four localities: 10 individuals from lakes (Canguçu: 5 ind.; Bananal: 5 ind.); 10 individuals from rivers (Canguçu: 5 ind.; Bananal: 5 ind.); 10 individuals from ponds (Coopergran: 5 ind.; Cooperformoso: 5 ind.); 10 individuals from ditches (Coopergran: 5 ind.; Cooperformoso: 5 ind.). To identify possible participation of the agriculture activity in the caiman food web, we also analyzed rice and soybean samples, the most harvest crops in the Araguaia irrigation projects. We selected seeds from Coopergran locality (rice: $n = 2$; soybean: $n = 3$) for essential amino acids $\delta^{13}\text{C}_{\text{EAA}}$ analysis. All samples were processed and analyzed for $\delta^{13}\text{C}_{\text{EAA}}$ at the Center for Stable Isotopes at the University of New Mexico (UNM-CSI). At the UNM-CSI facility, we can reliably make $\delta^{13}\text{C}$ measurements for 13 amino acids; however, for this analysis, we restricted measurements for seven amino acids that are considered essential for animals: isoleucine (Ile), leucine (Leu), lysine (Lys), phenylalanine (Phe), tyrosine (Tyr), threonine (Thr) and valine (Val).

Following established protocols (Whiteman *et al.* 2019), an aliquot about 1-2 mg from each lipid-extracted muscle sample was hydrolyzed to constituent amino acids in 1 mL of 6 N hydrochloric acid (HCl) at 110 °C for 20 hours; tubes were flushed with N_2 gas for 30 s and sealed before hydrolysis to prevent oxidation. After, all samples were transferred into 4 mL vials and dried down under a stream of N_2 gas for 1 hour at 110 °C in a Thermo Scientific®

Reacti-Therm heating module. This process converted the sample in a solid film in the vials that consisted of pure amino acids (Whiteman *et al.* 2019). To transform samples into more volatile forms, amino acids were derivatized to N- trifluoroacetic acid isopropyl esters using previously described methods (Silfer *et al.* 1991; Whiteman *et al.* 2019). In brief, samples were initially reacted with 1 mL of a 4:1, 2-propanol:acetyl chloride solution for an hour at 110 °C. Samples were then dried down under N₂ gas at room temperature and rinsed twice with dichloromethane (DCM). Lastly, samples were acetylated by adding a 1:1 trifluoroacetic anhydride:dichloromethane solution and reacting at 110 °C for 10 min.

For crop analysis, we used an aliquot of about 19-20 mg from each ground samples for both types. They followed all methods described for caiman muscle samples, but an additional step was made after hydrolysis. We made the Dowex purification step, which consisted in passing the hydrolyzed crop samples through a cation exchange resin column (Dowex 50WX8 100–200 mesh) to isolate amino acids from other metabolites (Amelung & Zhang 2001).

The $\delta^{13}\text{C}$ values of individual derivatized amino acids were measured in duplicate using a GC-C-IRMS system. Derivatized samples were injected into a 60-m BPX5 gas chromatography column for amino acid separation (0.32 ID, 1.0 μm film thickness, SGE Analytical Science, Ringwood, Victoria, Australia) in a Thermo Scientific Trace 1310 gas chromatography, coupled to an IsoLink combustion interface attached to a Thermo Scientific Delta Plus IRMS (Bremen, Germany). For amino acid $\delta^{13}\text{C}$ measurements, commercially available powdered amino acids (Sigma Aldrich, St. Louis, MO) were used as a primary reference material (PRM) that were derivatized and analyzed alongside each batch of unknown samples. $\delta^{13}\text{C}$ values for each underivatized (powdered) amino acid have been previously measured via EA-IRMS in the UNM-CSI. The within-run standard deviations of

measured $\delta^{13}\text{C}$ values among essential amino acids in the in-house reference material ranged from 0.2‰ (isoleucine) to 0.8‰ (lysine).

Measured $\delta^{13}\text{C}$ values of reference materials and unknown samples include carbon from reagents (isopropanol and N-trifluoroacetic acid anhydride) added during derivatization. By derivatizing and analyzing reference materials alongside unknown samples, we can calculate the $\delta^{13}\text{C}$ value of the intrinsic amino acid ($\delta\text{XAA}_{\text{sample}}$) using the following equation: $\delta\text{XAA}_{\text{sample}} = \delta\text{XAA}_{\text{dsa}} - \delta\text{XAA}_{\text{dst}} + \delta\text{XAA}_{\text{std}} (p_{\text{std}}) / p_{\text{std}}$, where δX is the isotope of interest ($\delta^{13}\text{C}$), $\delta\text{XAA}_{\text{dsa}}$ and $\delta\text{XAA}_{\text{dst}}$ refer to the derivatized sample and standard respectively, $\delta\text{XAA}_{\text{std}}$ refers to the underivatized standard, and p_{std} is equal to the proportion of the carbon derivative that was sourced from the amino acid (Silfer *et al.* 1991; O'Brien, Fogel & Boggs 2002).

Landscape metrics

We assessed human land use composition and wetland configuration through landscape metrics based on circular buffers of 500 m, 1 km, and 3 km centered at each animal in the site. First, the rasters of land use/cover were obtained from MapBiomias Project (<http://mapbiomas.org>, collection 4, year: 2016 and 2018). We grouped MapBiomias land use classes considering five categories: waterbody, forest, savanna (savanna, grassland, non-forest natural formation, and other non-forest natural formation classes), pasture (pasture and other non-vegetated area classes), agriculture (annual and perennial crop class), and urban (urban infrastructure class). To improve water coverage, we incorporated a hydrography raster generated from a vectorial database acquired from Secretaria do Meio Ambiente e Recursos Hídricos of State of Tocantins (<https://semarh.to.gov.br/car/base-vetorial-digital-tematica-do-car/>). Further, we improved MapBiomias land use due to differences between supervised coverage *in loco* and MapBiomias raster, reclassifying and redefining the topology guided by

Landsat 8 satellites images for the same months of caiman sampling in 2016 and 2018, with 30-m pixel spatial resolution obtained from the Instituto Nacional de Pesquisas Espaciais–INPE (Brazilian Space Agency; <http://www.inpe.br/>) using QGIS, version 3.12 (QGIS Development Team 2020).

Second, we calculated landscape metrics in class and landscape levels for each buffer using the R package LANDSCAPEMETRICS (Hesselbarth *et al.* 2019). At the landscape level, the landscape division index (LDI) was the metrics selected. In the class level, the metrics comprehended just the proportion of class (PCLASS) for all categories to describe the landscape composition, while the metrics in the patch level were restricted to water coverage to estimate wetland configuration: mean of Euclidean nearest-neighbor distance (ENN), largest patch index (LPI), patch cohesion index (COHESION), and mean of patch area (MPA). Such landscape metrics reflect aspects of proportion, isolation, patch dominance, aggregation, and physical connectivity, and landscape fragmentation (McGarigal & Marks 1995; Jaeger 2000). For standardization, each variable was named with prefix related to buffer, landscape attribute as a root word, and suffix related to class of land use; for example, “B_500m_PCLASS_Pasture” for pasture proportion in 500 m buffer, or “B_500m_LDI” for division index in the whole landscape in 500 m buffer.

Third, we minimized multicollinearity among landscape metrics using the variance inflation factor with a maximum value of 4 in the R package USDM (Naimi *et al.* 2014). This resulted in the retention of 14 metrics with a maximum correlation of $r = 0.67$ among them (Table S1). After, we calculated the mean values of landscape metrics at each site, applied a $\log(x + 1)$ transformation, and standardized around the mean with one standard deviation for posterior analyses.

Data analysis

We treated the missing values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from eight individuals; $n = 16$) and $\delta^{13}\text{C}$ values for muscle samples with a CN ratio > 4 ($n = 17$), representing 0.02% of all data ($n = 1650$), through imputation using the R package MISSFOREST (Stekhoven & Bühlmann 2012). Imputation is a viable solution where missing data can introduce bias and lead to incorrect conclusions due to masking biological patterns (Penone *et al.* 2014). The MISSFOREST is among the best imputation approaches for animal trait data (Stekhoven & Bühlmann 2012; Penone *et al.* 2014). It is a non-parametric method that relies on Random Forest algorithms, and thus, a machine learning technique that handles in an iterative imputation scheme by training a Random Forest on observed values, predicting the missing values, and then proceeding iteratively (Stekhoven & Bühlmann 2012). Its performance is assessed using the normalized root mean squared error (NRMSE), where an excellent performance leads to a value close to 0 (Stekhoven & Bühlmann 2012). In our case, the NRMSE was 0.03%.

We assessed differences in resource use and niche width between habitats through the standard ellipse space and estimated Bayesian standard ellipse area metric (SEAB ; in $\%0^2$) using the R package SIBER (Jackson *et al.* 2011). We estimated the SEAB through a Markov chain Monte Carlo simulation with 10^4 iterations, 10^3 burn-ins, and two chains. The SEAB generates a robust measure of isotopic niche width due to insensitivity to bias associated with sample size. Further, the generated standard ellipses produce more information about isotopic niche position than a simple point estimate from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means, retaining uncertainty from fluctuations in the ellipse location and shape (Jackson *et al.* 2011). Thus, the ellipse represents a suitable measure for the niche position, being a proxy of the richness and evenness of resources consumed by the population.

To verify differences and similarities in the isotopic niche width among habitats, we performed pairwise comparisons between-habitat for each tissue using SEAB values drew in

the simulations. We assumed the certainty of difference through the probability that one group was larger (reference group) than another: $SEA_{\text{groupA}} > SEA_{\text{groupB}}$ (Jackson *et al.* 2011). The probability of difference can range from 0.5 (equal probabilities or smaller certainty) to 1.00 (higher certainty). Furthermore, we assessed diet similarity between groups by niche overlap through the function *bayesianOverlap* set to 100 draws with other parameters in default values.

To assess the effect of landscape composition and wetland configuration on isotopic niche width of *C. crocodilus*, we estimated the niche width (SEA_B) in the site level for each tissue implementing the same setting parameters described above. Before analysis, we selected landscape metrics that had greater relevance to niche width through R package BORUTA (Kursa & Rudnicki 2010). Boruta is a Random Forest-based selection method that identifies *all-relevant variables* through a comparative approach of the importance (Z-score values) between original and “shadows” variables (obtained by shuffling values of the randomized original variables). Boruta performs eliminations of the irrelevant features ($Z\text{-scores}_{\text{Original var.}} < \text{maximum } Z\text{-scores}_{\text{Shadows var.}}$) to improve the accuracy and prediction of the model. We then used *nTree* of 2000, *maxRuns* of 2000, and default settings for the other parameters. We retained the landscape attributes with mean and normalized importance values above zero ($meanImp$ and $normImp > 0$), obtained through function *attStats* (Table S2).

We implemented a hierarchical Bayesian approach to model the spatial variation in the (i) isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) under effects of intraspecific traits of sex, ontogeny, and habitat; (ii) isotopic niche width of *C. crocodilus* under effects of land use composition and wetland configuration across landscapes in the Araguaia floodplain. Spatial hierarchical Bayesian models were structured by two powerful tools: Stochastic Partial Differential Equations (SPDE) combined with the Integrated Nested Laplace Approximations

(INLA) algorithm. SPDE handles the continuous spatial stochastic process from spatial/geostatistical data through a discretely indexed spatial random process, the Gaussian Markov Random Field representation (GMRF), using a Matérn covariance function (Lindgren, Rue & Lindström 2011; Lindgren & Rue 2015). Through a representation of neighborhood mesh designs with indexed nodes, a derived matrix connects the GMRF-on-the-mesh to the GMRF-on-the-data (Bakka *et al.* 2018). In this way, we construct a class of latent Gaussian model able to do Bayesian inference through the INLA approach, supporting the applicability to many related variants of additive and/or generalized models (Rue, Martino & Chopin 2009; Blangiardo & Cameletti 2015; Rue *et al.* 2017). INLA became a faster and accurate alternative for Bayesian inference than time-intensive Markov Chain Monte Carlo methods (Rue, Martino & Chopin 2009; Wang, Yue & Faraway 2018).

Thus, we implemented SPDE and INLA approaches using the R package R-INLA (Rue, Martino & Chopin 2009; Lindgren, Rue & Lindström 2011), accounting for the spatial dependency between sampling sites and for the effects of selected predictors. We performed separately models for each tissue, where response variables were $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and isotopic niche width, while the predictors were SVL, sex, habitat, and their interactions (for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ models) or landscape attributes (for isotopic niche width model). We applied backward stepwise procedures in INLA to obtain the best model using the *INLAstep* function in the R package INLAUTILS (Redding *et al.* 2017). Before, we standardized SVL around the mean with one standard deviation and applied an orthogonal contrast to categorical matrixes using *model.matrix* function.

For each model, we evaluated the performance of different mesh designs based on deviance information (DIC) and Watanabe-Akaike information (WAIC) criteria (Spiegelhalter *et al.* 2002; Watanabe 2010). We created five mesh designs using the constrained refined Delaunay triangulation based on individual positions (in case of the $\delta^{13}\text{C}$

and $\delta^{15}\text{N}$ models) or sampling site locations (for isotopic niche width model), by varying the sizes of triangles within and outside the sampled area (Figure S1), attempting to minimize any boundary effects (Lindgren & Rue 2015). Details about models, representation of the spatial Random Fields, and descriptions of the posterior estimates of hyperparameters from spatial hierarchical Bayesian approach are in Supporting Information.

We investigated whether $\delta^{13}\text{C}_{\text{EAA}}$ values could discriminate and classify categories separately, indicating that primary producers of *C. crocodilus* food webs across human-modified landscapes differ among habitats or localities, and what are the essential amino acids that best explains the pattern of classification. For that, we performed a linear discriminant analysis (LDA) using the R package MASS (Venables & Ripley 2002). We examined the reclassification error rate using a leave-one-out cross-validation approach (Larsen *et al.* 2013). In the LDA, we plotted the 95% confidence interval ellipses to evidence a clear distinction among groups and the dataset was not standardized. Additionally, we also used the LDA to predict and associate crop samples to discriminated categories of caiman samples (Larsen *et al.* 2009; Larsen *et al.* 2013). We know that crop samples (both rice and soybean) came from ditch systems in the Coopergran. Thus, a high reclassification rate of crop samples ($n = 5$) within their group establishes a reliable LDA analysis to link the possible contribution of the agricultural source to food webs of the associated habitats in modified landscapes. All statistical tests were performed in R, version 3.6.1 (R Development Core Team 2019).

RESULTS

We captured 275 caimans with a sampling effort per site ranging from 9 to 14 animals. The minimum capture per locality was in Canguçu ($n = 21$, in two sites – two habitat types) while the maximum capture was in Coopergran ($n = 49$, in six sites – four habitat types). The

sex ratio was 2:1 (males:females) but distributed disproportionally among habitats, where some localities presented exclusively males in river habitat (Table S3).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and trophic niche estimates

The hierarchical Bayesian approach demonstrated that mesh design had different performances in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ models as the DIC and WAIC information criteria (Table S4, Table S5). The spatial structure of mesh 1 was the best for all tissues in $\delta^{13}\text{C}$ models, while mesh 1 (plasma and claw) and mesh 5 (muscle) were the best spatial structures for $\delta^{15}\text{N}$ models. The isotopic models had similar random fields among tissues, with reduced spatial uncertainty met in the regions of sampled points (Figure S2; Figure S3).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ models differed in their spatial effects among tissues, i.e., time window (Figure 2A; Figure 2B). Predicted spatial distribution of $\delta^{13}\text{C}$ values enriched temporally from smaller values in plasma to high values in claw, and prominent difference among localities, especially in the Xavante, Cooperformoso, and Coopergran regions (high values) compared to other areas (Figure 2A; Figure S4A). Alternatively, predicted spatial distribution of $\delta^{15}\text{N}$ values had lower differences among tissues, nonetheless, the localities showed consistent variation: high values found in the Xavante, Cooperformoso, and Coopergran regions, and lower values in the Bananal and natural areas surrounded Cooperformoso and Coopergran (Figure 2B; Figure S4B).

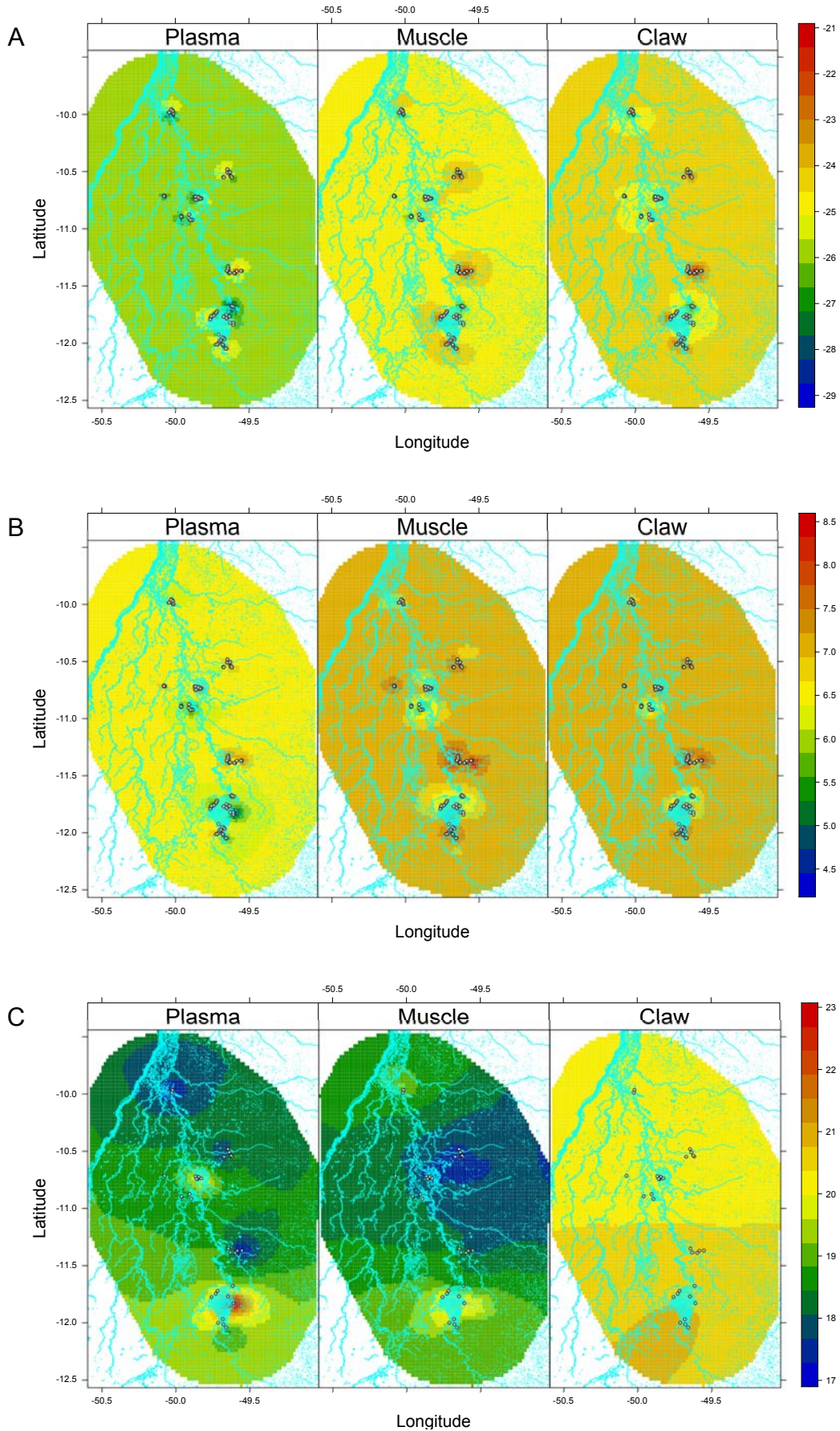


Figure 2. Predicted values from spatial hierarchical Bayesian best models for (A) $\delta^{13}\text{C}$, (B) $\delta^{15}\text{N}$, (C) isotopic niche width values of *Caiman crocodilus* according to tissue across

landscapes in the Araguaia floodplain. White points represent each sampled caiman (A and B) or sampling sites (C). The colors indicate levels of $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), isotopic niche width (‰²) mean values according to the associated legend. High values in bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are related to anthropogenic habitats, e.g., irrigation systems, but surrounding natural habitats of these areas present lower values, depicting a spatially isotopic variability. Additionally, the higher caiman isotopic niche width values were concentrated in the largest agricultural irrigation system and related to a greater proportion of pasture coverage. Some human-modified landscapes had similar niche width to natural landscapes in the Araguaia floodplain, suggesting the same intensity of resource use in these populations across the landscape.

In $\delta^{13}\text{C}$ models (Table 1), the only habitat affected that $\delta^{13}\text{C}$ in the plasma model (short-term scale) was pond, with evident positive effect. In muscle (middle-term scale) and claw (long-term scale) models, habitats differed in $\delta^{13}\text{C}$ values, demonstrating a clear effect in the pond (positive) and ditch (negative). The SVL had a negative effect on $\delta^{13}\text{C}$ in both models. The participation of sex was verified in the interaction of habitat:sex:SVL, which males in the lake had a positive effect in the SVL– $\delta^{13}\text{C}$ relationship.

Table 1. Posterior estimates (mean \pm SD and 95% credibility interval) from spatial hierarchical Bayesian best models relating sex, SVL, and habitat effects to $\delta^{13}\text{C}$ values of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Bold values indicate parameters significantly different from zero.

Tissue	Parameter	Mean	SD	Q _{0.025}	Q _{0.975}
Plasma	Intercept	-25.764	0.413	-26.609	-24.960
	Ditch	-0.174	0.336	-0.840	0.484
	Lake	-0.377	0.334	-1.039	0.274
	Pond	1.200	0.361	0.498	1.915
	Male	-0.103	0.115	-0.330	0.122
	SVL	-0.282	0.150	-0.576	0.012
	Ditch:Male	-0.027	0.169	-0.359	0.305
	Lake:Male	0.191	0.174	-0.150	0.532
	Ditch:SVL	-0.315	0.200	-0.708	0.078
	Male:SVL	-0.260	0.144	-0.544	0.023
	Ditch:Male:SVL	-0.216	0.200	-0.608	0.175
	Pond:Male:SVL	0.265	0.187	-0.102	0.632
	Intercept	-24.616	0.401	-25.446	-23.841
Ditch	-0.725	0.318	-1.354	-0.102	
Lake	0.417	0.332	-0.241	1.066	
Pond	0.851	0.341	0.187	1.530	
SVL	-0.451	0.149	-0.744	-0.158	

Muscle	Ditch:Male	-0.170	0.185	-0.534	0.194
	Lake:Male	0.398	0.223	-0.040	0.835
	Pond:Male	-0.183	0.217	-0.609	0.243
	Ditch:SVL	-0.208	0.216	-0.632	0.216
	Lake:SVL	0.340	0.261	-0.174	0.853
	Male:SVL	-0.142	0.144	-0.425	0.142
	Ditch:Male:SVL	-0.381	0.213	-0.800	0.038
	Lake:Male:SVL	0.642	0.273	0.104	1.178
	Pond:Male:SVL	0.111	0.222	-0.325	0.547
Claw	Intercept	-24.483	0.400	-25.301	-23.697
	Ditch	-0.759	0.312	-1.376	-0.145
	Lake	0.380	0.327	-0.270	1.017
	Pond	0.983	0.342	0.319	1.664
	SVL	-0.463	0.149	-0.757	-0.170
	Ditch:Male	-0.147	0.185	-0.511	0.218
	Lake:Male	0.301	0.226	-0.142	0.744
	Pond:Male	-0.098	0.221	-0.531	0.335
	Ditch:SVL	-0.374	0.219	-0.805	0.057
	Lake:SVL	0.480	0.275	-0.062	1.020
	Pond:SVL	0.243	0.254	-0.257	0.742
	Male:SVL	-0.200	0.146	-0.488	0.087
	Ditch:Male:SVL	-0.402	0.214	-0.822	0.017
	Lake:Male:SVL	0.680	0.277	0.135	1.224
	Pond:Male:SVL	0.294	0.256	-0.209	0.797

In $\delta^{15}\text{N}$ models (Table 2), for plasma, only habitat affected $\delta^{15}\text{N}$ values, which pond had a negative effect. In muscle, $\delta^{15}\text{N}$ differed among habitats, with a remarkable negative effect from the lake. Further, habitat influenced the SVL– $\delta^{15}\text{N}$ relationship, where ditch and pond had a negative and positive effect, respectively. Sex also affected the SVL– $\delta^{15}\text{N}$ relationship, with males having a negative and positive effect in the ditch and pond, respectively. Finally, for claw, the $\delta^{15}\text{N}$ was affected in the SVL– $\delta^{15}\text{N}$ relationship due to the habitat effect of the ditch, showing a negative effect. This same SVL– $\delta^{15}\text{N}$ relationship in the ditch differed according to sex; males demonstrated a negative effect.

Table 2. Posterior estimates (mean \pm SD and 95% credibility interval) from spatial hierarchical Bayesian best models relating sex, SVL, and habitat effects to $\delta^{15}\text{N}$ values of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Bold values indicate parameters significantly different from zero.

Tissue	Parameter	Mean	SD	Q _{0.025}	Q _{0.975}
Plasma	Intercept	6.400	0.218	5.960	6.837
	Ditch	0.273	0.143	-0.011	0.550
	Pond	-0.537	0.152	-0.834	-0.236
	SVL	0.080	0.068	-0.053	0.213
	Ditch:Male	-0.046	0.081	-0.206	0.114
	Pond:Male	0.105	0.093	-0.078	0.287
	Ditch:SVL	-0.154	0.100	-0.349	0.042
	Lake:SVL	0.096	0.109	-0.118	0.310
	Pond:SVL	0.215	0.116	-0.012	0.442
	Male:SVL	0.061	0.067	-0.071	0.192
	Ditch:Male:SVL	-0.182	0.098	-0.374	0.009
	Lake:Male:SVL	0.132	0.117	-0.096	0.362
	Pond:Male:SVL	0.219	0.116	-0.009	0.446
	Muscle	Intercept	7.024	0.197	6.632
Ditch		0.228	0.118	-0.005	0.458
Lake		-0.252	0.121	-0.489	-0.012
Pond		-0.214	0.122	-0.454	0.025
Male		-0.053	0.052	-0.156	0.050
SVL		0.040	0.053	-0.064	0.143
Ditch:Male		-0.135	0.085	-0.302	0.031
Lake:Male		0.152	0.101	-0.046	0.349
Pond:Male		0.047	0.100	-0.150	0.244
Ditch:SVL		-0.293	0.094	-0.478	-0.108
Lake:SVL		0.181	0.127	-0.068	0.431
Pond:SVL		0.329	0.114	0.104	0.554
Ditch:Male:SVL		-0.194	0.090	-0.370	-0.017
Lake:Male:SVL		0.132	0.126	-0.116	0.380
Pond:Male:SVL	0.262	0.116	0.034	0.490	
Claw	Intercept	7.062	0.182	6.695	7.421
	Ditch	0.119	0.147	-0.172	0.408
	Pond	-0.305	0.160	-0.620	0.008
	Male	-0.032	0.061	-0.151	0.087
	SVL	0.095	0.061	-0.025	0.214
	Ditch:Male	-0.104	0.096	-0.293	0.083
	Lake:Male	0.160	0.113	-0.062	0.382
	Pond:Male	0.026	0.112	-0.196	0.246
	Ditch:SVL	-0.279	0.107	-0.490	-0.069

Lake:SVL	0.246	0.144	-0.036	0.528
Pond:SVL	0.237	0.129	-0.016	0.489
Ditch:Male:SVL	-0.315	0.101	-0.514	-0.117
Lake:Male:SVL	0.224	0.138	-0.047	0.496
Pond:Male:SVL	0.258	0.131	0.000	0.514

Habitats differed in the isotopic niche width, varying their size differently across tissues (Figure 3). Overall, pond and river were larger and had higher probabilities of difference in the pairwise tests (Table S6). There were changes in the niche width across tissues. Pond and lake had larger niches in plasma. In muscle, lake decreased its niche, while river increased and joined to pond as higher niches. The pattern was maintained in claw, with a similarity between ditch and lake. Additionally, we observed a high niche overlap among habitats and no strong change in the niche position according to tissue time windows (Figure 3). Overall, the degree of the niche overlap increased from plasma to claw (Table S7; Figure S5).

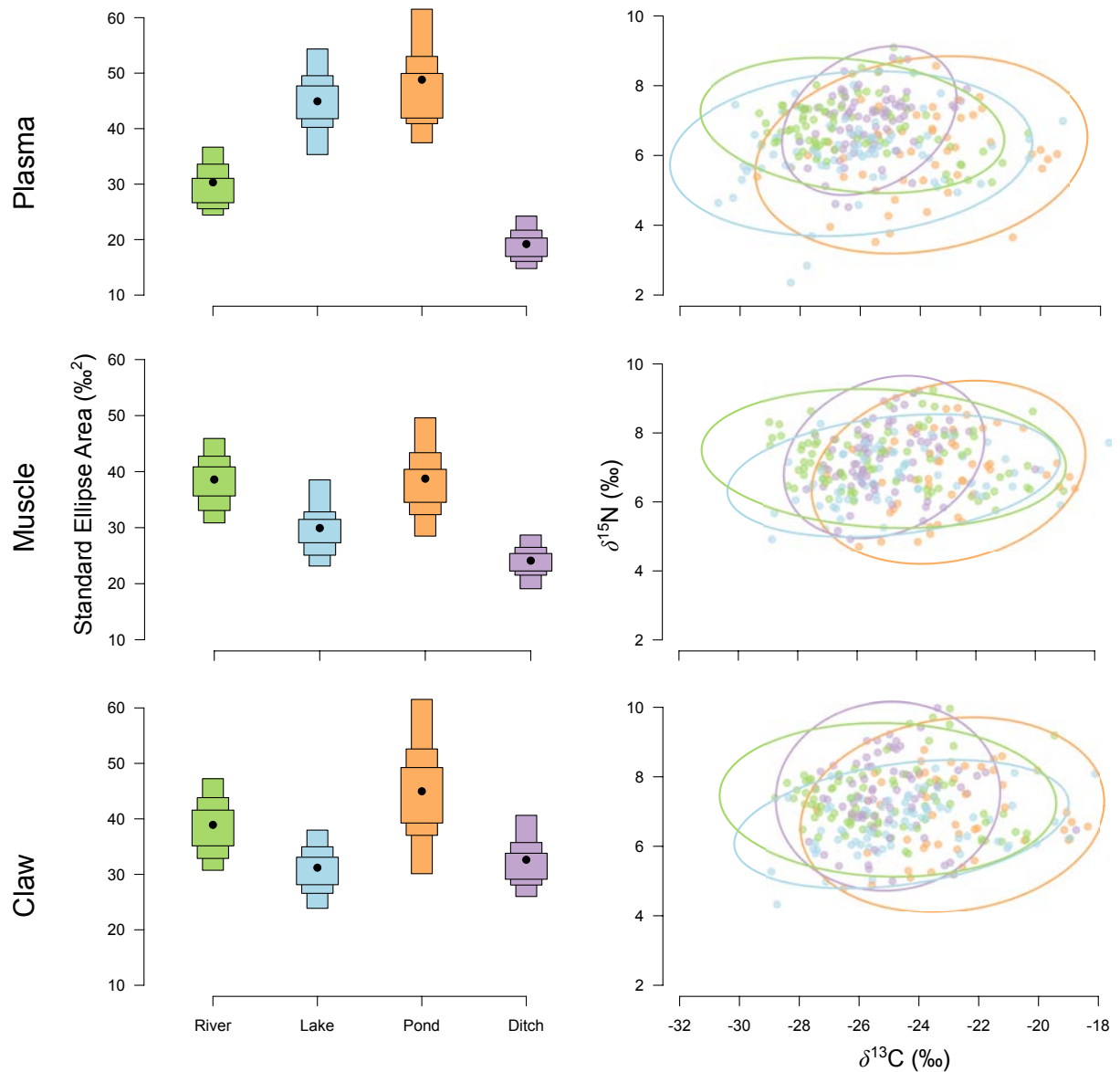


Figure 3. Isotopic niches and estimated niche width for habitats according to tissues of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Solid lines represent the core isotopic niche space. Black dots correspond to the mean, and boxes represent 50%, 75%, and 95% credibility intervals. Overall, habitats shared similar basal resources, reflecting a high niche redundancy. Otherwise, niche width shows that tissues demonstrate variability in resource use among habitats, but with a similar effect on long-term tissues. Caimans in the pond had a larger resource use, regardless of tissue, while other habitats had higher similarities.

Land use composition and wetland configuration effect on caiman niche width

We found similar DIC and WAIC values among mesh designs within each tissue model, suggesting that structures had similar spatial dependences in the hierarchical Bayesian approach for isotopic niche width (Table S8). However, we selected the mesh structure with

the lower value in the DIC and WAIC criteria: mesh 2 for plasma, mesh 5 for muscle, and mesh 1 for claw. The caiman niche width had different realizations of the spatial random fields according to tissue (Figure S2C; Figure S3C). Plasma and claw random fields had, overall, low spatial dependence and reduced uncertainty across the Araguaia floodplain, while muscle random field had high dependence and uncertainty, especially in the north and south.

Boruta and INLA stepwise selection procedures retained only the proportion of pasture coverage and the fragmentation index for models of isotopic niche width (Table 3). Just proportion of pasture coverage in 500-m buffer affected caiman niche width, with a positive effect in the plasma. The remaining predictors in their respective tissue models did not have effects on caiman niche width. The predicted isotopic niche width showed a spatial variability across sites with a higher range in plasma, medium in muscle, lower in claw (Figure 2C; Figure S4C). In plasma, caiman niche width was remarkably higher in Cooperformoso and Coopergran region ($\sim 23\text{‰}^2$), with other localities having lower values ($>19.5\text{‰}^2$). In muscle, the central region of the map had the lower niche width ($>19\text{‰}^2$), while Cooperformoso and Coopergran region maintained higher values ($\sim 20.5\text{‰}^2$). In claw, overall, the spatial distribution of niche width was higher compared to other tissues, but it distributed homogeneously across Araguaia floodplain (range: 20-21 ‰^2).

Table 3. Posterior estimates (mean \pm SD and 95% credibility interval) from spatial hierarchical Bayesian best models relating Boruta-selected landscape attributes to isotopic niche width (SE_{AB}) of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Bold values indicate parameters significantly different from zero.

Tissue	Parameter	Mean	SD	Q _{0.025}	Q _{0.975}
Plasma	Intercept	17.966	7.972	-3.315	33.467
	B_500m_PCLASS_Pasture	11.54	5.199	1.236	21.759
	B_3km_PCLASS_Pasture	-3.205	5.234	-13.511	7.144
Muscle	Intercept	16.833	10.301	-12.355	36.336
	B_3km_PCLASS_Pasture	4.413	2.682	-0.94	9.669
	B_3km_LDI	0.724	2.68	-4.523	6.074
Claw	Intercept	19.395	7.557	-1.691	33.682
	B_3km_PCLASS_Pasture	4.478	2.424	-0.323	9.254

Essential amino acids $\delta^{13}C$ analysis

In the LDA analysis, we found an overall successful reclassification rate of 65% for habitats, where they were correctly reclassified in 50% for pond, 60% for ditch, 70% for lake, and 80% for river (Appendix B, page 99). The linear discriminant axes explained 88% (LD1) and 9% (LD2) of the overall variation among habitats, which the most important EAA for distinguishing habitats were phenylalanine, leucine, and lysine. The LDA results showed a clear distinction in carbon sources from primary producers between natural and anthropogenic habitats (Figure 4A). Crop samples had a successful reclassification rate of 80%, just one rice sample was reclassified as river. The LDA space demonstrates a better characterization of anthropogenic habitats and possible contribution to the caiman food web in these habitats, evidencing proximity of crop samples to ellipses (Figure 4A).

The LDA had larger statistical support for separation among localities, with a correct reclassification rate of 85%, where they were correctly reclassified in 70% for Canguçu, 80% for Coopergran, 90% for Cooperformoso, and 100% for Bananal (Appendix C, page 100). The LD1 and LD2 explained respectively 80% and 10% of the variation, indicating a clear separation among localities, especially Bananal and Canguçu from Cooperformoso and Coopergran (Figure 4B). The most informative coefficients were phenylalanine, leucine, and lysine. Crop samples had a successful reclassification rate of 80%, just one Coopergran sample was reclassified as Bananal. The LDA maintained the affinity of crop samples to anthropogenic habitats but showed distant locations from habitat ellipses (Figure 4B).

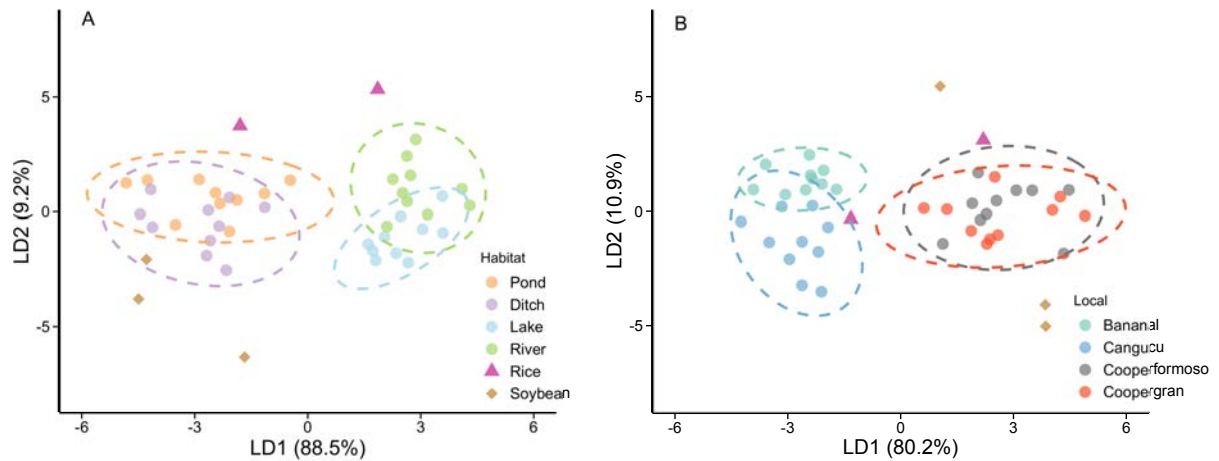


Figure 4. Multivariate discrimination of primary producer based on $\delta^{13}\text{C}_{\text{EAA}}$ values of *Caiman crocodilus* and crops (i.e., rice and soybean) according to habitat (A) and locality (B). Lake and river are natural habitats sampled in the localities of Bananal and Canguçu, while pond and ditch were anthropogenic habitats sampled in the Cooperformoso and Coopergran. Ellipses indicate a 95% confidence interval region for classified groups of *C. crocodilus*. Basal sources of the caiman food webs differed among natural and anthropogenic habitats, which altered habitats suggest a potential contribution from soybean-energy carbon due to correct discrimination and similarities in the $\delta^{13}\text{C}_{\text{EAA}}$ values with caimans.

DISCUSSION

We demonstrated that human-induced landscape modification impacts wetland food web in the Araguaia floodplain, identified through spatial representations in which related high values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and isotopic trophic niche of *Caiman crocodilus* to agricultural areas. Indeed, pasture coverage was the principal landscape feature that affected *C. crocodilus* niche width in a spatially explicit context, reflecting effects of land-use conversion, habitat alteration, and fragmentation. Moreover, sex, ontogeny, and habitat use had an influence and effect on the spatial patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across landscapes in the Araguaia floodplain. Habitats influenced the caiman diet and altered differently trophic niche width across tissue time windows, but their niche positions evidenced a similar pool in the resource supply. However, our study revealed by $\delta^{13}\text{C}_{\text{EAA}}$ analysis that natural and anthropogenic habitats differ in the basal source of carbon for *C. crocodilus* food webs, with soybean-derived energy possibly supporting food webs in anthropogenic habitats.

Crocodylians are highly mobile top predators with an opportunistic and generalist feeding behavior that can participate in several and distinct food webs in the landscape, where variations in their intraspecific trait regulate the strength and dynamics of trophic relations (Rosenblatt *et al.* 2013; Somaweera *et al.* 2020). This was corroborated in our study, ontogeny and sex influenced the resource use, with their effects varying with habitat. Such variations can be mediated by density-dependent mechanisms, such as hierarchical social and sexual body-sized groups, nutritional and/or physiological requirements to impose niche segregation at habitat and microhabitat level, and thus, decrease the competition in the population to coexistence (Pereira *et al. in prep.*, Marques *et al.* 2013; Caut *et al.* 2019).

The utilization of hierarchical Bayesian models for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values evidenced a marked spatial heterogeneity in small-scale across landscapes in the Araguaia floodplain. Overall, we found higher isotopic values in landscapes of irrigation systems, i.e., highly human-modified areas, but contrasting with lower values in natural environments surrounded them. Patterns of stable isotope variation in a small spatial scale are reported in man-made and natural freshwater ecosystems (Zambrano, Valiente & Vander Zanden 2010; Doi *et al.* 2013; Merlo-Galeazzi & Zambrano 2014). Such spatial variation can relate to different resources, trophic structures, and basal sources in the food webs due to distinct ecological processes and conditions across distinct habitats (Finlay & Kendall 2008; Boecklen *et al.* 2011; Zaia Alves *et al.* 2017). Otherwise, these findings can suggest an influence of anthropic activities and land-use changes on the food web functioning through agricultural N input or alterations in the C_3/C_4 resources availability and nutrient cycling (Bentivoglio *et al.* 2016; Parreira de Castro *et al.* 2016; Resasco *et al.* 2017; Magioli *et al.* 2019; Price *et al.* 2019; Burdon, McIntosh & Harding 2020). Therefore, the implications of spatial small-scale isotopic variability could result in a high similarity and no clear differentiation in the niche positions among habitats (Figure 3, Figure S5). High niche overlap degrees are seen in

human-modified areas in which food web members and functional groups exert a generalist feeding behavior and trophic flexibility in the community (Zambrano, Valiente & Vander Zanden 2010; Carvalho *et al.* 2015; Korotkevich *et al.* 2018; Magioli *et al.* 2019).

Communities in disturbed landscapes are usually represented by generalist and opportunistic species with broad trophic niche resulted from historical environmental- or biotic-filtering processes (Newbold *et al.* 2015; Siqueira, Lacerda & Saito 2015; Le Provost *et al.* 2020).

Concomitantly to spatial small-scale isotopic variability, movements and feeding behavior of caimans can contribute to high niche redundancy among habitats across tissue time windows, motivated by factors of habitat suitability and seasonal floodplain dynamic (Pereira *et al. in prep.*). Habitat suitability can relate to food provision and availability, where some waterbodies couldn't sustain a complex food web with larger animals in which allochthonous subsidy complements autochthonous production, for instance in small pools and man-made ponds where adjacent habitats and/or surrounding land use matrix influences food supplementation (Jardine *et al.* 2017). Some studies show that the terrestrial food web can be more important in supporting crocodylians than the aquatic food web (Adame *et al.* 2018; Santos *et al.* 2018). Moreover, seasonal floodplain dynamic through flood pulse mediates hydric connectivity among waterbodies and population dynamics (occupation, dispersal, and movement) of wetland species across interconnected habitats (Pereira *et al. in prep.*). Larger niches can reflect a season with a high food supply, while smaller niche widths can reflect a season with a low food supply (Sepúlveda-Lozada *et al.* 2017).

Alternatively, studies in fragmented environments report that smaller niches reflect a collapsed food web due to disruption of energy flow caused by reductions in diversity of potential prey for consumers (Layman *et al.* 2007; Korotkevich *et al.* 2018; Burdon, McIntosh & Harding 2020). Such trends could be observed in ditches in our study. However, trophic niche mechanisms are non-exclusive and some populations can reflect smaller niches due

promoted by abundant low-diversified resources simultaneously to other generalist populations in the region (Burdon, McIntosh & Harding 2020). Caimans can be taking advantage of the ditch systems through the stable and closed water system, predation facility, natural predation release, and food provision from associated biodiversity, which provide an optimal diet and body condition (Pereira and Colli *in prep.*). These populations could trigger a shift in feeding behavior to a site specialist population (Thomson *et al.* 2012) mediated by ecological opportunity mechanism (Araújo, Bolnick & Layman 2011), in which individuals cope with the cost of habitat selection and adaptation and foraging preferences to improve populational and individual fitness (Bolnick *et al.* 2003).

Then, what are the landscape attributes (composition and/or configuration) that affect the isotopic niche width of caimans? The spatial distribution of trophic niche width was affected by pasture coverage in multiple scales in the landscapes in Araguaia floodplain, with high values clustered in the largest irrigation system, Cooperformoso and Coopergran areas. Our finding that pasturelands influence caiman trophic niche corroborates with evidence of land-use cover affects the trophic dynamic of aquatic food webs (Merlo-Galeazzi & Zambrano 2014; Carvalho *et al.* 2015; Bentivoglio *et al.* 2016; Parreira de Castro *et al.* 2016).

Pasture coverage changes the terrestrial carbon biomass (from C₃ to C₄ source) and alters soil hydro-physical proprieties that maximize the susceptibility of aquatic ecosystems receive pasture inputs through erosion, sedimentation, and leaching processes (Latrubesse *et al.* 2009; Coe *et al.* 2011; Hunke *et al.* 2014), including under reduction of riparian vegetation and geomorphology conditions in the watershed (Cordeiro *et al.* 2020). Coarse grass fragments or attached to the soil particles can enter the aquatic ecosystem and alter biogeochemical constituents - increasing $\delta^{13}\text{C}$ values for dissolved inorganic carbon and particulate organic matter in the waterbody (Martinelli *et al.* 2007). However, aquatic food webs have demonstrated low assimilations of the source from C₄ pathway, with

autochthonous production (C_3 pathway) supporting the food web in rivers (Wantzen, Fellerhoff & Voss 2010; Thorp & Bowes 2016; Villamarín *et al.* 2017), which was corroborated by our data. Those few individuals in our study with low $\delta^{13}C$ values ($> 20\text{‰}$) could be directly related to terrestrial prey. C_4 carbon can be introduced through the consumption of insectivorous-omnivorous fishes or terrestrial grazer prey (insects or vertebrates) coming from pasture or savanna vegetation (Wantzen, Fellerhoff & Voss 2010). In our context, caimans in the man-made ponds have prominent susceptibility to this allochthonous subsidy (Jardine *et al.* 2017; Adame *et al.* 2018; Santos *et al.* 2018).

Otherwise, food webs in pasturelands show a high variation of $\delta^{13}C$ and $\delta^{15}N$ values in basal resources (particulate organic matter, algae, periphyton; all C_3 pathway) for consumers, such as macroinvertebrates and fishes (Turner & Edwards 2012; García *et al.* 2017). As consequence, all trophic chain members can repercuss higher isotopic variability and larger isotopic trophic niches, summed to feeding plasticity of some organisms (Carvalho *et al.* 2015; Parreira de Castro *et al.* 2016). Thus, variations in the proportion of pasture coverage can drive to greater alteration in the basal resources, generalist feeding behaviors, and niches sizes of consumers. Large areas of pasture can imply in higher susceptibility of wetland food webs suffer such bottom-up effect in a large spatial extension, which it can impact farther terrestrial and aquatic food webs (Rooney, McCann & Moore 2008; McCoy, Barfield & Holt 2009; Tschardtke *et al.* 2012). Using spatially explicit Bayesian models, we evidenced these effects on the food web through top predator, which caiman trophic niche varies according to pastureland proportion in human-modified landscapes in the Araguaia floodplain.

Distinct modes of human modifications alter the structural state of the landscape from an ongoing process over time that results in habitat loss and fragmentation (McGarigal & Marks 1995; Jaeger 2000; Fahrig 2003). However, the amount of loss mediates the effects of habitat fragmentation (Ewers & Didham 2006; Villard, Metzger & Saura 2014). Land-use

conversion is a clear outcome and irreversible change (in sense of intangible recovery of prior state), disrupting ecological patterns and processes that drive food webs (Fischer & Lindenmayer 2007; Jordan *et al.* 2012; Tschardtke *et al.* 2012; Haddad *et al.* 2015). In this sense, the relevant importance of fragmentation index on the isotopic trophic niche of *C. crocodilus* in the spatial Bayesian model of the claw (a tissue with long-term incorporation time) suggest the chronic effect of landscape modification and habitat disturbance on terrestrial and aquatic food webs through land-use conversion, expanding an agricultural matrix over natural vegetation. Overall, the Cerrado biome suffers a historical and constant pressure of pasturelands and croplands expansions (Barretto *et al.* 2013; Dias *et al.* 2016), including in the Araguaia River Basin (Ferreira *et al.* 2008; Coe *et al.* 2011; Garcia *et al.* 2017). Favorable climate, topography, and soil physical properties in Araguaia floodplain linked to government incentives through technological, mechanical, and financial supports had converged this region to an agricultural frontier (Fragoso *et al.* 2013; Phalan *et al.* 2013; Araújo *et al.* 2019). Although studies report prospective reductions in the expansion of agribusiness relied on the agricultural intensification and protected area delimitations (Barretto *et al.* 2013; Carranza *et al.* 2014; Dias *et al.* 2016; Garcia *et al.* 2017), it's plausible that areas of natural vegetation will still be fragmented and converted to pasturelands or croplands, with Cerrado species facing a huge challenger to persist (Lemes, de Andrade & Loyola 2019).

The evidences that carbon origins of caiman food webs differed among habitats by $\delta^{13}\text{C}_{\text{EAA}}$ analysis reveal the masked impact of matrix expansion and fragmentation on the Araguaia floodplain food web didn't note by bulk tissue SIA. In part due to similar isotopic variability of bulk $\delta^{13}\text{C}$ between aquatic basal sources and the most common crops harvested in agricultural matrixes (soybean and rice) in the Araguaia floodplain, such as Figure S6 (Zaia Alves *et al.* 2017). Natural producers are consistent to have a unique $\delta^{13}\text{C}_{\text{EAA}}$ composition,

determined by species-specificity biochemical pathways in the synthesis of the amino acids and conserved across environmental gradients (Larsen *et al.* 2009; Larsen *et al.* 2013; McMahon *et al.* 2016). The $\delta^{13}\text{C}_{\text{EAA}}$ analysis confirms that basal carbon source for river food webs is associated with autochthonous primary production via algae (Thorp & Bowes 2016; Bowes, Thorp & Delong 2019); otherwise, anthropogenic changes also are observed via $\delta^{13}\text{C}_{\text{EAA}}$ values in watershed scale by altering hydrogeomorphic changes and primary productivity in freshwater ecosystems (Bowes, Thorp & Delong 2019). In our case, essential amino acids demonstrated the distinction between natural and anthropogenic habitats in basal carbon source, resembling among localities in their pairs and demonstrating a remarkable effect of human influence on energy and nutrient flow of caiman food web in altered habitats.

Our findings suggest that crop-derived energy can be incorporated in the caiman food web with decisive participation in the agricultural ditch systems. The results were consistent with the turnover rate and integration time of muscle tissue associated with soybean cultivation and harvesting in the dry period in the Araguaia floodplain region, from May to September (Oliveira *et al.* 2015); period before tissue collection (September) and comprehended for $\delta^{13}\text{C}$ turnover time estimated in caiman muscle – four months or more considering the body size (Caut 2013; Vander Zanden *et al.* 2015). Additionally, rice-derived energy could probably have more participation in the caiman food web during the rainy period (October to April), when rice crop is cultivated in the Araguaia floodplain (Oliveira *et al.* 2015). Both soybean and rice could be part of the annual carbon source for the basal food web in anthropogenic habitats. To verify this possible influence, future studies should focus on collecting muscle samples in the late wet season. However, the caiman food web cannot be exclusively supported by crop-derived energy, incorporating resources from another basal source, as observed by variability in the LDA representation. The population dynamic, movements between natural–anthropogenic habitats, and seasonality of the Araguaia

floodplain favor variability in the basal source (Pereira et al. *in prep.*). Unfortunately, our study didn't sample primary producers from natural sites in the research area for $\delta^{13}\text{C}_{\text{EAA}}$ analysis due to logistic and financial constraints, but bulk tissue SIA with caimans in Amazonian floodplain infers that autochthonous production (C_3 pathway) supports caiman food web, mainly evidencing interspecific niche partitioning among sympatric caiman species and elucidating terrestrial allochthonous subsidy according to habitat use (Villamarín *et al.* 2017).

Concluding remarks

Our results highlight the effect of agricultural activities and disturbances on the trophic ecology of a semi-aquatic top predator driven by land-use conversion in landscapes along the Araguaia floodplain. Further, we evidenced that basal sources of food webs in natural habitats differ from anthropogenic habitats, which are supported in part by crop energy in agricultural areas. To our knowledge, this was the first study to assess the effects that landscape modification has upon species trophic niche based on SIA methodology and multi-scale gradient study design relied on landscape attributes (composition and configuration metrics). We advocate that the use of spatially explicit Bayesian models explore the relationship between landscape characteristics and ecological responses of species, considering variations in intraspecific traits, and avoid dichotomic/categorical evaluations of landscape (e.g., Resasco *et al.* 2017; Korotkevich *et al.* 2018; Magioli *et al.* 2019) that does not reflect spatial variations and effects of the mechanisms that moderate the landscape use by organisms (Tscharntke *et al.* 2012; Wang, Blanchet & Koper 2014; Riva & Nielsen 2020). Landscape configuration and composition drive food web structure and trophic interactions (Rooney, McCann & Moore 2008; Pillai, Gonzalez & Loreau 2011; Liao *et al.* 2016; Liao, Bearup & Blasius 2017b). Realistic ecological responses of landscape alteration effects arise

from consideration of species traits (e.g., trophic level, feeding behavior, body size, dispersal ability) and species-oriented habitat perception (Ewers & Didham 2006), which interacts with landscape characteristics to model species' sensitivity and tolerance in the face of the gradient of landscape alteration to persist in human-modified landscapes (Villard, Metzger & Saura 2014).

Our finding of crop supplementation for caiman food web support evidences that agricultural energy availability integrates and mediates food web structure (Thompson & Townsend 2005; Larson *et al.* 2013), providing high primary productivity to ecosystems in agricultural landscapes (Finlay 2011; Bastos *et al.* 2018). In these systems, food web functioning and stability could be achieved through weak indirect interactions and short food chains under predator-prey control (Canning & Death 2017). Omnivorous community plays crucial importance to maintain the food web functioning in human-modified areas, which bottom-up control is replaced by the predominant top-down control regime but top predators have secondary importance (Pillai, Gonzalez & Loreau 2011; Jordan *et al.* 2012). Empirical studies report that trophic controls change and energy flow pathways are lost, making unfeasible a food web support a top predator in long-term (Layman *et al.* 2007; Liao, Bearup & Blasius 2017b), triggering trophic cascade with strong and severe impacts to processes of ecosystem resilience and resistance to disturbances (Scheffer *et al.* 2001; Duffy *et al.* 2007; Hooper *et al.* 2012). The fragmentation threshold for species extinction can be dependent on community and landscape contexts (Villard, Metzger & Saura 2014; Liao, Bearup & Blasius 2017a). The potential for anthropogenic landscapes to support biodiversity and ecological and conservation values relies on an evaluation of the key attributes of species, food web, and ecosystem processes in their spatial context of landscape proprieties (Rooney, McCann & Moore 2008; McCoy, Barfield & Holt 2009).

Sustainable land and water management rely on the management of landscape attributes (extension, composition, and configuration) to increase landscape heterogeneity and quality (Tscharntke *et al.* 2012). Landscape complexity through environmental diversification and land cover types via local management can drive biodiversity patterns and dynamics to support more species, rather than simplified or in complex landscapes (Tscharntke *et al.* 2005). Inter-dependent ecological processes emerge from landscape complexity across multiple spatial scales, supplying ecological requirements of biodiversity for population processes and dynamics (Villard, Metzger & Saura 2014; Riva & Nielsen 2020). As consequence, energy flow pathways increase to structure and stabilize spatially the food webs (McCann, Rasmussen & Umbanhowar 2005; Rooney, McCann & Moore 2008). In general, landscape attributes are still neglected or unapplied in spatial food web models to elucidate the mechanisms of functioning, especially in ongoing landscape modification worldwide (Pillai, Gonzalez & Loreau 2011; Liao *et al.* 2016; Liao, Bearup & Blasius 2017a). However, our results emphasized the process of landscape modification that reverberates in resource use patterns and trophic interactions of a semi-aquatic top predator. Therefore, it provides new insights on how landscape fragmentation affects food web dynamics in a human-modified floodplain, enhancing our understanding and contributing with critical information for environmental policies, conservation planning, and land use management.

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SUPPORTING INFORMATION

APPENDIX A – Spatial hierarchical Bayesian models with INLA and SPDE

Geostatistical data are realizations of a stochastic process indexed by space (*random field*)

$$Y(s) \equiv \{y(\mathbf{s}), \mathbf{s} \in \mathcal{D}\},$$

where *random field* is characterized by a spatial index \mathbf{s} which varies continuously in the fixed domain \mathcal{D} (Blangiardo & Cameletti 2015; Krainski *et al.* 2018; Gómez-Rubio 2020). Typically, \mathbf{s} is a two-dimensional vector, such as latitude and longitude. In this sense, the actual data are represented by a collection of observations $\mathbf{y} = \{y(\mathbf{s}_1), \dots, y(\mathbf{s}_n)\}$, where the set of n points $(\mathbf{s}_1, \dots, \mathbf{s}_n)$ indicate the locations at which the measurements are taken. Such spatial process, a latent Gaussian Random Field (GRF), follows a multivariate Normal distribution with mean $\boldsymbol{\mu} = \{\mu(\mathbf{s}_1), \dots, \mu(\mathbf{s}_n)\}$ and spatially structured covariance matrix $\boldsymbol{\Sigma} = \{C(\mathbf{s}_1, \mathbf{s}_n)\}$, which is related to the Matérn spatial covariance function (Rue, Martino & Chopin 2009; Lindgren, Rue & Lindström 2011; Blangiardo & Cameletti 2015; Rue *et al.* 2017). Additionally, the latent GRF must assume a Gaussian form with additional conditional independence properties, which reflects to a Gaussian Markov Random Fields (GMRF) form, with huge computational benefits because pairs of conditionally independent values result in zeros in the matrix; thus, this implies great importance in Bayesian inferential methods based on Integrated Nested Laplace Approximations – INLA (Rue *et al.* 2017). The Stochastic Partial Differential Equations (SPDE) approach is implemented by constructing a continuously indexed approximation of the latent GRF defined on the entire study area through a discretely indexed spatial random process (i.e., a GMRF) associated to use of the Matérn covariance function, where the parameters used in SPDE have one-to-one correspondence (Lindgren, Rue & Lindström 2011; Blangiardo & Cameletti 2015; Bakka *et al.* 2018).

In INLA, the spatial hierarchical Bayesian model has a structure similar to the Generalized Linear Mixed Model framework, where the response (η) is a linear predictor and the measured parameter, where observations have an associated likelihood. The models estimate the mean (μ) of the observed data using a structured additive predictor η through a link function $g(\cdot)$, such that $g(\mu_i) = \eta$, for example:

$$y_i \sim \text{Normal}(\mu_i, \sigma_\epsilon^2) \quad i = 1, \dots, n$$

$$g(\mu_i) = \eta$$

$$\eta_i = \beta_0 + \sum_j \beta_j z_{ij} + \xi_i + \varepsilon_i$$

where: σ_e^2 is the hyperparameter of variance of the measurement error e_i which is supposed to be normally distributed and independent; β_0 is the intercept; z are fixed covariates with linear effects; β_j are the linear regression coefficients of the z predictors; the term ξ_i represents the random effect, which is the realization of the latent GF using a Gaussian multivariate distribution $\xi(\mathbf{s}) \sim \text{MVNormal}(0, \Sigma)$, where the mean is zero and the precision matrix Σ relates to Matérn spatial covariance function and by which captures the spatial correlation through mesh structures; finally, ε_i is an error term (Blangiardo *et al.* 2013; Rue *et al.* 2017; Krainski *et al.* 2018; Gómez-Rubio 2020). All these components constitute the (non-observable) latent field defined as $\theta = \{\beta_0, \beta_j, \xi\}$, where β and ξ are the covariates and smooth functions included in the linear predictor. In the SPDE approach, the mesh structures are representations of latent fields of domain \mathcal{D} in triangular subdivisions of mosaic with indexed node (vertices), and thus, used to construct observation matrix A that connects the GMRF-on-the-mesh to the GMRF-on-the-data (Lindgren & Rue 2015; Bakka *et al.* 2018).

Then, we performed the spatial hierarchical Bayesian models where the responses were bulk isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) from each individual and isotopic niche width (SEA_B) at each site across landscapes in the Araguaia floodplain. Each sampled tissue had separated model, where the predictors for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ models were sex, snout-vent length (SVL), habitat, and their interactions; otherwise, the SEA_B model had the previously selected by Boruta, which were B_500m_PCLASS_Pasture, B_3km_PCLASS_Pasture, and B_3km_LDI (Table S2). Following Blangiardo and Cameletti (2015), we constructed three models to test for each response: (i) null model; (ii) full model without accounting for spatial process; (iii) full model accounting for spatial process. Overall, the simplified models tested were:

1. $\delta^{13}\text{C}$ (all tissues):
 - i. Null = 1
 - ii. Non-SPDE = $\beta_0 + \beta_1\text{Habitat} + \beta_2\text{Sex} + \beta_3\text{SVL} + \beta_4\text{Habitat:Sex} + \beta_5\text{Habitat:SVL} + \beta_6\text{Habitat:Sex:SVL}$
 - iii. SPDE = $\beta_0 + \beta_1\text{Habitat} + \beta_2\text{Sex} + \beta_3\text{SVL} + \beta_4\text{Habitat:Sex} + \beta_5\text{Habitat:SVL} + \beta_6\text{Habitat:Sex:SVL} + \xi$
2. $\delta^{15}\text{N}$ (all tissues):
 - i. Null = 1
 - ii. Non-SPDE = $\beta_0 + \beta_1\text{Habitat} + \beta_2\text{Sex} + \beta_3\text{SVL} + \beta_4\text{Habitat:Sex} + \beta_5\text{Habitat:SVL} + \beta_6\text{Habitat:Sex:SVL}$
 - iii. SPDE = $\beta_0 + \beta_1\text{Habitat} + \beta_2\text{Sex} + \beta_3\text{SVL} + \beta_4\text{Habitat:Sex} + \beta_5\text{Habitat:SVL} + \beta_6\text{Habitat:Sex:SVL} + \xi$
3. SEA_B :
 - a. Plasma and Muscle

- i. Null
 - = 1
 - ii. Non-SPDE
 - = $\beta_0 + \beta_1 B_{500m_PCLASS_Pasture}$
 - + $\beta_2 B_{3km_PCLASS_Pasture}$
 - + $\beta_3 B_{3km_LDI}$
 - iii. SPDE
 - = $\beta_0 + \beta_1 B_{500m_PCLASS_Pasture}$
 - + $\beta_2 B_{3km_PCLASS_Pasture}$
 - + $\beta_3 B_{3km_LDI} + \xi$
- b. Claw
 - i. Null
 - = 1
 - ii. Non-SPDE
 - = $\beta_0 + \beta_1 B_{3km_PCLASS_Pasture}$
 - iii. SPDE
 - = $\beta_0 + \beta_1 B_{3km_PCLASS_Pasture} + \xi$

However, we obtained the best model designed from these previous models using a backward stepwise procedure in the *INLAstep* function from R package INLAUTILS (Redding *et al.* 2017). The best models are reported in the Table 1-3 of main text. For these best models, hyperparameters estimated are given in Table S9.

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APPENDIX B – Linear discriminant analysis output for habitat categorization of essential amino acids analysis ($\delta^{13}C_{EAA}$)

Prior probabilities of groups

Ditch	Lake	Pond	River
0.25	0.25	0.25	0.25

Group means

Habitat	Thr	Ile	Leu	Val	Lys	Phe	Tyr
Ditch	-17.0	-24.8	-31.0	-27.5	-23.8	-28.9	-28.9
Lake	-16.1	-24.0	-30.0	-27.4	-23.2	-30.9	-30.4
Pond	-17.3	-24.0	-29.9	-26.4	-22.3	-27.9	-28.2
River	-19.0	-25.6	-31.7	-28.5	-23.9	-32.4	-31.5

Coefficients of linear discriminants

Parameter	LD1	LD2	LD3
Thr	0.108	-0.622	0.306
Ile	0.149	0.375	-0.220
Leu	0.793	-1.325	-0.686
Val	-0.105	1.063	0.017
Lys	0.798	0.708	-0.125
Phe	-1.721	-0.147	-0.259
Tyr	-0.214	-0.066	0.466

Proportion of trace

LD1	LD2	LD3
0.8856	0.0922	0.0222

Linear discriminant analysis (LDA) classification table.

	Ditch	Lake	Pond	River	Percent correct
Ditch	6	0	4	0	60
Lake	0	7	0	3	70
Pond	4	0	5	1	50
River	0	2	0	8	80

Bold numbers represent correct reclassification of the LDA.

APPENDIX C – Linear discriminant analysis output for locality categorization of essential amino acids analysis ($\delta^{13}C_{EAA}$)

Prior probabilities of groups

Bananal	Canguçu	Cooperformoso	Coopergran
0.25	0.25	0.25	0.25

Group means

Locality	Thr	Ile	Leu	Val	Lys	Phe	Tyr
Bananal	-17.0	-25.1	-30.9	-27.3	-23.4	-31.6	-30.8
Canguçu	-18.0	-24.5	-30.8	-28.6	-23.8	-31.7	-31.1
Cooperformoso	-16.3	-23.8	-30.1	-26.1	-23.3	-28.2	-29.0
Coopergran	-18.0	-25.0	-30.8	-27.7	-22.9	-28.6	-28.0

Coefficients of linear discriminants

Parameter	LD1	LD2	LD3
Thr	-0.164	0.406	0.320
Ile	-0.137	-1.103	-0.735
Leu	-0.957	-0.987	-0.171
Val	0.265	1.160	-0.692
Lys	-0.700	0.698	0.689
Phe	1.688	-0.152	-0.238
Tyr	0.192	-0.159	0.560

Proportion of trace

LD1	LD2	LD3
0.8024	0.1094	0.0881

Linear discriminant analysis (LDA) classification table

	Bananal	Canguçu	Cooperformoso	Coopergran	Percent correct
Bananal	10	0	0	0	100
Canguçu	3	7	0	0	70
Cooperformoso	0	0	9	1	90
Coopergran	0	0	2	8	80

Bold numbers represent correct reclassification of the LDA.

TABLES

Table S1. Landscape attributes retained by Variance Inflation Factor (VIF) in the Araguaia floodplain. The VIF threshold had a value of 4 for *theta* parameter. NS: landscape attributes with collinearity problem (VIF value > 4) and that were excluded of the posterior analysis.

Variables	VIF
B_500m_PCLASS_Forest	3.61
B_500m_PCLASS_Savanna	2.19
B_500m_PCLASS_Pasture	2.51
B_500m_PCLASS_Water	2.99
B_3km_PCLASS_Forest	2.73
B_3km_PCLASS_Pasture	2.94
B_1km_MPA_Water	2.37
B_3km_MPA_Water	1.56
B_1km_ENN_Water	1.25
B_3km_ENN_Water	1.59
B_500m_COE_Water	1.92
B_3km_COE_Water	2.64
B_500m_LDI	3.24
B_3km_LDI	1.78
B_1km_PCLASS_Crop	NS
B_1km_LPI_Water	NS
B_3km_PCLASS_Crop	NS
B_500m_LPI_Water	NS
B_3km_PCLASS_Water	NS
B_500m_PCLASS_Crop	NS
B_1km_PCLASS_Water	NS
B_1km_PCLASS_Savanna	NS
B_1km_PCLASS_Pasture	NS
B_1km_PCLASS_Forest	NS
B_1km_LDI	NS
B_1km_COE_Water	NS
B_500m_MPA_Water	NS
B_3km_PCLASS_Savanna	NS
B_3km_LPI_Water	NS

Table S2. Summary of importance parameters of Boruta selection for isotopic niche width (SEA_B) according to tissue of *C. crocodilus* related to landscape attributes measured in the Araguaia floodplain: mean, minimum, maximum, and normalized importance based on the fraction of random forest runs in which the attributes were more important than shadow values.

Tissue	Predictor	<i>meanImp</i>	<i>minImp</i>	<i>maxImp</i>	<i>normHits</i>
Plasma	B_500m_PCLASS_Pasture	18.545	11.571	23.735	0.974
	B_3km_PCLASS_Pasture	7.665	2.483	12.249	0.652
	B_3km_LDI	0.703	-2.080	3.127	0.035
	B_3km_COE_Water	-0.708	-3.312	1.656	0.000
	B_500m_PCLASS_Water	-0.752	-2.167	1.151	0.000
	B_500m_LDI	-0.924	-3.708	2.202	0.009
	B_500m_COE_Water	-1.365	-3.226	1.502	0.000
	B_500m_PCLASS_Forest	-1.571	-2.938	0.256	0.000
	B_3km_MPA_Water	-1.816	-5.548	1.548	0.009
	B_3km_ENN_Water	-2.140	-3.918	-0.161	0.000
	B_1km_MPA_Water	-2.218	-2.805	-0.928	0.000
	B_1km_ENN_Water	-2.243	-3.796	-0.289	0.000
	B_3km_PCLASS_Forest	-2.431	-4.442	-0.998	0.000
	B_500m_PCLASS_Savanna	-2.608	-3.835	-1.052	0.000
	Muscle	B_3km_PCLASS_Pasture	7.077	0.224	14.523
B_3km_LDI		3.586	0.704	9.267	0.001
B_500m_PCLASS_Pasture		2.978	-0.923	5.982	0.001
B_500m_PCLASS_Forest		0.147	-1.861	2.622	0.000
B_3km_PCLASS_Forest		-0.084	-2.571	1.718	0.000
B_3km_ENN_Water		-0.839	-2.176	1.453	0.000
B_500m_LDI		-1.086	-2.633	0.209	0.000
B_500m_PCLASS_Water		-1.087	-3.138	0.187	0.000
B_1km_ENN_Water		-1.569	-3.499	0.400	0.000
B_500m_PCLASS_Savanna		-1.739	-4.086	0.889	0.000
B_3km_MPA_Water		-2.571	-4.714	-1.136	0.000
B_500m_COE_Water		-3.010	-5.122	-0.803	0.000
B_1km_MPA_Water		-3.702	-4.586	-1.407	0.000
B_3km_COE_Water		-3.862	-5.526	-1.882	0.000
Claw		B_3km_PCLASS_Pasture	9.619	3.059	16.860
	B_3km_PCLASS_Forest	1.126	-1.128	2.265	0.000
	B_3km_ENN_Water	0.080	-2.150	2.238	0.000
	B_1km_ENN_Water	0.039	-1.449	2.182	0.000
	B_500m_PCLASS_Savanna	-0.262	-2.620	4.933	0.000
	B_500m_COE_Water	-0.519	-4.286	1.562	0.000
	B_3km_LDI	-0.740	-1.951	0.661	0.000
	B_500m_PCLASS_Pasture	-0.865	-1.781	0.764	0.000
	B_500m_PCLASS_Water	-1.124	-2.577	-0.133	0.000
	B_500m_LDI	-1.620	-4.024	1.341	0.000

B_500m_PCLASS_Forest	-1.828	-3.870	0.046	0.000
B_3km_MPA_Water	-2.017	-3.209	-0.672	0.000
B_1km_MPA_Water	-2.358	-4.476	-0.887	0.000
B_3km COE Water	-2.362	-4.111	-1.173	0.000

Table S3. Description of the sampled population of the *Caiman crocodilus* and Boruta-selected landscape attributes in the Araguaia floodplain.

Locality	Number of sites	Habitat	N	Sex ratio (Male:Female)	500 m Buffer		3 km Buffer			
					PCLASS_Pasture (%)		PCLASS_Pasture (%)		LDI	
					Mean	SD	Mean	SD	Mean	SD
Bananal	2	Ditch	12	7:5	0.13	0.35	0.30	0.04	0.48	0.09
	1	Lake	12	7:5	0.00	0.00	0.00	0.00	0.33	0.02
	1	River	12	9:3	0.11	0.39	0.31	0.05	0.86	0.02
Canguçu	1	Lake	9	4:5	11.59	15.15	25.85	8.80	0.57	0.12
	1	River	12	12:0	9.13	13.86	15.81	11.98	0.74	0.12
Cooperformoso	1	Ditch	10	7:3	0.35	0.63	4.53	3.48	0.67	0.06
	2	Lake	11	9:2	20.76	29.63	39.76	16.10	0.67	0.09
	1	Pond	12	6:6	60.34	9.07	38.62	0.37	0.81	0.01
	1	River	12	10:2	28.49	16.89	54.33	22.80	0.78	0.05
Coopergran	1	Ditch	12	9:3	0.00	0.00	4.25	4.70	0.27	0.26
	2	Lake	14	11:3	15.05	16.80	29.65	5.07	0.84	0.04
	2	Pond	10	7:3	38.15	8.31	26.61	6.58	0.72	0.04
	1	River	13	12:1	57.11	13.92	51.32	4.90	0.67	0.01
Cristalândia	2	Ditch	12	6:6	0.00	0.00	17.80	26.18	0.70	0.01
	1	Lake	10	8:2	31.46	5.40	50.56	1.52	0.86	0.00
	1	Pond	6	3:3	29.44	9.82	48.75	3.38	0.80	0.06
	1	River	11	11:0	7.54	7.54	27.54	3.53	0.76	0.02
Lagoa	1	Ditch	13	6:7	1.04	2.42	18.94	2.67	0.89	0.01
	1	Lake	7	2:5	26.28	9.10	19.98	1.08	0.88	0.02
	1	Pond	8	4:4	59.64	24.80	23.04	0.07	0.86	0.01
	2	River	14	8:7	13.99	15.35	18.84	2.77	0.84	0.04
Xavante	1	Ditch	12	1:1	0.84	1.39	3.25	3.12	0.64	0.08
	1	Lake	10	9:1	20.63	10.18	43.36	1.32	0.77	0.01
	2	Pond	11	7:4	59.84	10.78	37.64	0.26	0.71	0.08
	1	River	10	4:6	18.07	2.50	25.82	0.38	0.79	0.01

Table S4. Accuracy information criteria of mesh designs from different spatial hierarchical Bayesian models for each tissue relating $\delta^{13}\text{C}$ values of *Caiman crocodilus* to sex, ontogeny, and habitat across landscapes in the Araguaia floodplain. Bold values indicate mesh design and model chose for posterior analysis. Model descriptions are described in Appendix A.

Tissue	Mesh	DIC				WAIC			
		Null	Non-SPDE	SPDE	Best model	Null	Non-SPDE	SPDE	Best model
Plasma	Mesh 1	1215.587	1184.973	1062.336	1054.824	1215.735	1186.426	1071.379	1059.407
	Mesh 2	1215.587	1184.973	1076.590	1070.672	1215.735	1186.426	1082.268	1072.129
	Mesh 3	1215.587	1184.973	1078.516	1072.786	1215.735	1186.426	1084.668	1074.338
	Mesh 4	1215.587	1184.973	1076.542	1070.820	1215.735	1186.426	1082.216	1072.125
	Mesh 5	1215.587	1184.973	1078.549	1072.897	1215.735	1186.426	1084.700	1074.331
Muscle	Mesh 1	1224.719	1189.252	1079.481	1075.445	1224.725	1188.863	1086.761	1080.745
	Mesh 2	1224.719	1189.252	1088.368	1086.907	1224.725	1188.863	1092.801	1088.798
	Mesh 3	1224.719	1189.252	1088.705	1087.096	1224.725	1188.863	1093.203	1089.531
	Mesh 4	1224.719	1189.252	1088.281	1086.704	1224.725	1188.863	1092.889	1088.659
	Mesh 5	1224.719	1189.252	1088.952	1087.048	1224.725	1188.863	1093.421	1089.500
Claw	Mesh 1	1220.159	1185.034	1078.919	1076.872	1220.238	1185.340	1085.464	1081.347
	Mesh 2	1220.159	1185.034	1088.800	1084.906	1220.238	1185.340	1093.042	1087.417
	Mesh 3	1220.159	1185.034	1087.318	1085.589	1220.238	1185.340	1091.489	1087.377
	Mesh 4	1220.159	1185.034	1088.929	1084.875	1220.238	1185.340	1093.154	1087.503
	Mesh 5	1220.159	1185.034	1087.314	1085.573	1220.238	1185.340	1091.505	1087.545

Table S5. Accuracy information criteria of mesh designs from different spatial hierarchical Bayesian models for each tissue relating $\delta^{15}\text{N}$ values of *Caiman crocodilus* to sex, ontogeny, and habitat across landscapes in the Araguaia floodplain. Bold values indicate mesh design and model chose for posterior analysis. Model descriptions are described in Appendix A.

Tissue	Mesh	DIC				WAIC			
		Null	Non-SPDE	SPDE	Best model	Null	Non-SPDE	SPDE	Best model
Plasma	Mesh 1	795.551	762.731	656.718	648.695	796.364	765.030	662.052	652.016
	Mesh 2	795.551	762.731	657.561	655.927	796.364	765.030	661.620	657.650
	Mesh 3	795.551	762.731	652.109	650.449	796.364	765.030	655.783	652.030
	Mesh 4	795.551	762.731	657.538	652.334	796.364	765.030	661.559	653.666
	Mesh 5	795.551	762.731	652.227	650.473	796.364	765.030	655.958	652.027
Muscle	Mesh 1	733.805	736.360	646.003	643.957	733.691	737.380	647.630	643.734
	Mesh 2	733.805	736.360	648.844	644.890	733.691	737.380	649.672	644.297
	Mesh 3	733.805	736.360	641.496	639.384	733.691	737.380	642.458	638.706
	Mesh 4	733.805	736.360	648.834	644.879	733.691	737.380	649.662	644.304
	Mesh 5	733.805	736.360	641.423	639.375	733.691	737.380	642.368	638.660
Claw	Mesh 1	794.461	784.527	709.619	705.288	794.469	785.074	713.007	706.877
	Mesh 2	794.461	784.527	719.626	715.522	794.469	785.074	720.990	715.024
	Mesh 3	794.461	784.527	709.160	707.033	794.469	785.074	710.657	706.655
	Mesh 4	794.461	784.527	719.641	715.475	794.469	785.074	721.012	715.034
	Mesh 5	794.461	784.527	709.116	707.027	794.469	785.074	710.605	706.667

Table S6. Probability of difference between groups of habitats according to tissues of *Caiman crocodilus* across landscapes in the Araguaia floodplain. The first group was the largest group (reference for comparisons).

Tissue	Mean SEAB ‰² (95% credible interval)	Comparison	Probability
Plasma		SEA _{pond} > SEA _{ditch}	1.00
	River = 30.32 (23.73 – 36.66)	SEA _{pond} > SEA _{river}	1.00
	Lake = 44.93 (35.39 – 54.35)	SEA _{river} > SEA _{ditch}	1.00
	Pond = 48.82 (36.32 – 61.46)	SEA _{lake} > SEA _{ditch}	1.00
	Ditch = 19.2 (14.07 – 24.19)	SEA _{lake} > SEA _{river}	0.99
		SEA _{pond} > SEA _{lake}	0.62
Muscle		SEA _{pond} > SEA _{ditch}	1.00
	River = 38.59 (30.85 – 45.92)	SEA _{river} > SEA _{ditch}	0.99
	Lake = 29.93 (22.21 – 37.87)	SEA _{pond} > SEA _{lake}	0.94
	Pond = 38.74 (28.42 – 48.23)	SEA _{river} > SEA _{lake}	0.92
	Ditch = 24.11 (19.13 – 28.76)	SEA _{lake} > SEA _{ditch}	0.91
		SEA _{river} > SEA _{pond}	0.51
Claw		SEA _{pond} > SEA _{lake}	0.96
	River = 38.92 (30.23 – 47.24)	SEA _{pond} > SEA _{ditch}	0.94
	Lake = 31.20 (23.87 – 38.07)	SEA _{river} > SEA _{lake}	0.89
	Pond = 44.98 (29.85 – 59.87)	SEA _{river} > SEA _{ditch}	0.87
	Ditch = 32.63 (24.83 – 40.38)	SEA _{pond} > SEA _{river}	0.82
		SEA _{ditch} > SEA _{lake}	0.65

Table S7. Niche overlap area (%²) among habitats in the (A) plasma, (B) muscle, and (C) claw of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Values in mean (95% credible interval).

Tissue		Lake	Pond	Ditch
Plasma	River	26.53 (21.38–32.16)	21.89 (16.49–27.18)	16.62 (13.38–19.90)
	Lake		33.19 (26.41–39.95)	16.60 (13.03–20.14)
	Pond			16.71 (12.34–21.03)
Muscle	River	26.19 (20.74–31.71)	25.55 (20.45–30.29)	21.30 (17.50–25.06)
	Lake		23.05 (18.47–27.58)	18.27 (14.67–21.86)
	Pond			18.43 (13.71–23.11)
Claw	River	25.99 (20.58–31.28)	28.23 (21.00–35.13)	27.84 (21.99–33.99)
	Lake		25.65 (20.27–30.81)	21.12 (16.34–26.19)
	Pond			24.57 (17.56–31.45)

Table S8. Accuracy information criteria of mesh designs from different spatial hierarchical Bayesian models for each tissue relating isotopic niche width (SEAB) of *Caiman crocodilus* to Boruta-selected landscapes attributes in the Araguaia floodplain. Bold values indicate mesh design and model chose for posterior analysis. Model descriptions are described in Appendix A. NA means that step for model construction was not performed.

Tissue	Mesh	DIC				WAIC			
		Null	Non-SPDE	SPDE	Best model	Null	Non-SPDE	SPDE	Best model
Plasma	Mesh 1	275.724	273.581	273.152	271.674	277.406	274.294	273.625	271.041
	Mesh 2	275.724	273.581	273.105	271.154	277.406	274.294	273.509	270.938
	Mesh 3	275.724	273.581	273.038	271.721	277.406	274.294	273.490	271.278
	Mesh 4	275.724	273.581	273.071	271.580	277.406	274.294	273.441	270.969
	Mesh 5	275.724	273.581	273.073	271.313	277.406	274.294	273.452	270.939
Muscle	Mesh 1	249.977	251.260	250.992	248.951	251.478	251.166	250.850	247.842
	Mesh 2	249.977	251.260	250.880	248.872	251.478	251.166	250.896	247.987
	Mesh 3	249.977	251.260	250.810	248.838	251.478	251.166	250.804	247.971
	Mesh 4	249.977	251.260	250.953	248.819	251.478	251.166	250.719	247.901
	Mesh 5	249.977	251.260	250.661	248.830	251.478	251.166	250.746	247.870
Claw	Mesh 1	254.029	252.517	252.535	NA	254.453	252.371	252.477	NA
	Mesh 2	254.029	252.517	252.658	NA	254.453	252.371	252.629	NA
	Mesh 3	254.029	252.517	252.560	NA	254.453	252.371	252.509	NA
	Mesh 4	254.029	252.517	252.542	NA	254.453	252.371	252.502	NA
	Mesh 5	254.029	252.517	252.572	NA	254.453	252.371	252.528	NA

Table S9. Posterior estimates of hyperparameters (mean \pm standard deviation and 95% credibility interval) from spatial hierarchical Bayesian best models for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and isotopic niche width (SEA_B) of *Caiman crocodilus* according to tissue across landscapes in the Araguaia floodplain.

Response	Tissue	Hyperparameter	Mean	SD	Q _{0.025}	Q _{0.975}
$\delta^{13}\text{C}$	Plasma	Precision for the Gaussian observations	0.44	0.04	0.36	0.53
		Range for spatial random field	-5.69	0.49	-6.67	-4.76
		SD for spatial random field	3.84	0.43	3.02	4.71
	Muscle	Precision for the Gaussian observations	0.41	0.04	0.34	0.49
		Range for spatial random field	-5.29	0.51	-6.29	-4.28
		SD for spatial random field	3.60	0.47	2.67	4.51
	Claw	Precision for the Gaussian observations	0.41	0.04	0.33	0.49
		Range for spatial random field	-5.18	0.50	-6.17	-4.20
		SD for spatial random field	3.52	0.47	2.61	4.44
$\delta^{15}\text{N}$	Plasma	Precision for the Gaussian observations	1.93	0.18	1.59	2.31
		Range for spatial random field	-4.58	0.40	-5.38	-3.81
		SD for spatial random field	3.51	0.41	2.73	4.33
	Muscle	Precision for the Gaussian observations	1.93	0.18	1.60	2.30
		Range for spatial random field	-4.94	0.91	-6.83	-3.27
		SD for spatial random field	3.62	0.57	2.56	4.82
	Claw	Precision for the Gaussian observations	1.57	0.15	1.29	1.89
		Range for spatial random field	-4.81	0.52	-5.84	-3.80
		SD for spatial random field	3.81	0.44	2.94	4.68
SEA_B	Plasma	Precision for the Gaussian observations	0.00	0.00	0.00	0.01
		Range for spatial random field	-1.64	2.43	-5.81	3.68
		SD for spatial random field	2.99	2.27	-0.69	8.05
	Muscle	Precision for the Gaussian observations	0.01	0.00	0.00	0.01
		Range for spatial random field	-3.00	2.54	-7.84	2.12
		SD for spatial random field	1.51	1.93	-2.05	5.50
	Claw	Precision for the Gaussian observations	0.01	0.00	0.00	0.01
		Range for spatial random field	-1.41	2.16	-5.08	3.31
		SD for spatial random field	2.83	2.34	-1.20	7.92

FIGURES

Figure S1. Meshes used in the SPDE approach to INLA model selection. First, we constructed five meshes with a specified non-convex boundary ($\text{convex} = -0.15$) with *inla.nonconvex.hull* function. Next, we built non-convex meshes using the *inla.mesh.2d* function with fixed values for *cutoff* and *offset* parameters ($\text{cutoff} = 0.01$ and $\text{offset} = (0.1, 0.2)$) and varying values of the *max edge* parameter: Mesh I ($\text{max edge} = (0.05, 0.1)$), Mesh II ($\text{max edge} = (0.1, 0.2)$), Mesh III ($\text{max edge} = (0.15, 0.2)$) and Mesh IV ($\text{max edge} = (0.1, 0.3)$), and Mesh V ($\text{max edge} = (0.15, 0.3)$).

Figure S2. Posterior mean of the spatial random effect, Gaussian random field, from spatial hierarchical Bayesian best models for (A) $\delta^{13}\text{C}$, (B) $\delta^{15}\text{N}$, and (C) isotopic niche width according to tissue of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Points represent individuals (for A and B) and sites (C) within determined locality. The colors indicate levels of spatial random effect according to the associated legends.

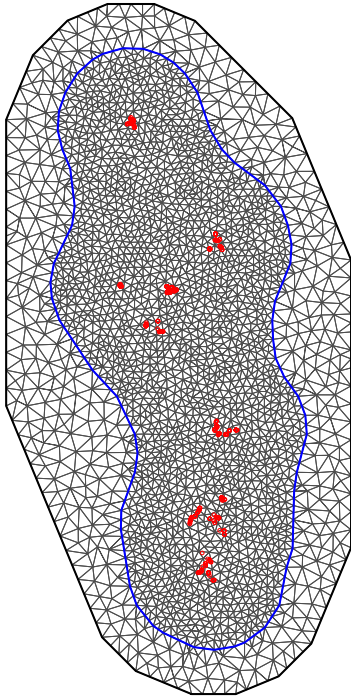
Figure S3. Posterior standard deviation of the spatial random effect, Gaussian random field, from spatial hierarchical Bayesian best models for (A) $\delta^{13}\text{C}$, (B) $\delta^{15}\text{N}$, and (C) isotopic niche width according to tissue of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Points represent individuals (for A and B) and sites (C) within determined locality. The colors indicate levels of spatial random effect according to the associated legends.

Figure S4. Predicted standard deviation of the spatial hierarchical Bayesian best models for (A) $\delta^{13}\text{C}$, (B) $\delta^{15}\text{N}$, and (C) isotopic niche width according to tissue of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Points represent individuals (for A and B) and sites (C) within determined locality. The colors indicate levels of responses according to the associated legends.

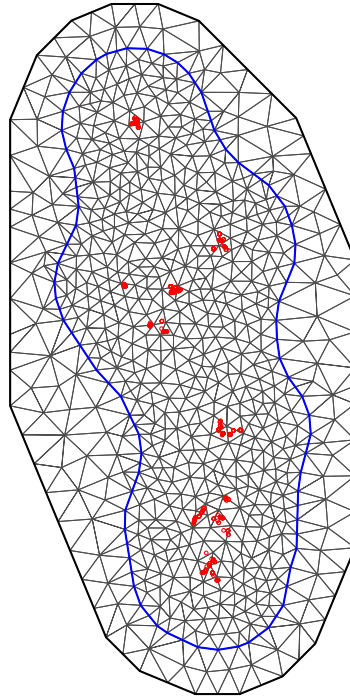
Figure S5. Isotopic niches of the habitats for each locality in (A) plasma, (B) muscle, and (C) claw of *Caiman crocodilus* across landscapes in the Araguaia floodplain. Solid lines represent the core isotopic niche space. Overall, habitats had high niche redundancy (i.e., high niche overlap) in all localities.

Figure S6. Values of isotope composition (A) and means \pm SD (B) from primary carbon sources collected by Zaia Alves *et al.* (2017) in the Araguaia River Basin and from samples of crops (rice and soybean) and caimans collected for our study. A high isotopic variability along $\delta^{13}\text{C}$ axis occurs in basal sources, including with agricultural samples, and caimans.

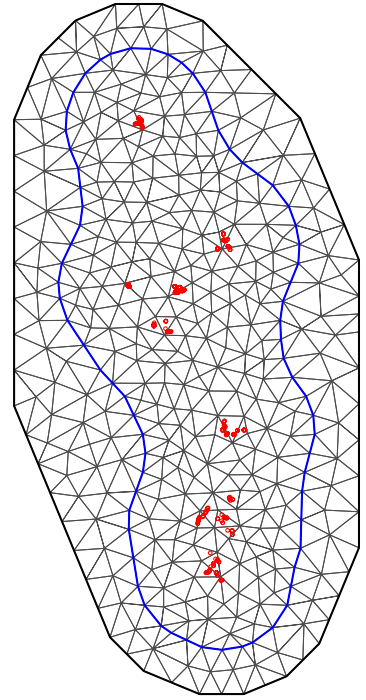
Mesh 1



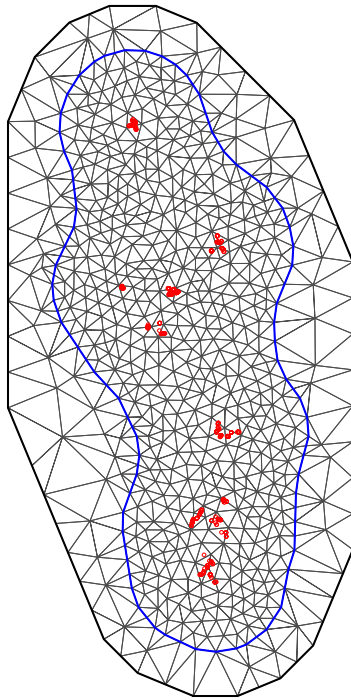
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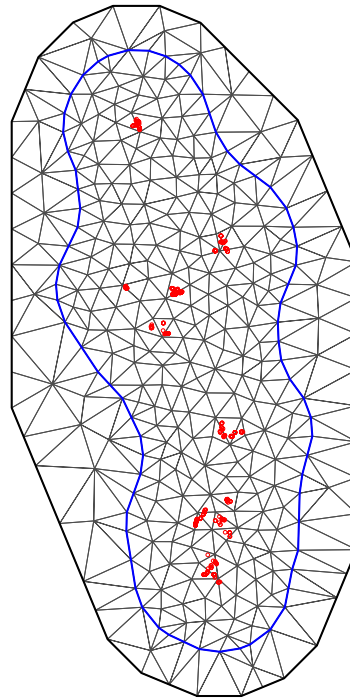
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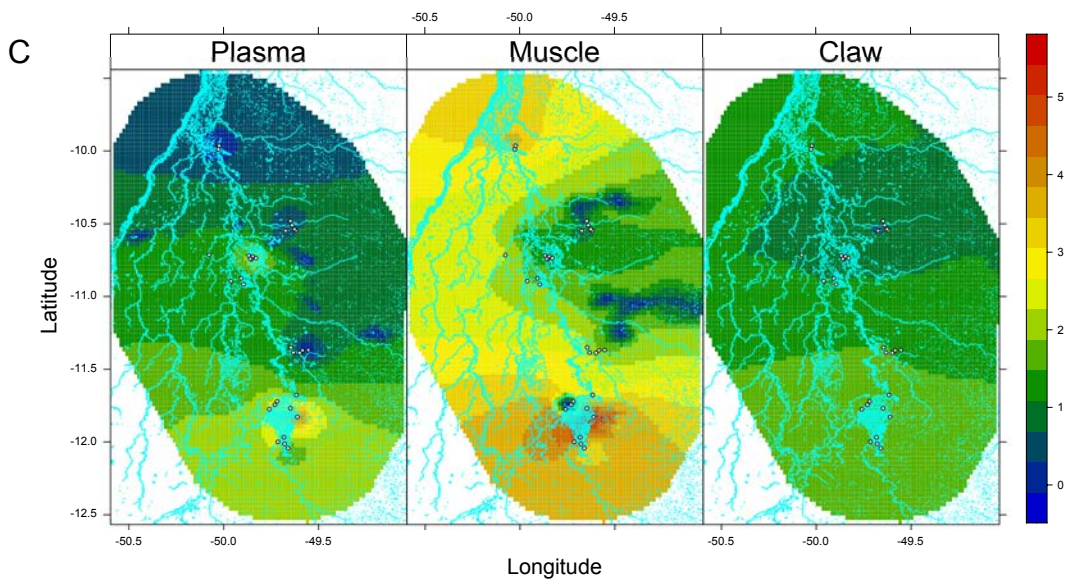
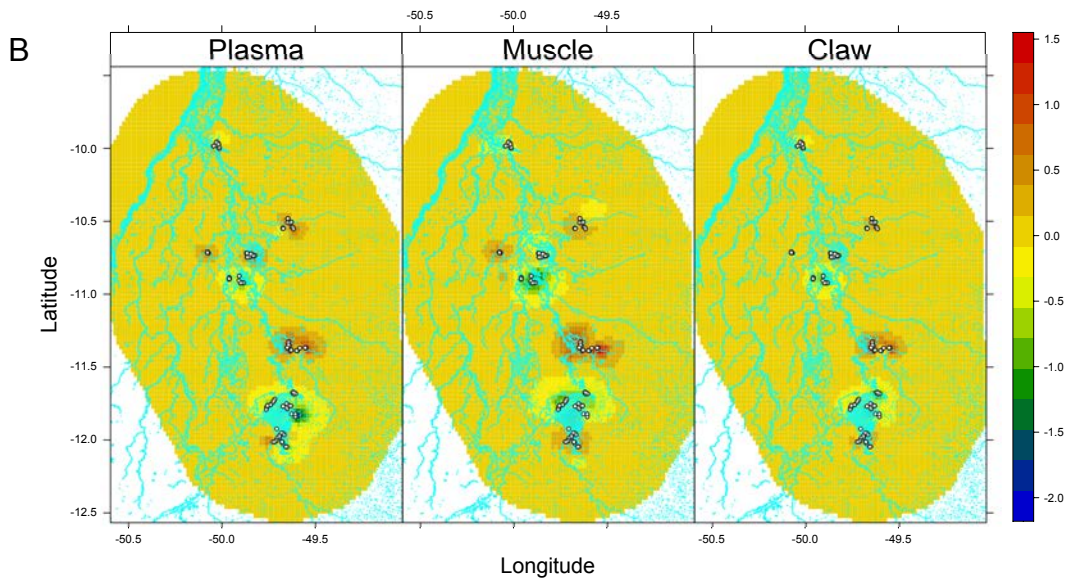
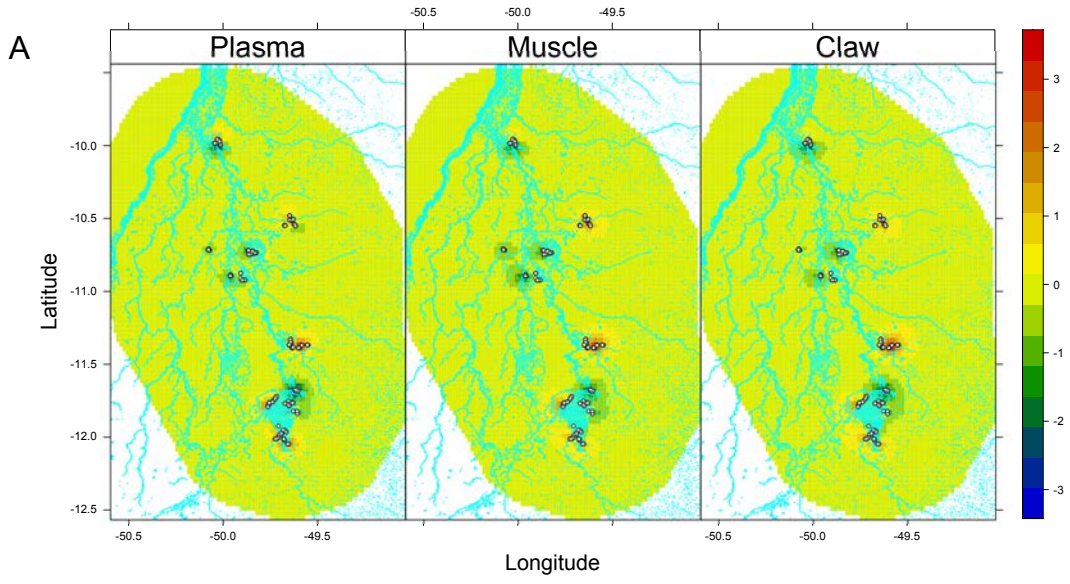


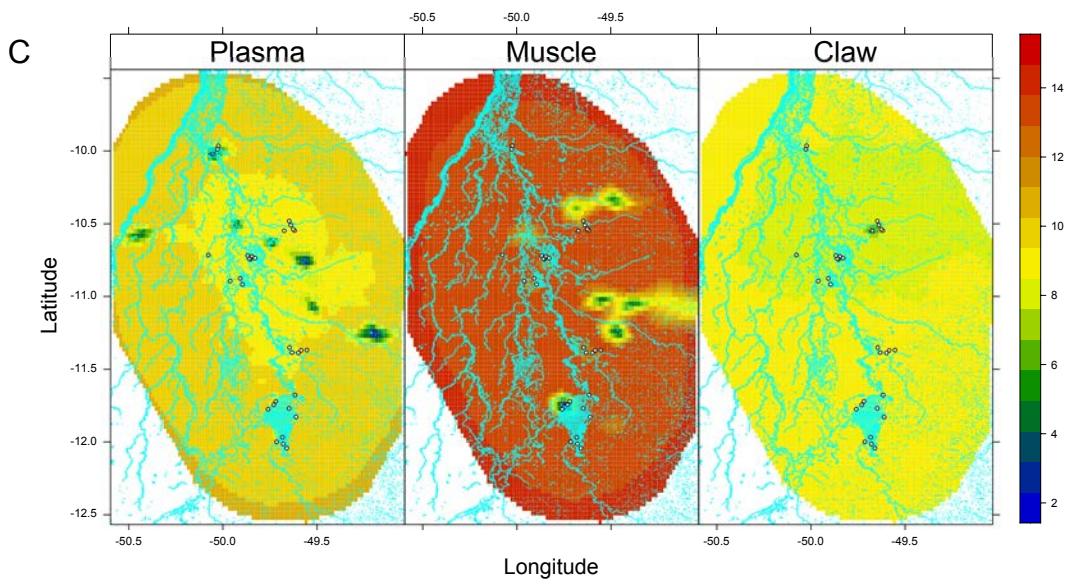
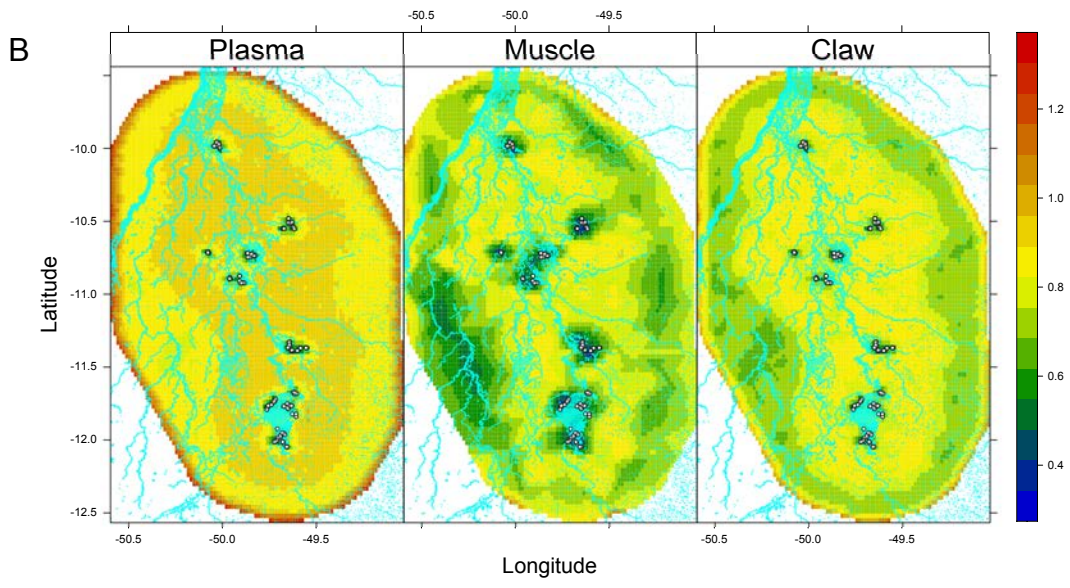
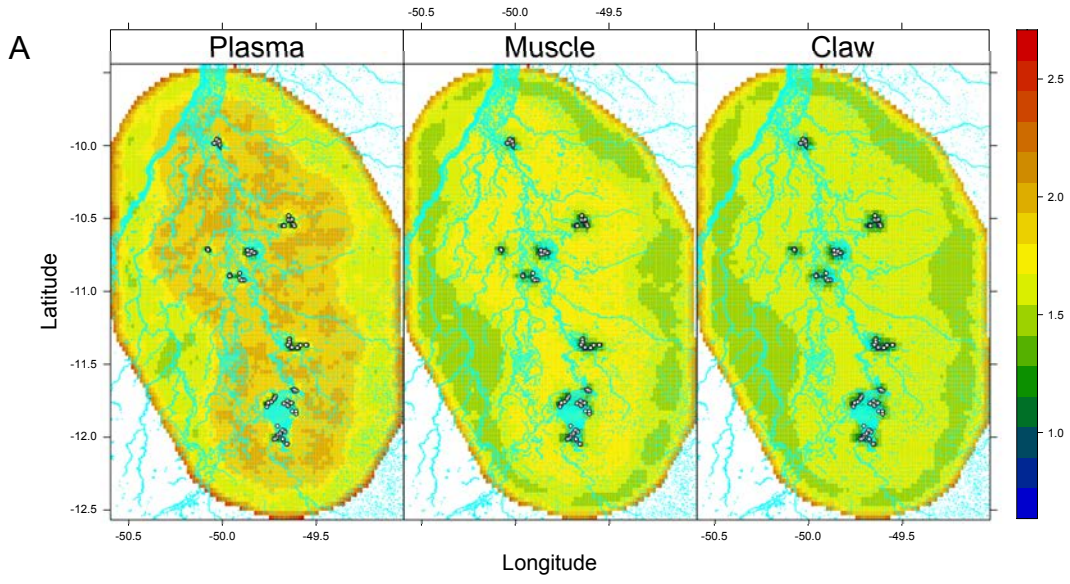
Mesh 4

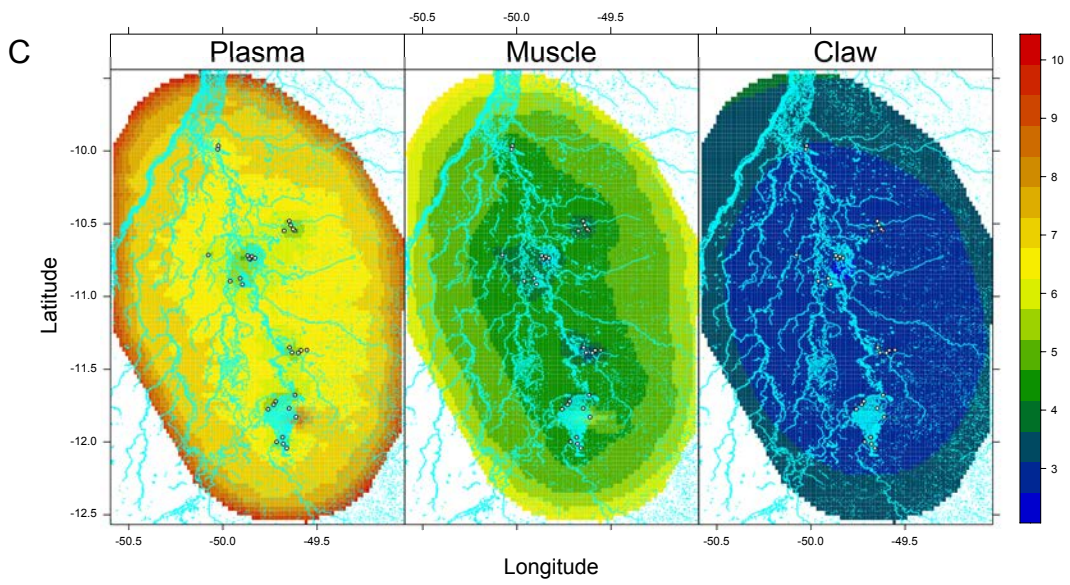
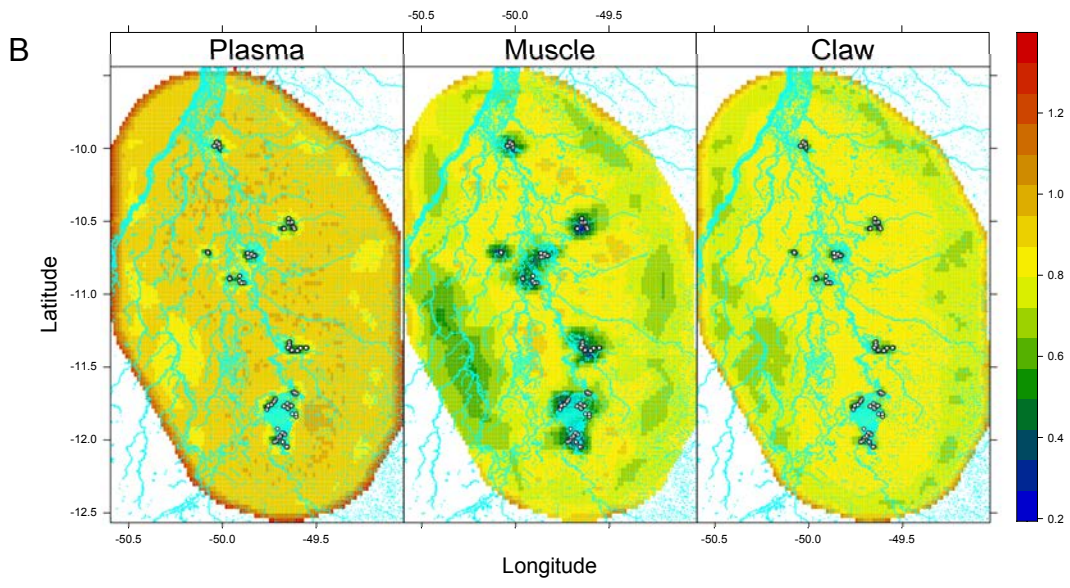
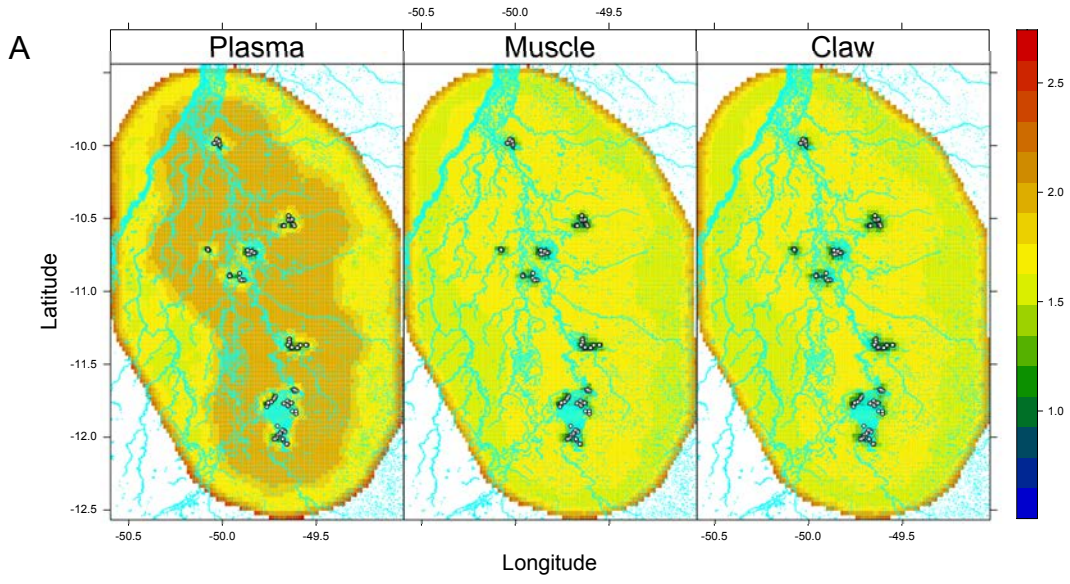


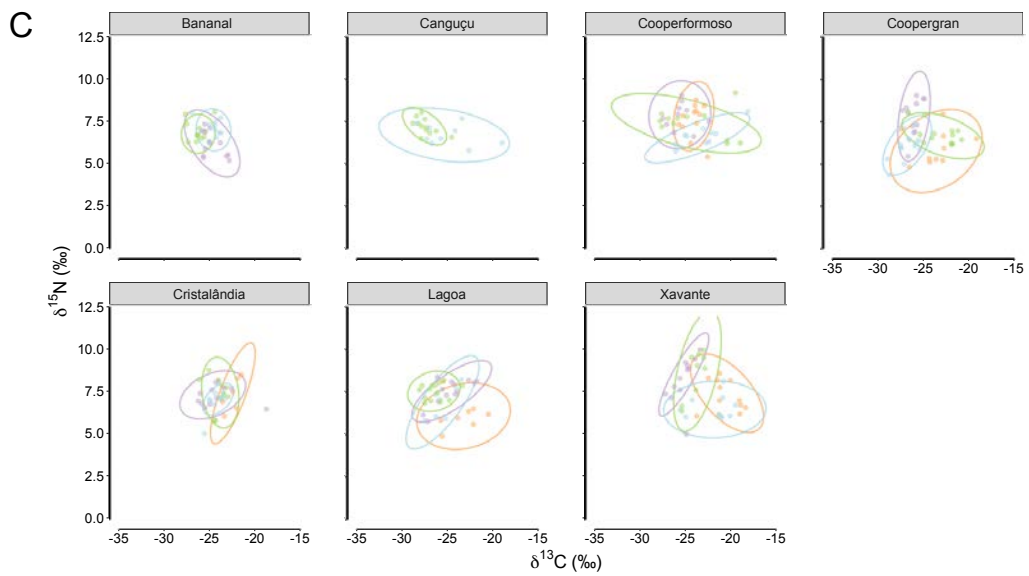
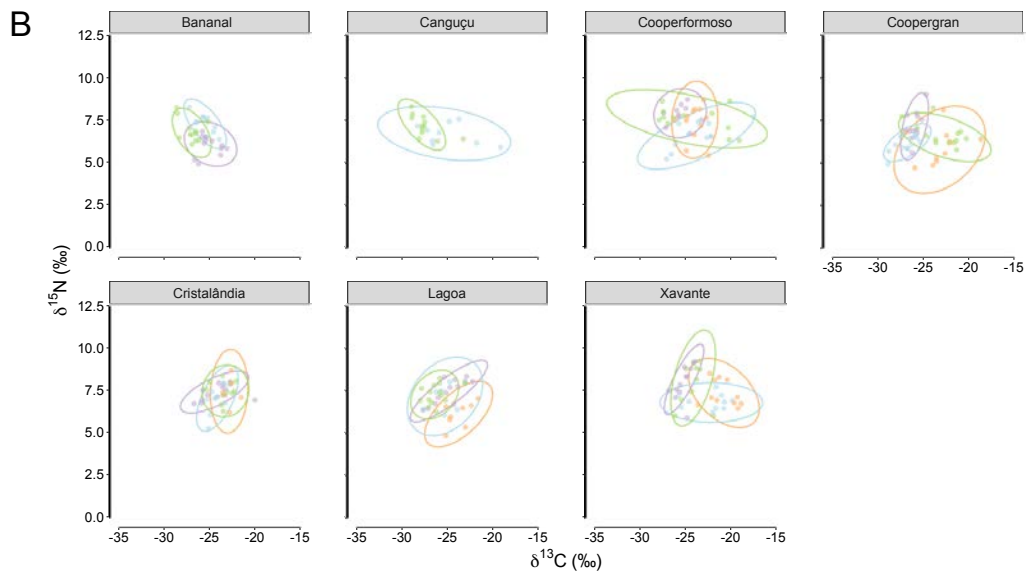
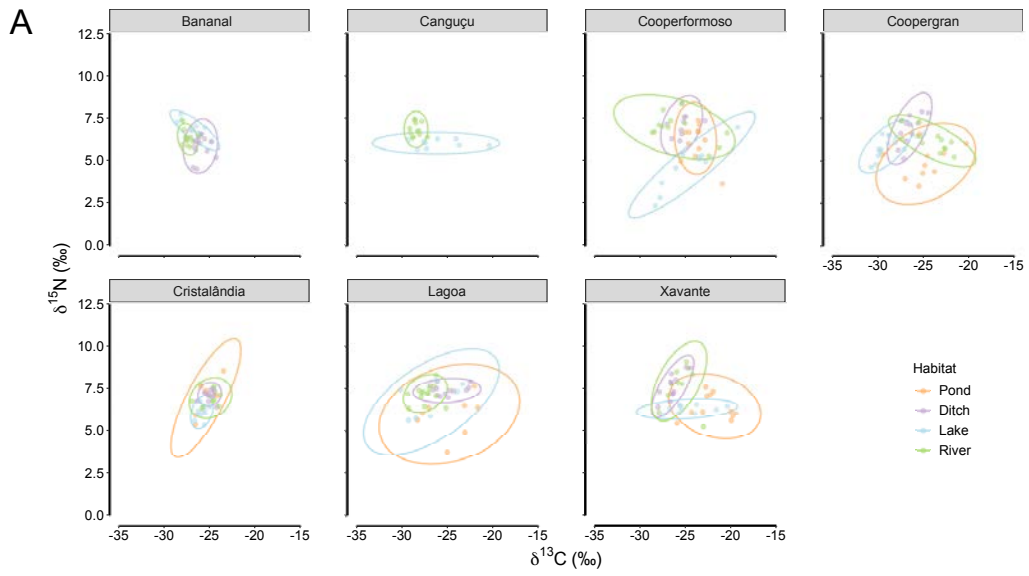
Mesh 5

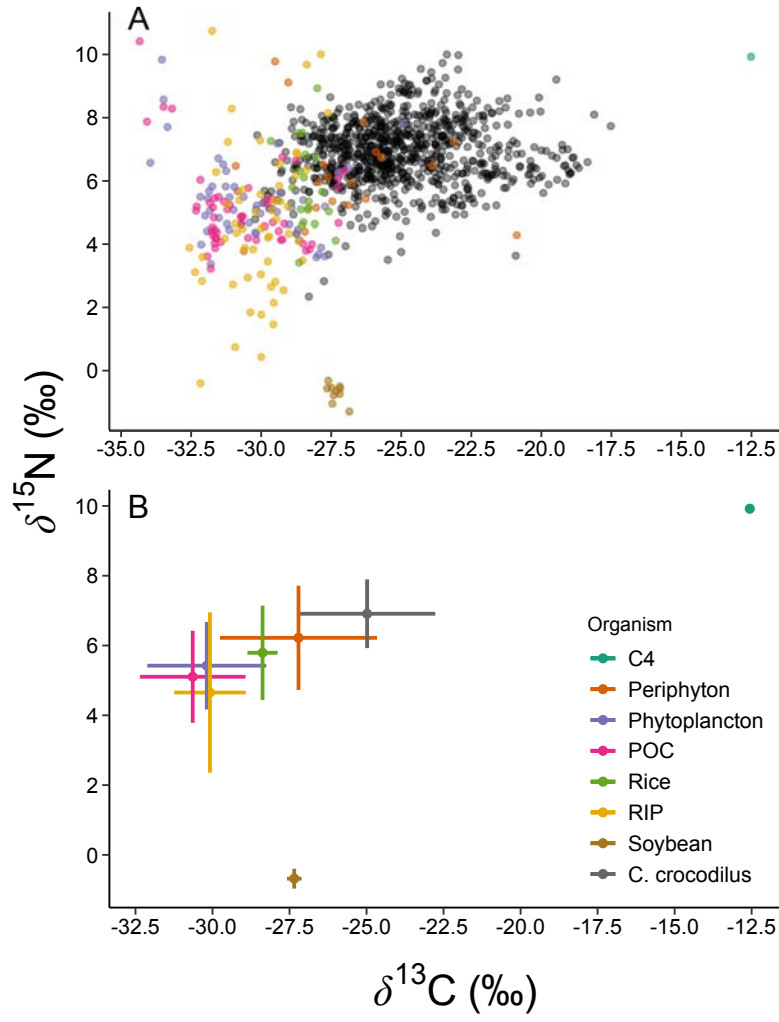












CAPÍTULO 3. IRRIGATED-RICE LANDSCAPES CAN SUPPORT HEALTHY POPULATIONS OF *CAIMAN CROCODILUS* (CROCODYLIA, ALLIGATORIDAE)

ABSTRACT

1. Landscape modifications cause environmental degradation that affects habitat suitability for species' persistence, with initial effects observed through individuals' and populations' physiological responses. However, some species can take advantage of landscape alteration and anthropogenic habitats. The landscape features that enable wildlife populations to persist in human-modified landscapes are still overlooked. We investigated what landscape features affect the body condition of *Caiman crocodilus* (Crocodylia, Alligatoridae) in human-modified landscapes with different land uses in the Araguaia floodplain, central Brazil.

2. Across seven distinct agricultural landscapes in the floodplain, we estimated the body condition index (SMI) of *C. crocodilus* captured in natural and anthropogenic habitats. Further, we verified and recorded the incidence of body injuries in individuals. To assess landscape modification, we measured land use composition and wetland configuration at different spatial scales. Next, we used a spatial Bayesian model averaging approach to assess the effects of body injuries and landscape attributes on caiman body condition.

3. Caimans had higher SMI in anthropogenic than in natural habitats and in ditches and man-made ponds than in lakes or rivers. The caiman SMI was affected only by wetland cohesion (an aggregation and connectivity metric), suffering a negative effect. However, wetland cohesion ranged from 80 to 99% in the human-modified landscapes. Otherwise, landscape composition did not influence caiman SMI, though ditch habitats relate to irrigated rice systems. Further, illnesses (i.e., leeches and body injuries) did not affect SMI.

4. *Caiman crocodilus* can thrive in anthropogenic waterbodies, such as stable water, closed systems of irrigation, apparently benefitting from higher prey availability.

Additionally, irrigated rice yields favored caimans by providing resources from associated biodiversity, becoming a high-quality matrix for caiman persistence.

5. Our findings highlight landscape features that support the persistence of caiman populations in altered landscapes. Anthropogenic waterbodies and irrigated rice fields provide suitable landscape conditions for caimans, supporting population maintenance across the landscape through waterbody availability and connectivity. In this sense, artificial wetlands can conciliate human-oriented and biodiversity-oriented purposes, providing ecosystem services and semi-natural habitats for some tolerant biota to habitat modifications.

Environmental policies should incorporate these semi-natural habitats in an integrative strategy of landscape-based management and monitoring water resources to achieve sustainable and conservation goals.

Keywords: body condition, disturbance, connectivity, fragmentation, Araguaia floodplain

INTRODUCTION

Anthropogenic ecosystems are becoming increasingly ubiquitous as humans modify natural landscapes for their purposes (Ellis & Ramankutty, 2008). Irrigation ditches and canals, livestock watering ponds, roadside ponds, and agricultural dams are examples of anthropogenic freshwater ecosystems in croplands and rangelands. These artificial waterbodies can vary with the degree and intent of modification, and their conditions for wildlife are not necessarily inadequate from their anthropogenic origins (Clifford & Heffernan, 2018). On the contrary, man-made waterbodies often can support many ecological processes and high biodiversity (Chester & Robson, 2013; Herzon & Helenius, 2008). In

landscapes where natural wetlands were suppressed, abundant and heterogeneous anthropogenic waterbodies can provide shelter and functional connectivity for wetland species (Clarke, 2015; Guareschi, Laini, Viaroli, & Bolpagni, 2019; Sayer, 2014; Thiere et al., 2009). Thus, improving habitat quality in agroecosystems through land and water management to enhance biodiversity, ecological processes, and ecosystem services is an active area of research (Biggs, von Fumetti, & Kelly-Quinn, 2016; Dollinger, Dagès, Bailly, Lagacherie, & Voltz, 2015; Maltchik, Stenert, & Batzer, 2017; Perfecto & Vandermeer, 2008; Sayer, 2014).

Such emergent ecological significance is threatened by well-known harmful human effects on wetland ecosystems and biodiversity, caused by environmental degradation and pollution, fragmentation and suppression of natural habitats, and land-use conversion (Allan, 2004). Changes in landscape composition and configuration can affect how species use, exploit, and access habitats and food, consequently influencing their persistence (Bennett, Radford, & Haslem, 2006; Fischer & Lindenmayer, 2007; Villard, Metzger, & Saura, 2014). The stressor factors can initially affect individuals and, posteriorly, entire populations; thus, population parameters may not inform habitat or landscape quality in a short-time (Gilroy & Edwards, 2017). Therefore, a quick health assessment of individuals may reveal environmental or anthropogenic stressors operating at small spatial scales before the entire population declines (Ellis, McWhorter, & Maron, 2012; Janin, Léna, & Joly, 2011).

Physiological traits, often measured through non-destructive or non-invasive alternative approaches, can help understand and predict wildlife responses under stressors (Ellis et al., 2012; Romero, 2004; Sheriff, Dantzer, Delehanty, Palme, & Boonstra, 2011). Body condition indexes indicate an animal's energetic state, health, or quality (i.e., physiological and nutritional condition), assuming a positive relationship with fitness and survival, being indirectly related with habitat suitability for the long-term persistence of

populations (Peig & Green, 2009, 2010; Stevenson & Woods, 2006). Ecological and conservation studies have profitably used body condition indexes to reveal some silent environmental and anthropogenic threats, including habitat loss, habitat disturbance, and pesticides (reviewed in Stevenson & Woods, 2006), and also to evaluate restoration actions and water management practices (Fujisaki, Rice, Pearlstine, & Mazzotti, 2009; Mazzotti et al., 2009). For instance, body condition can increase with the aggregation and proximity of habitat fragments in the landscape (Janin et al., 2011) and be lower in anthropogenic habitats due to reduced habitat quality (Battles, Whittle, Stehle, & Johnson, 2013; Gallego-Carmona, Castro-Arango, & Bernal-Bautista, 2016; Smyth, Smee, Godfrey, Crowther, & Phalen, 2014).

Smaller patch size is known to reduce food and refugia; consequently, the body condition of freshwater species is expected to have a positive relationship with increased waterbody size (Ellis et al., 2012; Ewers & Didham, 2006; Fahrig, 2003). Additionally, artificial habitats are surrounded by a non-native matrix that can vary in hostility, degree of permeability, and functional connectivity for biodiversity (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013; Ewers & Didham, 2006; Fischer & Lindenmayer, 2007). For example, irrigated rice systems can provide stable, interconnected, and heterogeneous habitats (Clarke, 2015; Maltchik et al., 2017; Perfecto & Vandermeer, 2008), while forest patches enhance the matrix quality and help maintain the life cycles, population dynamics, and body condition of wetland species (Janin et al., 2011; Quesnelle, Lindsay, & Fahrig, 2015). Conversely, homogeneous pastures are less favorable to such species due to reduced dispersal and elevated risk under more extreme abiotic conditions (Ribeiro, Colli, Batista, & Soares, 2017).

The ecological processes affecting body condition can vary among species in the same landscape, mainly related to differences in dispersal ability and body size driving their susceptibility to landscape modification (Ewers & Didham, 2006; Fischer & Lindenmayer,

2007). Crocodylians are semi-aquatic, large-bodied top predators in wetland ecosystems, which use multiple habitats in the landscape to meet their nutritional requirements, alternating resources from terrestrial and aquatic food webs (Somaweera et al., 2020). Crocodylians experience an ontogenetic dietary shift, from small invertebrates as juveniles to large vertebrates as adults, reflecting an associated increase in home range size and movements, including incursions in terrestrial environments (Grigg & Kirshner, 2015). As an ectothermic and a wetland-dependent species, prolonged periods overland may negatively impact physiological parameters and body condition (Barão-Nóbrega et al., 2017; Campbell, Micheli, & Abe, 2008). Changes in landscape characteristics may impact the trophic ecology, physiology, occupancy, and persistence of crocodylian populations (Somaweera, Brien, Platt, Manolis, & Webber, 2019). Therefore, crocodylians are a useful ecological indicator for detecting and monitoring the effects of anthropogenic disturbance (Somaweera et al., 2020; Mazzotti et al., 2009).

Here, we investigate the effects of landscape features on the body condition of *Caiman crocodilus* (Crocodylia, Alligatoridae) across a gradient of anthropogenic disturbance in the middle Araguaia River floodplain, central Brazil. We also use the incidence of ectoparasites (e.g., ticks and leeches) and body injuries (amputations, lesions, fractures, and lacerations) as indicators of general health. We use the top predator *C. crocodilus* (spectacled caiman) as an indicator species due to (1) its broad range of seasonal and ontogenetic movements across a variety of terrestrial and aquatic habitats in the floodplain (Gorzula, 1978; Ouboter & Nanhoé, 1988); (2) its public appeal as an iconic element of the Araguaia River basin; and (3) the presence in anthropogenic habitats in the floodplain, including irrigated crop systems and livestock watering ponds, which are essential for the conservation of crocodylian populations (Borteiro, Gutiérrez, Tedros, & Kolenc, 2008; Marques et al., 2016). We hypothesize that

anthropogenic disturbance should negatively affect the body condition and health of *C. crocodilus*.

METHODS

Study sites

The middle Araguaia River floodplain is in the highly dynamic and complex Cerrado–Amazonia ecotone in Brazil (Marques et al., 2019). The annual flood pulse drastically changes the landscape, spanning about 88,000 km² at maximum flood level and interconnecting several waterbodies, while only 3.3% (2,930 km²) of water area is present in the dry season (Irion et al., 2016). The Araguaia floodplain supports a rich and abundant biota, including many endemic and endangered species, protected by a RAMSAR site (Ilha do Bananal; n°. 624), some parks, and indigenous lands (RAMSAR, 2002; SEPLAN, 2012).

However, the Araguaia floodplain is under sustained pressure from agricultural development due to favorable topography and hydrology, which turned this region into one of the leading producers of irrigated rice in Brazil (CONAB, 2015). The production is based on irrigated systems, where crops are cultivated according to the hydrological regime: rice in the wet season alternating with other crops (e.g., soybeans, beans, watermelon) in the dry season (Oliveira, Viola, Mello, Giongo, & Coelho, 2015). During the last decades, Tocantins state expanded the cultivated area from 49,000 to 120,000 ha between 1989 and 2015, with maximum of 160,000 ha in 2008 (IBGE, 2016; Santos & Rabelo, 2008). The agribusiness has severely impacted the Araguaia Basin, and less than 50% of native vegetation remains (Coe, Latrubesse, Ferreira, & Amsler, 2011; Ferreira, Ferreira, Latrubesse, & Mizziara, 2008). In the middle Araguaia River floodplain, there was a reduction of 26% of native vegetation cover between 1975-2013, driven mainly by the expansion of pasturelands (Garcia, Sawakuchi, Ferreira, & Ballester, 2017).

Study design

We carried out fieldwork during the dry seasons (July to September) of 2016 and 2018 in seven localities across the middle Araguaia River floodplain (Figure 1). In each locality, we sampled animals in natural (e.g., rivers and lakes) and artificial habitats (e.g., ponds, reservoirs, and irrigation ditches), distributed among anthropogenic landscapes under different land uses and cover and natural landscapes, inside and outside of protected areas. To maximize their spatial independence, we chose localities at least 20 km from each other and sites within each locality as apart as possible from each other.

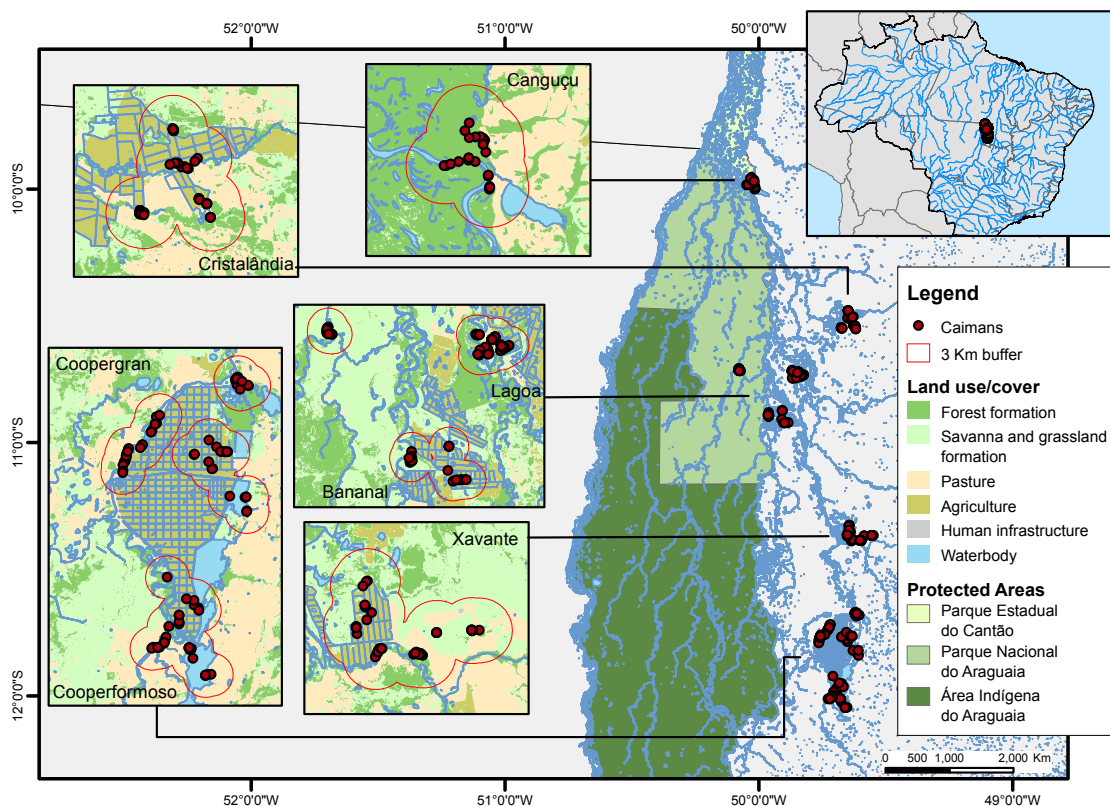


FIGURE 1 Location of seven sampling landscapes in the middle Araguaia River floodplain, central Brazil. Hydrograph and protected areas in the region are depicted. Red points represent the location of captured caimans in sampling sites. The 3-km buffer indicates the maximum spatial region for data acquisition of landscape attributes.

For assessment and measurement of human disturbance, we recorded landscape metrics using 500-m, 1-km, and 3-km circular buffers centered at each animal associated with the raster of land use/cover from MapBiomias Project (<http://mapbiomas.org>, collection 4, year: 2016 and 2018). Such buffer distances represent suitable distances for habitat utilization based on home range and movement studies for *C. crocodilus* (Gorzula, 1978; Ouboter & Nanhoé, 1988). We redefined MapBiomias land use classes considering five categories: water, forest, savanna (savanna, grassland, non-forest natural formation, and other non-forest natural formation classes), pasture (pasture and other non-vegetated area classes), agriculture (annual and perennial crop class). We excluded the urban class due to low representativeness in the coverage. To improve water coverage, we incorporated a hydrography raster generated from a vectorial database acquired from Secretaria do Meio Ambiente e Recursos Hídricos of State of Tocantins (<https://semarh.to.gov.br/car/base-vetorial-digital-tematica-do-car/>). Further, we improved MapBiomias land use mapping due to differences between supervised *in loco* coverage and MapBiomias raster, reclassifying and redefining the topology guided by Landsat 8 satellites images for the same months of caiman sampling in 2016 and 2018, with 30-m pixel spatial resolution obtained from the Instituto Nacional de Pesquisas Espaciais–INPE (Brazilian Space Agency; <http://www.inpe.br/>) using QGIS, version 3.12 (QGIS Development Team, 2020).

For each buffer, we calculated landscape metrics for the designated classes with the R package LANDSCAPEMETRICS (Hesselbarth, Sciaini, Nowosad, & Hanss, 2019): the percentage of the landscape of class (PCLASS) and mean patch area (MPA) for all classes; the mean of Euclidean nearest-neighbor distance (ENN), patch cohesion index (COHESION), and largest patch index (LPI) restricted to waterbody class. At the landscape level, we estimated the landscape shape index (LSI) and landscape division index (LDI). Such landscape metrics relate to composition characteristics, such as PCLASS, LPI, and MPA, which describe the

proportion of different types of classes, dominance of largest patch on class area, and mean area of class patches within the buffer area; and configuration characteristics, such as ENN, COHESION, LSI, and LDI. These characteristics reflect aspects of isolation, physical connectivity, and landscape fragmentation, respectively (McGarigal & Marks, 1995).

Field methods

We captured caimans in nocturnal spotlight surveys with the aid of locking cable snares or by hand after locating the animals by eye-reflection (Brien & Manolis, 2016; Fitzgerald, 2012). We physically restrained mouth and limbs with ropes and adhesive tape (Brien & Manolis, 2016). The capture effort was independent of animal size for all study habitats. We recorded the snout-vent length (SVL; with a 0.1-cm precision tape), tail length (from the posterior margin of the cloaca to the end of tail), body mass (with 0.1-kg precision spring scale), and sex, determined by cloacal examination and palpation of the penis (Reed & Tucker, 2012). Moreover, we recorded the presence of ectoparasites (e.g., ticks and leeches) and severe injuries (amputations, lesions, fractures, and lacerations) in the animals caught (Figure 2). We placed a permanent and individual mark in caimans by notching tail scutes as a standardized numerical code and released at the same local of capture (Plummer & Ferner, 2012). We conducted this study under permits SISBIO #13324-6 and #57940-3 (issued by Instituto Chico Mendes de Conservação da Biodiversidade), FUNAI #08620.005147/2018-38 (Fundação Nacional do Índio), and CEUA-UnB #94/2017 (Comissão de Ética no Uso de Animais da Universidade de Brasília).



FIGURE 2 *Caiman crocodilus* specimens in the middle Araguaia River floodplain: (a) released in an irrigation canal; (b) with leeches; (c) with hindlimb amputation; (d) with thorax laceration; (e) with partial tail loss; (f) with mouth lesion.

We estimated the body condition of *Caiman crocodilus* using the scaled mass index – SMI (Peig & Green, 2009), based on body mass and snout-vent length data in Equation (1):

$$SMI_i = M_i * \left[\frac{SVL_0}{SVL_i} \right]^{b_{SMA}} \quad (1)$$

where M_i and SVL_i are the body mass and the size of individual i , respectively; SVL_0 is the mean size in the study population; and b_{SMA} is a scaling factor. We computed b_{SMA} from a standardized major axis (SMA) regression of $\log(M)$ on $\log(L)$, using the R package LMODEL2 (Legendre, 2014). SMI is more efficient than conventional methods of estimating body condition, with isometric growth and invariability regarding sex and ontogeny, predicting

measures of fat and protein reserves of individuals, and being employed in several vertebrate taxa (Peig & Green, 2009, 2010).

Data analysis

We initially performed descriptive analyses, with values expressed mean \pm standard deviation (min – max). We performed a Chi-square test of independence with 1000 Monte Carlo simulations to investigate whether the frequency of ectoparasites and injuries were related to sex, habitat, and locality.

To assess the effects of land use and illnesses on *C. crocodilus* body condition, we used a Bayesian model averaging (BMA) approach to identify the most important predictors for body condition (Hoeting, 2002; Hoeting, Madigan, Raftery, & Volinsky, 1999), with R package BMS (Zeugner & Feldkircher, 2015). In this analysis, SMI was the response variable, while habitat, sex, tail length, presence of injury, presence of ectoparasite, landscape metrics (ENN, MPA, PCLASS, COHESION, LPI, LDI and LSI) for each buffer, and the interaction between sex and habitat were predictors. The predictors of landscape metrics and tail length were standardized around the mean with one standard deviation. For ectoparasite and injury, individuals had a record of presence-absence, represented as a binary variable (1 or 0, respectively). For this purpose, we excluded hatchlings (SVL < 20 cm) due to the low survivor rate and influence of environmental conditions on the mass-SVL relationship during embryonic development (Campos, 1993; Grigg & Kirshner, 2015).

Before analysis, we reduced the multicollinearity of the predictors by retaining landscape metrics with Variance Inflation Factors (VIF) smaller than 2 (Table S1), using the R package USDm (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014). Next, we selected those with greater predictive accuracy for caiman body condition among the remaining landscape metrics, using R package BORUTA (Kursa & Rudnicki, 2010). Boruta is a Random

Forest-based selection method that identifies all-relevant variables through a comparative approach of the importance (Z -score values) between original and “shadow” variables (obtained by shuffling values of the randomized original variables). Boruta eliminates irrelevant features ($Z\text{-scores}_{\text{Original var.}} < \text{maximum } Z\text{-scores}_{\text{Shadow var.}}$) to improve model predictive accuracy. We used $n\text{tree} = 2000$, $\text{maxRuns} = 2000$, and default settings of the other parameters. We retained the landscape attributes that had a positive decision (Table S2).

We incorporated in the BMA procedures to address model uncertainty in the presence of spatial autocorrelation due to the inherent spatial dependencies among the observations (Legendre, 1993). Spatial dependencies are removed through a semiparametric spatial filtering approach based on selected eigenvectors extracted from the spatial weight matrix (Tiefelsdorf & Griffith, 2007). Considering the critical effects that uncertainty in the type of spatial weight matrix (neighborhood relationships) can have on model parameter estimates, the spatial Bayesian model averaging method addresses both the uncertainty over model specification and the uncertainty regarding the choice of neighborhood relationships in the spatial regression model (Cuaresma & Feldkircher, 2013).

We implemented spatial Bayesian model averaging using the R package SPATBMS (Feldkircher, 2010) in 5 chains, using 10^7 iterations, 10^6 burn-in draws, the reversible-jump model-sampler algorithm, retention of the 500 best models, and default settings for the other parameters. We used nine different spatial weight matrices built with R package SPDEP (Bivand, Pebesma, & Gómez-Rubio, 2008): k nearest-neighbors ($k = 89\text{-}91$), Delaunay’s triangulation, Gabriel graph, relative neighbor graph, sphere of influence graph, and distance-based neighbors (distance = $17 \times \text{dngb}$, $20 \times \text{dngb}$, and $23 \times \text{dngb}$) – calculated from the minimum distance (dngb) at which all points have at least one neighbor, and then multiplied as many times as needed (i.e., 17, 20, and 23 times) to improve the contiguity. In this sense, we respected the contiguity condition for the choice of graph-based neighbor schemes, where

all graph schemes had all the points and areas linked, producing a unique mesh (Bivand et al., 2008). To assess the adequacy of the spatial filtering, we verified P -values of the Moran's I test for spatial autocorrelation obtained from the 100 best models (Feldkircher, 2010). We implemented all statistical tests in the R platform (R Development Core Team, 2019).

RESULTS

We caught 294 *Caiman crocodilus* across localities, with mean SVL of 57.40 ± 20.24 cm (15.4 – 104 cm) and body mass of 6.32 ± 5.98 kg (0.056 – 26.6 kg). The resulting b_{SMA} was 3.217, producing a mean SMI of 4.45 ± 0.46 (2.05 – 5.83). We recorded parasitism by leeches ($n = 15$) and injuries ($n = 19$), which included perforations and lacerations in the jaw, head, dorsum, and the loss of limbs and part of the tail (Figure 2). The presence of leeches was independent of sex ($\chi^2 = 1.228$; $P = 0.390$), but significantly associated with lake habitat ($\chi^2 = 11.472$; $P = 0.008$) and Cooperformoso and Bananal localities ($\chi^2 = 12.428$; $P = 0.499$). On the other hand, the occurrence of body injuries was dependent of sex ($\chi^2 = 4.693$; $P = 0.047$), with males having more injuries than females, but independent of habitat ($\chi^2 = 0.320$; $P = 0.950$) and locality ($\chi^2 = 12.355$; $P = 0.056$).

The best predictor of body condition was COHESION of waterbodies in a 3-km buffer (Table 1; Figure 3a), with 70.3% of posterior inclusion probability, a 95% credibility interval that did not include zero, and the largest standardized coefficient, but a negative correlation with body condition in all models that it was present (Figure 4a). COHESION was alone in the top model, contributing 35% to the posterior model probabilities. The null model was the second-best model, adding 21% to the posterior model probabilities, while the third-best model (COHESION and habitat) added just 9.6% to the posterior model probabilities (Figure 3a). The second-best predictor was habitat, with a 95% credibility interval that did not include zero, but just with 29.8% of posterior inclusion probability. Habitat had a positive coefficient,

that is, caiman body condition increased from river to ditch [predicted SMI river: 4.43 ± 0.05 ($4.36 - 4.56$); lake: 4.47 ± 0.09 ($4.34 - 4.59$); pond: 4.46 ± 0.08 ($4.39 - 4.64$); ditch: 4.48 ± 0.06 ($4.39 - 4.65$); Figure 4b]. The remaining predictors had lower importance ($PIP < 10\%$), lower standardized coefficients, and meager contributions to posterior model probability, indicating a small predictive power (Table 1, Figure 3a). The spatial BMA analysis indicated that the spatial weight matrix based on Delaunay's triangulation graph had the highest posterior model probability above 99%, with successful removal of the spatial autocorrelation from the regression residuals (Figure 3b).

TABLE 1 Bayesian model averaging of *Caiman crocodilus* body condition for landscape mosaic in the middle Araguaia River floodplain, central Brazil.

Predictor	PIP	Post Mean	Post SD	Post Sign	2.5% PostCI	97.5% PostCI
COHESION (water) 3-B	0.703	-0.078	0.058	0.000	-0.175	-0.047
Habitat	0.298	0.023	0.039	1.000	0.015	0.138
Sex	0.070	-0.008	0.033	0.000	-0.234	-0.008
MPA (water) 1-B	0.039	-0.002	0.011	0.000	-0.105	0.007
MPA (agriculture) 3-B	0.036	0.002	0.011	1.000	-0.009	0.111
MPA (forest) 1-B	0.033	-0.001	0.009	0.000	-0.094	0.007
MPA (water) 3-B	0.030	-0.001	0.009	0.000	-0.092	0.011
MPA (forest) 3-B	0.030	-0.001	0.009	0.001	-0.101	0.008
Habitat:Sex	0.027	0.000	0.006	0.474	-0.065	0.052
PCLASS (agriculture) 0.5-B	0.020	0.001	0.010	1.000	-0.025	0.139
MPA (pasture) 3-B	0.016	0.001	0.007	1.000	-0.037	0.091
Injury	0.012	-0.001	0.014	0.000	-0.271	0.102
MPA (savanna) 1-B	0.012	0.000	0.004	0.179	-0.071	0.038
ENN (water) 3-B	0.011	0.000	0.003	0.999	-0.029	0.064
Tail length	0.011	0.000	0.003	1.000	-0.033	0.065
COHESION (water) 0.5-B	0.010	0.000	0.003	0.077	-0.072	0.047
MPA (pasture) 1-B	0.010	0.000	0.003	0.980	-0.047	0.077
Ectoparasites	0.009	0.000	0.010	0.049	-0.240	0.186

PIP: posterior inclusion probabilities, i.e., sum of posterior model probabilities for all models wherein a predictor was included. *Post Mean*: standardized coefficients averaged over all models. *Post SD*: standard deviations of standardized coefficients. *Post Sign*: posterior probability of a positive coefficient expected value conditional on inclusion. *2.5% and 97.5% PostCI*: credibility interval of the posterior probability distribution. Buffers: 0.5-B for 500-m buffer; 1-B for 1-km buffer; 3-B for 3-km buffer.

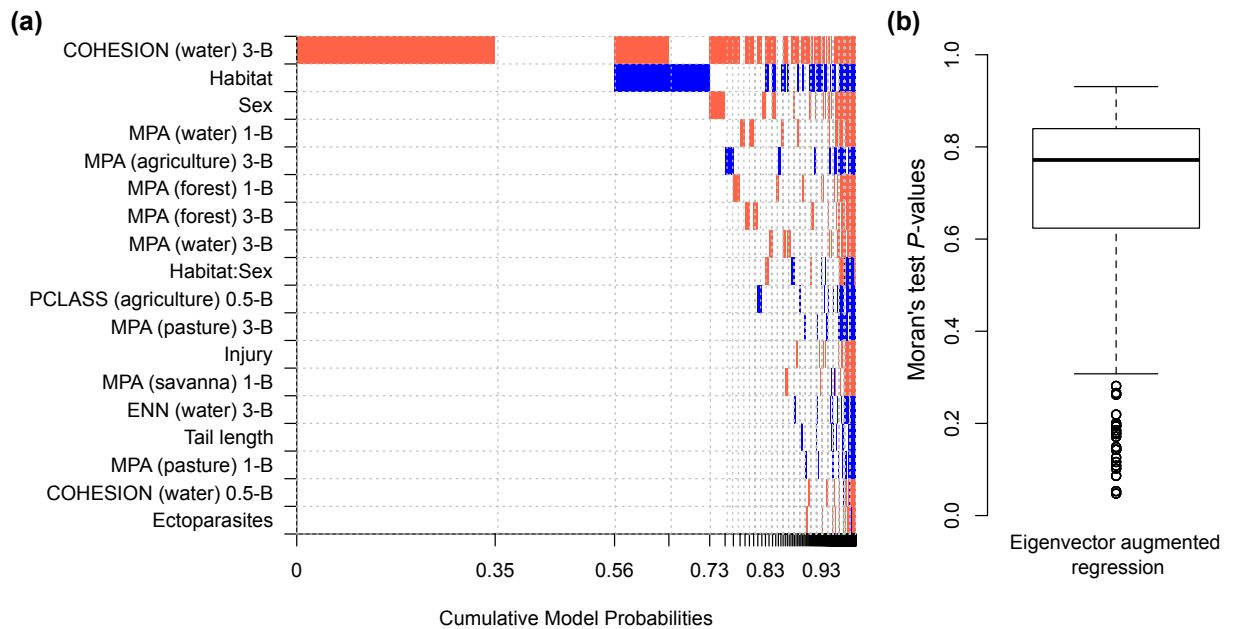


FIGURE 3 Bayesian model averaging of *Caiman crocodilus* body condition across landscapes in the middle Araguaia River floodplain: (a) cumulative model probabilities; (b) Moran's test P -values from spatial filtering of Delaunay's triangulation graph. The Y-axis contains the predictors of body condition, while the X-axis is scaled by the posterior model probabilities. Colors relate to predictor inclusions in models: positive coefficients are in blue, negative coefficients are in red, and non-inclusion are in white. Buffers: 0.5-B for 500-m buffer; 1-B for 1-km buffer; 3-B for 3-km buffer.

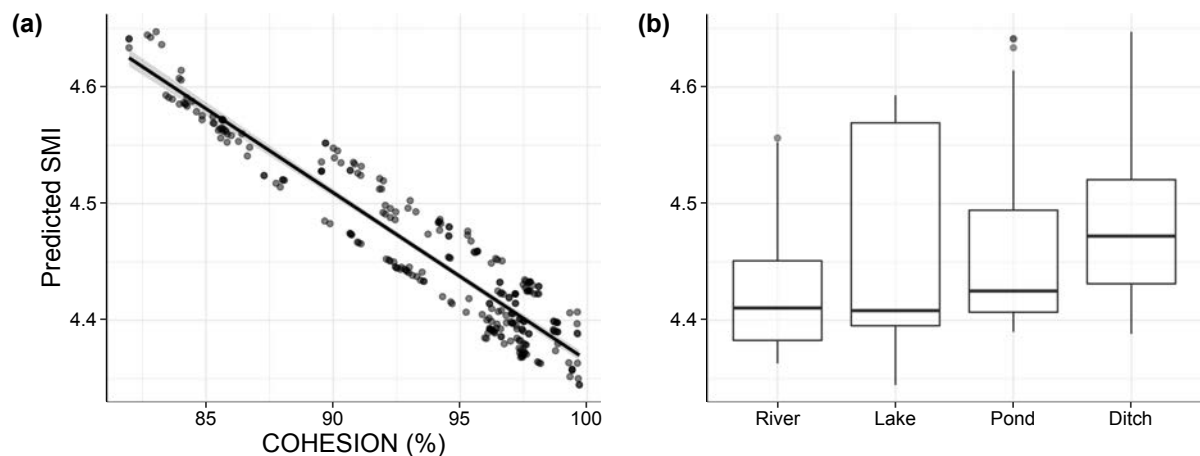


FIGURE 4 Effect of (a) patch cohesion index (COHESION) in 3-km buffer and (b) habitat on *Caiman crocodilus* body condition across landscapes in the middle Araguaia River floodplain.

DISCUSSION

Overall, the caiman body condition indicated good population health, suggesting suitable environmental conditions for populations' persistence in the Araguaia floodplain. Contrary to

our prediction, *Caiman crocodilus* had better body condition in anthropogenic waterbodies than their natural counterparts. Landscape features across human-modified areas in the Araguaia floodplain demonstrated that only waterbody connectivity affected caiman health, while other land-use composition and structure features did not directly influence. Our results illustrate how this species tolerates and even benefits from anthropogenic modifications.

Injuries and leeches were infrequent in *Caiman crocodilus*, and they were not included among important predictors of body condition. Although leech infestation rate and degree (number of leeches per individual) tend to increase with body size (Cott, 1961), habitat selection may be central for infestation intensity on individuals by using areas with high parasite load (Magnusson, 1985). Natural and anthropogenic waterbodies in our study indicated a low prevalence of ectoparasites, where the leech infestation did not indicate any obvious sign of disease or pathogenicity and no effect on *C. crocodilus* body condition. Still, leeches can transmit pathogens and hemoparasites, such as *Trypanosoma* and *Haemogregarina* (Fermino et al., 2015; Khan, Forrester, Goodwin, & Ross, 1980).

Injuries affect the physiologic functioning of individuals, reallocating energy for the immune system, regeneration, and recovery (Pressinotti et al., 2013; Siroski, Pina, Larriera, Merchant, & Di Conza, 2009), and depending on their severity, they may reflect apparent poor body condition and physical deterioration, e.g., weight loss (Huchzermeyer, 2003). In our study, injuries were more frequent in males than females, but unrelated to either anthropogenic waterbodies or higher human disturbance areas. Prevalence of injuries may relate to density-dependent factors through social interactions, such as crowding, hierarchy, and territory, where males usually demonstrate antagonistic behaviors during disputes for territory or females in the breeding season (Cott, 1961; Grigg & Kirshner, 2015; Huchzermeyer, 2003; Padilla & Weber, 2016). Nonetheless, the occurrence of crocodylians in some anthropogenic waterbodies may increase conflicts with humans due to human

occupation or threat to the rural livelihood, and thus, crocodylians may suffer injuries from human attacks, with fatal consequences for local populations (Das & Jana, 2017; Dunham, Ghiurghi, Cumbi, & Urbano, 2010; Fukuda, Manolis, & Appel, 2014; García-Grajales & Buenrostro-Silva, 2019). We postulate the low occurrence of injuries in our study is the reason for the lack of effect on *Caiman crocodilus* body condition, since we recorded injuries with great potential for physical impairments. Amputations and lesions can affect the body condition of crocodylians by restricting prey capture indirectly through hunt constrains (attack, locomotion, pursuit) or directly the food ingestion through feeding movement constrains (review of feeding mechanics of crocodylians in Grigg & Kirshner, 2015). For instance, we found a *C. crocodilus* without a tongue with poor physical aspect corresponding to one of the lowest values of body condition, likely due to reduced food intake.

Effects of landscape attributes upon *C. crocodilus* body condition were restricted to patch cohesion index, an indicative of aggregation and physical connectivity of waterbodies. Body condition decreased with a higher patch cohesion index in the 3-km buffer, indicating that our prediction was not supported. Higher aggregation and connectivity could indicate unfavorable conditions for foraging activities with a negative effect on *C. crocodilus* body condition. For example, more clumped wetlands could have high caiman densities, driving higher competition and resource deprivation (Hoare et al., 2006). Under the hypothesis that landscape influences population dynamics, with habitat quality and selection imposing costs and gains to individuals to achieve the best fitness (Hengeveld, van Langevelde, Groen, & de Knegt, 2009; Tschardt et al., 2012), anthropogenic pressures can reduce resource availability and diversity, lowering body condition in a spatial configuration of clumped wetlands (Battles et al., 2013; Gallego-Carmona et al., 2016; Smyth et al., 2014).

In our study, the waterbody cohesion index in 3-km buffer ranged from 80 to 99%, which can mask more harmful effects of extensive matrices in human-modified landscapes

with scarce and isolated wetlands, like pasturelands. In these circumstances, a severe dry season may intensify environmental constraints (reduced resource and habitat availability and depreciated physical-chemical conditions) to impact crocodylian body condition. A remarkable factor of stress is overheating and dehydration associated with restricted access to waterbodies or vegetation, with impact on physiological mechanisms of thermoregulation and body water balance able to conduct to lethal level (Campbell et al., 2008; Grigg & Kirshner, 2015; Somaweera et al., 2019). *Caiman crocodilus* females have a more prominent effect of dehydration in the breeding period when reproductive females reduce food acquisition and water access during nest attendance (Barão-Nóbrega et al., 2017; Barão-Nóbrega et al., 2016). Campbell et al. (2008) found expressive weight loss and reduction in physiological parameters (plasmatic glucose and triglycerides) in smaller *C. yacare* animals that inhabit Pantanal dry grassland with restricted access to water in high population density compared to animals inhabited in permanent ponds, indicating food deprivation by territorialism. Even though in estivation mode, crocodylians over three months without access to water were able to lose ~13% of their body weight, maintaining the same proportion of body mass in ~75% (Christian, Green, & Kennett, 1996). In circumstances of isolated waterbodies, an animal in poor health condition may reduce its survival rate during movement in a hostile agricultural matrix. For instance, the severe events in the dry seasons in 2016, 2017, and 2019 conducted to deaths of caimans in some isolated lakes in the Araguaia region (<https://g1.globo.com/to/tocantins/noticia/dezenas-de-jacares-morrem-apos-lagoas-secarem-na-ilha-do-bananal.ghtml>, <http://g1.globo.com/to/tocantins/noticia/2016/08/jacares-morrem-presos-lama-apos-lago-secar-no-sudeste-do-tocantins.html>, and <https://g1.globo.com/jornal-nacional/noticia/2019/09/30/no-tocantins-a-seca-severa-transforma-rios-em-lagos.ghtml>).

Forest formation is pivotal to support wetland species in agricultural landscapes (Bennett et al., 2006; Quesnelle et al., 2015). Some species relate mainly to the mounds of

vegetation formed next to wetlands (a complementary habitat), such as amphibians and reptiles that require different habitat types to complete their life cycles (i.e., foraging, dispersion, and breeding activities) (Guareschi et al., 2019; Quesnelle et al., 2015; Ribeiro et al., 2017). Vegetation influences directly crocodylians through nesting ecology, spatial habitat occupation according to body size, thermoregulation behavior, population survival, communication, and foraging activities across different spatial scales (reviewed in Somaweera et al., 2019). However, our spatial BMA modeling indicated no effect of forest area (represented by MPA of forest in 1-km buffer) upon *C. crocodilus* body condition, but intrinsically driven by wetland amount via cohesion index. The effect of vegetation coverage varies with animal taxa, and thus, though a wetland-dependent species is linked to wetland amount (Guareschi et al., 2019; Quesnelle et al., 2015). As the landscape integrates nearby protected areas and high waterbody connectivity, the spillover of caimans across habitats, including between irrigated rice fields and natural ecosystems, could reduce the negative impacts of landscape modifications upon body condition (Tschardt et al., 2012).

Our findings did not support our prediction that *Caiman crocodilus* population in natural habitats (e.g., rivers and lakes) should have higher body condition than populations in anthropogenic habitats; instead, *C. crocodilus* population in ditches had the best health, followed by populations in man-made ponds. This finding suggests that anthropogenic waterbodies met some characteristics for *C. crocodilus* to achieve better health. Man-made ponds and drainage networks in rice irrigation systems may become closed aquatic systems for aquatic animals during the dry season, with stable standing water or slow flow and shallow depths (Bambaradeniya & Amerasinghe, 2003; Biggs et al., 2016; Davies, Biggs, Williams, Lee, & Thompson, 2008), promoting suitable conditions to increase food intake. With a diet based on fish (Da Silveira & Magnusson, 1999; Laverty & Dobson, 2013; Thorbjarnarson, 1993), crocodylians experiment better body conditions in the dry season,

when feeding opportunity increases due to reduction of depth and area in waterbodies, concentrating aquatic and terrestrial prey in smaller wetlands (Fujisaki et al., 2009; Mazzotti et al., 2012). Whereas not equally comparable to natural habitats in pristine wetlands, waterbodies in agricultural landscapes can support expressive and representative freshwater biodiversity, including native, rare, threatened, and endangered species from diverse taxa (Bambaradeniya & Amerasinghe, 2003; Chester & Robson, 2013; Davies et al., 2008; Davies et al., 2008; Davis & Moore, 2016; Herzon & Helenius, 2008; Verdonschot, Keizer-Vlek, & Verdonschot, 2011). High α and γ taxonomic diversities are found in some agricultural landscapes, highlighting an important role of small natural and anthropogenic waterbodies for biodiversity conservation (Biggs et al., 2016; Davies et al., 2008; Ishiyama, Sueyoshi, Watanabe, & Nakamura, 2016; Thiere et al., 2009; Verdonschot et al., 2011). Man-made aquatic habitats such as irrigated rice yields could support generalist and opportunistic species by facilitating access to widespread prey associated with agricultural areas, amplifying the number of habitats and the structural connectivity between natural aquatic waterbodies.

However, the occurrence in anthropogenic habitats puts caution on these results because the susceptibility to exposure to agrochemicals, which are known to be harmful to biodiversity (Lee & Choi, 2020; Tavalieri et al., 2020; Warner et al., 2020). In irrigated agricultural systems in the Araguaia floodplain, the application of fungicides and herbicides apparently has low concentrations of their contaminants in the water, such as atrazine, propiconazole, tebuconazole, and tetraconazole (Guarda et al., 2020). However, negative effects are being detected through histological analyses of living tissues (liver, epithelium, and reproductive system) in amphibians (Lima, Malvasio, & Moraes, 2020). Although our study did not apply ecotoxicological approach, studies with crocodilians demonstrated harmful effects of pesticides on these predators, including through genotoxicity, enzymatic and metabolic alterations that affects fetal development and animal reproductive and immune

systems (Di Lorenzo et al., 2020; Galoppo et al., 2020; Guillette & Iguchi, 2003; Poletta et al., 2011; Siroski et al., 2016; Tavalieri et al., 2020). Body condition index also are negatively correlated with pesticide concentrations and distance to application area (Grant, Woudneh, & Ross, 2013). As indicator species and top predator that suffers effects from bioaccumulation and/or biomagnification processes, caiman body conditions can reflect a direct health loss or an indirect effect of trophic relations with reduction of prey (Grant et al., 2013). This ecotoxicological approach with caimans emerges as an open area for investigation in future studies in agricultural landscapes in the Araguaia floodplain.

Environmental heterogeneity plays a pivotal role for the populations of wetland species in agricultural wetlands (Bennett et al., 2006; Guareschi et al., 2019; Thiere et al., 2009). Local management can be effective to support rich biodiversity through an intermediate landscape complexity hypothesis, where the mosaic comprises natural and semi-natural habitats (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005; Tscharntke et al., 2012). For instance, agroecological systems integrate components for biodiversity- and human-oriented purposes, improving landscape attributes to a high-quality matrix and functional landscape heterogeneity (Fahrig et al., 2011; Perfecto & Vandermeer, 2008). Anthropogenic origins do not imply limitations to harbor wetland biodiversity when suitable landscape features are involved, mainly when associated with their natural counterparts. Artificial habitats can support functions for: maintenance of life cycle stages (e.g., breeding, foraging, temporal refuges) with higher habitat heterogeneity and availability for animal species; persistence, as an immediate refuge in the landscape with scarce natural freshwater habitats, considering the habitat suitability and representativeness in the landscape for the species; and dispersion and movement, as stepping-stones habitats able to have high connectivity value between freshwater habitats (natural or anthropogenic), mainly for

dispersive species (Bennett et al., 2006; Chester & Robson, 2013; Guareschi et al., 2019; Thiere et al., 2009).

Our study emphasizes the importance of anthropogenic waterbodies in agricultural areas and landscape configuration for a wetland-dependent species. Albeit of human origin, irrigated-rice landscapes could still have high conservation and ecological value (Chester & Robson, 2013; Clifford & Heffernan, 2018). Management of these habitats is the key for improving biodiversity, when considering strategies to incorporate and enhance ecological goals and possible new ecosystem services (Clifford & Heffernan, 2018). Under the strategic view, better responses can be achieved with proper management in local and catchment scales (Allan, 2004). In local scale management, both human-oriented and biodiversity-oriented purposes aggregate attributes to provide ecosystem services and increase biodiversity, such as in ponds (Biggs et al., 2016; Bolpagni et al., 2019; Sayer et al., 2012), ditches (Clarke, 2015; Dollinger et al., 2015; Needeman, Kleinman, Strock, & Allen, 2007), and other man-made habitats (Chester & Robson, 2013). A catchment and landscape-based management benefits biodiversity conservation, integrating connectivity in a river-floodplain system for protective and restorative actions of diverse waterbody types (Allan, 2004; Eros & Grant, 2015; Sayer, 2014).

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SUPPORTING INFORMATION

TABLE S1 Landscape attributes retained by Variance Inflation Factor (VIF) in the Araguaia floodplain. The VIF threshold had a value of 2 for the theta parameter. NS: landscape attributes with collinearity problem (VIF value > 2) and that were excluded from the posterior analysis.

Landscape attribute	VIF
ENN (water) 0.5-B	1.157
MPA (agriculture) 3-B	1.234
PCLASS (agriculture) 0.5-B	1.243
ENN (water) 1-B	1.251
MPA (pasture) 1-B	1.501
ENN (water) 3-B	1.584
MPA (pasture) 3-B	1.601
MPA (savanna) 1-B	1.621
COE (water) 3-B	1.652
MPA (forest) 1-B	1.658
MPA (forest) 3-B	1.688
MPA (water) 3-B	1.712
MPA (savanna) 0.5-B	1.725
MPA (water) 1-B	1.799
COE (water) 0.5-B	1.913
LPI (water) 1-B	NS
MPA (agriculture) 0.5-B	NS
PCLASS (savanna) 3-B	NS

PCLASS (agriculture) 3-B	NS
PCLASS (forest) 1-B	NS
LSI 3-B	NS
PCLASS (savanna) 0.5-B	NS
PCLASS (forest) 3-B	NS
LDI 3-B	NS
MPA (pasture) 0.5-B	NS
PCLASS (water) 0.5-B	NS
PCLASS (water) 1-B	NS
PCLASS (savanna) 1-B	NS
LSI 0.5-B	NS
PCLASS (agriculture) 1-B	NS
MPA (savanna) 3-B	NS
LDI 0.5-B	NS
PCLASS (forest) 0.5-B	NS
LPI (water) 0.5-B	NS
MPA (forest) 0.5-B	NS
PCLASS (water) 3-B	NS
LDI 1-B	NS
COE (water) 1-B	NS
PCLASS (pasture) 0.5-B	NS
MPA (water) 0.5-B	NS
LPI (water) 3-B	NS
PCLASS (pasture) 1-B	NS
MPA (agriculture) 1-B	NS
PCLASS (pasture) 3-B	NS
LSI 1-B	NS

TABLE S2 Importance of landscape features selected by Boruta as predictors of the body condition of *Caiman crocodilus* in the Araguaia floodplain. Decision, mean, minimum, maximum, and normalized importance based on the fraction of random forest runs in which the attributes were more important than shadow values.

Landscape metric	Decision	<i>meanImp</i>	<i>minImp</i>	<i>maxImp</i>	<i>normHits</i>
MPA (water) 1-B	Confirmed	18.591	14.866	22.851	1.000
COHESION (water) 3-B	Confirmed	17.346	13.758	22.448	1.000
COHESION (water) 0.5-B	Confirmed	15.542	11.667	19.451	0.999
MPA (water) 3-B	Confirmed	15.346	11.159	19.483	0.999
MPA (forest) 3-B	Confirmed	11.281	7.278	15.753	0.985
MPA (forest) 1-B	Confirmed	10.401	6.272	13.468	0.979
PCLASS (agriculture) 0.5-B	Confirmed	9.507	4.201	15.884	0.956
MPA (pasture) 3-B	Confirmed	8.984	5.142	12.053	0.953
MPA (savanna) 1-B	Confirmed	8.833	5.322	11.799	0.946

ENN (water) 3-B	Confirmed	7.657	4.169	10.747	0.905
MPA (pasture) 1-B	Confirmed	5.316	1.405	8.942	0.683
MPA (agriculture) 3-B	Confirmed	4.527	-0.272	8.125	0.555
ENN (water) 0.5-B	Rejected	3.741	0.654	7.188	0.214
MPA (savanna) 0.5-B	Rejected	3.640	0.548	6.328	0.084
ENN (water) 1-B	Rejected	3.383	1.255	5.294	0.006

CONSIDERAÇÕES FINAIS

As paisagens estudadas na planície de inundação do Araguaia apresentaram-se como uma composição mista de áreas antropogênicas com atividades agrícolas e de áreas naturais. Ambientes aquáticos naturais e antropogênicos se alternaram ao longo da paisagem e proveram diversidade e heterogeneidade de habitat para a biodiversidade. Assim, a maior disponibilidade e diversidade de corpos hídricos reconfiguram a paisagem sustentando propriedades essenciais para as espécies de áreas alagáveis, nas quais as implicações ecológicas apoiam-se na manutenção da dinâmica populacional, interações tróficas e persistências de certas espécies tolerantes a modificações da paisagem.

Nossos resultados sugerem adequáveis condições e importância ecológica de habitats antropogênicos para persistência das populações de jacarés. No entanto, ressalva-se que *C. crocodilus* possui comportamento de tolerância a perturbações, com favorecimento das condições impostas pelas modificações da paisagem devido a sua alta mobilidade, tamanho corporal e comportamento de forrageio, como apontado por esse estudo. No entanto, algumas espécies especializadas em ambientes naturais e/ou com habilidade limitada de dispersão são prejudicadas frente a reconfiguração e perda de habitats em paisagens modificadas. A importância de ambientes antropogênicos para a biodiversidade ainda carece de mais estudos e informações detalhadas da contribuição destes ambientes para toda biodiversidade. Estudos remetem a uma diversidade taxonômica com certo grau de plasticidade ecológica e ausentes espécies de grupos tróficos funcionais importantes na funcionalidade ecossistêmica, demonstrando limitações do conhecimento para estes ambientes antropogênicos.

Frente aos efeitos deletérios não mensurados neste estudo, relativos às atividades agrícolas, que são capazes de serem averiguados por outras abordagens complementares, como ecotoxocologia para contaminação por agrotóxicos, há de se investigar e manter contínuo monitoramento dessas áreas agrícolas. O contínuo crescimento científico desses ambientes sob distintas abordagens contribui para fomentar práticas e ações de manejo quanto aos recursos hídricos e de controle fitossanitário dos cultivos agrícolas voltados para sustentabilidade e conservação destes ecossistemas. As áreas agrícolas são componentes dominantes ao longo da paisagem, inclusive com perspectivas futuras de aumento devido ao potencial agrícola na planície de inundação do Araguaia, a conservação efetiva da biodiversidade apoia-se também na matriz agrícola e seu manejo aliado a delimitações de áreas protegidas. Os agroecossistemas emergem com novos paradigmas ao abarcar a

conservação da biodiversidade e perspectivas de paisagem, demonstrando estratégias de manejo integradas em ampla escala espacial. Em nosso estudo, sistemas irrigados de produção de arroz demonstraram serem matrizes agrícolas de alta qualidade para *C. crocodilus* ao aumentar habitats aquáticos, facilitar movimentação e dispersão, e disponibilizar e fornecer itens alimentares associados a estes ambientes. Há um papel relevante dos gestores e proprietários de terras no manejo da atividade agrícola com manejo dos recursos hídricos e uso da terra as quais mantem certas condições ambientais e de hábitat para a biodiversidade, bem como uma heterogeneidade com diferentes corpos hídricos em diferentes regimes hídricos e de formação vegetal, propiciando a manutenção de certos serviços ecossistêmicos.

O efeito da paisagem sobre processos ecológicos teve evidências por esse estudo, os quais influenciaram o nicho trófico e condição corporal *C. crocodilus*. Desta forma, cresce a atenção ao manejo dessas paisagens mistas, que quando integrada a estratégias de gestão de recursos hídricos em escala de bacias hidrográficas, unifica-se ecossistemas terrestres e aquáticos com um delineamento para alcançar propriedades ecológicas da paisagem que dão a funcionalidade para toda biodiversidade associada, como conectividade, heterogeneidade, permeabilidade de ambientes aquáticos e terrestres, com possibilidades efetivas de manejo da paisagem. Assim, prioridades de conservação de áreas naturais integram-se com áreas antropogênicas como componentes de uma paisagem mista adequada a biodiversidade, com parcial compensação da perda de complexidade da paisagem comparada a paisagens preservadas.