ORIGINAL ARTICLE



Deforestation leads to prey shrinkage for an apex predator in a biodiversity hotspot

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Received: 16 September 2020 / Accepted: 21 January 2021 © Mammal Research Institute, Polish Academy of Sciences, Bialowieza, Poland 2021

Abstract

Deforestation is a key driver of biodiversity reduction worldwide and impacts ecosystem functioning, ecological processes, and species behavior. Here, we investigated the effects of deforestation on the diet of puma (*Puma concolor*) in the Brazilian Atlantic Forest. We characterized puma diets in the largest continuous Atlantic Forest remnant and compiled literature data on their diet across the biome for comparison. We divided localities (N = 16) into two systems, namely, preserved areas (>40% forest cover) and human-modified landscapes (HMLs; <40%), and compared the diets in terms of percentage of occurrence, mean weight of mammalian prey (MWMP), and niche breadth. We classified prey according to their body mass (small- to large-sized) and partitioned the contribution of vertebrates (mammals, birds, reptiles, and fish) and mammalian prey (10 orders). The puma diets varied widely across the Atlantic Forest, with prey size decreasing from preserved areas to HMLs. As deforestation increased, the proportion of small-sized prey also increased, leading to a reduction in the MWMP. Niche breadth varied independently of the context or forest cover. Ungulates, large rodents, and xenarthrans were the main prey for pumas in preserved areas, while small rodents and birds accounted for 55% in HMLs. Ungulate predation increased with forest cover augmentation, with the opposite pattern observed for small rodents. The puma diet parameters in the Atlantic Forest and across Neotropical regions were similar, whereas both differed from that of North America, where large-sized prey was more consumed. Deforestation drove pumas to feed on smaller prey (<1 kg), thus highlighting that the effects of deforestation can be even larger and affect the assemblage trophic structure.

Keywords Atlantic Forest · Diet · Felids · Feeding habits · Trophic ecology

Introduction

Deforestation is one of the main causes of reduced biodiversity in tropical forests worldwide, and it is mainly driven by

Communicated by: Krzysztof Schmidt

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the increasing proportion of agricultural lands and the expansion of urbanized areas (Gibbs et al. 2010). These factors along with overhunting are responsible for extirpating sensitive species and large-bodied animals (Dirzo et al. 2014), resulting in the erosion of large herbivore and top predator populations (Ripple et al. 2014, 2015). In particular, the extirpation of large carnivores in response to habitat loss, reduced occurrence area, prey base loss, and retaliatory hunting (Ripple et al. 2014) may result in cascading effects, with severe consequences for ecosystem functioning and ecological processes (Estes et al. 2011).

In the Neotropical realm, jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the remaining extant apex predators. Jaguars suffered contractions along their original distribution area, with biomes such as the Atlantic Forest in South America being classified as the most urgent concern for conservation (Sanderson et al. 2002), which is corroborated by recent studies (Galetti et al. 2013; Paviolo et al. 2016). The puma is the second largest felid that lives in the Atlantic Forest of Brazil, and although widespread in the biome and inhabiting both preserved areas and human-modified landscapes (HMLs) (e.g., Magioli et al. 2014, 2016; Bovo et al. 2018), pumas are threatened in Brazil (ICMBio 2018). Habitat loss and fragmentation and prey base loss are the main threats to pumas (Nielsen et al. 2015), and these negative impacts are compounded by the effects of other factors, such as retaliatory hunting (Marchini and Crawshaw 2015), genetic drift (Miotto et al. 2014), and roadkill (Abra et al. 2019).

Due to its behavioral plasticity, puma consumes a large number of prey species (Sunquist and Sunquist 2002), including small- to large-sized vertebrates, with proportions varying within its distribution area (Iriarte et al. 1990). In the tropical portion of its distribution, the species feed mainly on smalland medium-sized prey (from 1 to 15 kg), with an increased number of species consumed in comparison to temperate regions (Sunquist and Sunquist 2002; Nielsen et al. 2015). However, in highly modified landscapes with low forest cover, pumas persist by consuming large amounts of even smaller vertebrates (< 1 kg) (e.g., Rocha-Mendes et al. 2010; Ghelercosta et al. 2018), such as rodents, birds, and reptiles, and these prey survive by inhabiting and feeding on agricultural areas (Magioli et al. 2014, 2019).

Thus, in the context of the Atlantic Forest, which is a Neotropical biome with high levels of deforestation and habitat fragmentation (Ribeiro et al. 2009), we raised an important question: how do deforestation affect qualitative aspects of the puma diet? To answer this question, we assessed different aspects of puma diets across the Brazilian Atlantic Forest, in preserved areas, and HMLs and then evaluated the effects of forest loss on the diet parameters. To do this, we collected primary data on puma feeding habits in two localities of the largest continuous Atlantic Forest remnant and compiled data from the literature on the puma diet across the biome for comparison.

At the landscape scale, areas with more than 40% forest cover have higher odds of supporting wildlife assemblages containing forest-dependent species (Arroyo-Rodríguez et al. 2020), which includes key prey for pumas in the Neotropics (e.g., ungulates). Thus, we considered areas with more than 40% forest cover at the landscape scale to be preserved areas and areas with less than 40% forest cover to be HMLs (see details in the "Data analysis" section). Since pumas tend to feed on prey that are more common and vulnerable (Sunquist and Sunquist 2002), we expect that (1) as deforestation increases, the proportion of smaller prey (e.g., small rodents and birds) in the puma diet will increase because large vertebrates (e.g., ungulates) tend to vanish in response to high levels of deforestation (Bogoni et al. 2020) and (2) the changes in prey composition in response to deforestation will result in a reduction of the mean weight of puma prey from preserved areas (> 40% of forest cover) to HMLs (< 40%).

Methods

Primary data collection

We selected four sampling sites within the largest continuous Atlantic Forest remnant in the state of São Paulo, Brazil, and grouped them in two blocks: (1) Corredor Ecológico de Paranapiacaba (CEP), which is composed of two contiguous state parks, Carlos Botelho and Intervales, and (2) Núcleo Santa Virgínia (NSV), which is an administrative division of the Serra do Mar State Park and composed of two research bases, Itamambuca and Vargem Grande (Fig. S1 in Online Resource). These sites present mammalian assemblages that are similar to what is expected in pristine areas (Galetti et al. 2017), including the main prey species of pumas, such as armadillos (*Dasypus* spp., *Cabassous tatouay, Euphractus sexcinctus*), deer (*Mazama* spp.), and peccaries (*Pecari tajacu* and *Tayassu pecari*).

Between October 2014 and July 2016, we conducted 16 sampling campaigns lasting five days each (four campaigns in each sampling site) to collect fecal samples, and an interval of at least 2 months occurred between campaigns. We collected samples on pre-existing dirt roads and trails at each site (Fig. S2 in Online Resource), resulting in a sampling effort of 850 km traversed and the collection of 45 fecal samples. The samples were placed in plastic bags labeled with the site of collection, date, and trail or dirt road traversed and then stored in a refrigerator at the Wildlife Ecology, Management and Conservation lab (LEMaC), Forest Science Department, University of São Paulo (ESALQ/USP). Sample collection was authorized by SISBIO permit #43680-3, and access to sampling sites was authorized by COTEC permit #260108 – 003.547/2014.

Predator and prey identification

To identify the predator and prey species, we first screened the fecal samples by adapting the method proposed by Korschgen (1980), which consists of fragmenting and soaking the samples in water with detergent and alcohol for at least a day and subsequently washing them in running water with a 1×1 mm mesh sieve. Then, we dried the resulting material in an oven at 50 °C and screened it by separating food items (e.g., hair, bones, claws, feathers, teeth). Later, we placed the items in plastic bags for the identification of prey species and predators. Approximately 50% of the samples collected in the field (N = 20) had characteristic marks associated with them, e.g., tracks or placed in front or over scratches on the ground, which helped us to identify them as belonging to pumas. From the 45 samples collected in the field, those that were collected in the same sampling campaign, containing the same prey species and presented similar signs of decay, were excluded from the analysis because we considered them to be from the same animal (N = 5). Thus, 40 samples were retained for analysis.

After the screening process, we identified guard hairs from predators (pumas) and prey mainly based on the hair microstructure (cuticle imprints and medullar analysis) by adapting the method proposed by Quadros (2002). First, we cleaned guard hairs with 70% alcohol and dried them with absorbent paper. Then, we deposited the hairs over a slide containing a thin layer of partially dried transparent nail polish and covered it with another slide. We pressed the set of slides in a manual vise and left it to rest for ~30 min. Finally, we carefully removed the hairs from the slide and observed and photographed its imprints under a microscope at ×400 magnification. For the medullar analysis, we deposited a guard hair over a slide containing a drop of water and covered it with a glass cover. Then, we observed and photographed the medullar patterns under a microscope at ×400 magnification. To identify hair cuticle imprints and medullar patterns, we compared our records with photos from Quadros (2002), Miranda et al. (2014), and Magioli et al. (2016) and slides from reference collections of museum specimens. Items such as claws, scales, feathers, and others also helped in the identification of prey. Puma hair was found in ~63% of the samples (N = 25); eight samples were only identified by vestiges (tracks and scratches); and another seven samples were identified by fecal DNA (unpublished data). We conducted all laboratory procedures at LEMaC - ESALQ/USP.

Data analysis

Diet parameters

First, we classified prey items into size groups for standardization: small (< 1 kg), medium (from 1 to 15 kg), and large (> 15 kg). We calculated the proportion of occurrence (PO) of vertebrate prey, i.e., the frequency of each prey in the diet divided by the sum of the frequencies of all prey recorded (Maehr and Brady 1986). We calculated the niche breadth (B) for all vertebrate prey using Levins' index (Levins 1968) and standardized it (*B*') according to Hurlbert (1978):

$$B = 1/\sum PO^{2}$$

 $B' = (B-1)/(N-1)$

where *N* is the total number of species in the diet. To avoid bias in the calculation of niche breadth considering that diet studies identify species at different taxonomic levels, we grouped mammals into orders (Primates, Xenarthra, Marsupialia, Artiodacyla, Perissodactyla, Rodentia (small and large), Carnivora, Lagomorpha, and Chiroptera) and other vertebrates in birds, reptiles, and fish. We also calculated the mean weight of mammalian prey (MWMP) as a geometric mean following Jaksic (1983). Except for mammals, most of the other small vertebrates are difficult to identify at the species or even genus level (e.g., birds and reptiles). Thus, we chose to calculate the mean weight of prey only for mammalian species, which are the main prey groups for pumas. We compiled the mean body mass of mammals from Paglia et al. (2012).

Puma diet in a deforestation gradient

To assess the differences in the diet parameters of pumas (PO, niche breadth, and MWMP) and test the influence of forest cover on these parameters, we compiled studies from the literature on puma feeding habits in the Atlantic Forest for comparison. Different combinations of keywords in the titles and abstracts of studies were searched in the Web of Science and Google Scholar: puma(s), Puma concolor, diet, feeding habit(s), and Atlantic Forest. We also performed a Google search with the same keywords in English and Portuguese. We selected studies published in indexed and nonindexed journals and complemented them with gray literature, such as graduate and undergraduate dissertations, to maximize the number of studies in the analysis. We selected studies that presented the number of samples collected, number of prey items, and geographical coordinates of the study locality (checked in Google Earth Pro). We compiled 14 studies in different localities of the Atlantic Forest conducted between 2000 and 2018.

To perform the comparison, we classified the 16 study localities (two from this study and 14 from the literature) into two different systems based on the percentage of forest cover at the landscape scale: preserved areas (>40% of forest cover) and HMLs (< 40%). Recent evidence shows that landscapes with more than 40% forest cover can ensure the persistence of forest-dependent species (Arroyo-Rodríguez et al. 2020). Thus, to classify the study localities, we created buffers of 10 km radius (~340 km²) using the central point of the sampling areas as a reference and then calculated the percentage of native forest in the buffer zone (Fig. S3 in Online Resource). We adopted this buffer radius based on the home range of pumas (Oliveira and Cassaro 2006; de Azevedo et al. 2013; Azevedo et al. 2020). We used the MapBiomas land use map (collection 5) of 2020 (Projeto MapBiomas 2020) to calculate the percentage of forest cover. Forest cover varied from 5.5 to 99.5% between study localities; eleven localities were classified as preserved areas; and five were classified as HMLs (Table S1 in Online Resource).

For the comparison of diet parameters between systems, we tested the data for normality (Shapiro-Wilk normality test), with the Welch two-sample *t* test used for normally distributed data and the Wilcoxon rank-sum test used for nonnormal data, and the MWMP was log-transformed. To assess the influence of forest cover on the diet parameters of pumas, we fitted logistic regressions for proportion data (PO and niche breadth)

and used the log-transformed number of samples collected in the studies as weight for the models. The MWMP was logtransformed, and a generalized linear model was fitted, with the log-transformed number of samples used as weight for the model.

Additionally, we compared the differences in the proportion of vertebrate prey between systems by dividing them into categories (mammals, birds, reptiles, and fish) and the differences in mammalian prey by dividing them into orders as recorded in the data: Primates, Xenarthra, Marsupialia, Artiodacyla, Perissodactyla, Rodentia (small (< 1 kg) and large (> 1 kg)), Carnivora, Lagomorpha, and Chiroptera. We tested data for normality and then used the Welch two-sample t test for normally distributed data and the Wilcoxon rank-sum test for nonnormally distributed data. To assess the influence of forest cover on the proportion of vertebrate prey and mammalian orders consumed by pumas, we fitted logistic regressions and used the log-transformed number of samples collected in the studies as weights for the models. We also compared the diet parameters of pumas in the Atlantic Forest with parameters obtained for pumas across the Neotropics and North America (Iriarte et al. 1990; Oliveira 2002). One-way ANOVA and Tukey's HSD test were used to assess the differences in diet parameters. All analyses were performed in R 4.0.3 (R Core Team 2020) using RStudio 1.2.5042 (RStudio Team 2020), and the package "ggplot2" (Wickham 2016) was used for graphical implementation.

Results

Puma diet in the largest continuous Atlantic Forest remnant

We identified 16 prey items consumed by pumas in our sampling sites, of which 14 were mammals from 10 families and five orders (Table 1). The percentage of occurrence of largesized prey was high in NSV (67%), particularly white-lipped peccaries (*Tayassu pecari*) (44%), while both medium- and large-sized prey were important in CEP (48% each). Ungulates were most consumed prey in both areas (48.0 and 55.6% in CEP and NSV, respectively). The MWMP was also higher in NSV (21.8 kg) than in CEP (12.7 kg), and the niche breadth was narrower for pumas in CEP (0.53) than in NSV (0.67).

Puma diet variation across the Atlantic Forest

The percentage of occurrence, MWVP, and niche breadth of pumas varied widely across the Atlantic Forest (for all 16 study sites) within and between systems (Fig. 1; Table S1 in Online Resource). The percentage of occurrence of large-sized prey was higher in preserved areas (Wilcoxon rank-

sum test; W = 45, p = 0.05); the consumption of small-sized prey (Welch two-sample *t* test; t = -3.18, df = 5.22, p = 0.02) was higher in HMLs (Fig. 2a; Table S1 in Online Resource); and the percentage of medium-sized prey was higher in preserved areas with marginal statistical support (t = 2.21, df = 5.71, p = 0.07).

The proportion of mammals in puma diets was significantly higher in preserved areas (t = -2.94, df = 6.59, p = 0.02), while the opposite was observed for birds in HMLs (W = 47.5, p = 0.03) (Fig. 3a). For reptiles (W = 21.5, p = 0.52) and fish (W = 25, p = 0.59), there were no significant differences between areas (Table S2 in Online Resource). Ungulates, large rodents, and xenarthrans (mostly armadillos) were the most consumed prey in preserved areas, while small rodents were consumed to a greater degree than any other mammal in HMLs (Fig. 3b; Table S3 in Online Resource). Ungulate consumption was significantly higher in preserved areas (W = 3.5, p < 0.01), while the opposite was observed for small rodents in HMLs (W = 47, p = 0.03). None of the other mammalian orders presented significant differences between preserved areas and HMLs.

The MWMP of pumas was significantly higher in preserved areas than in HMLs (t = 2.83, df = 6.23, p = 0.03) (Fig. 2b), and the standardized niche breadth did not present any difference within or between systems (t = -0.10, df = 7.01, p = 0.92) (Fig. 2c; Table S1 in Online Resource).

A comparison of the diet parameters across the global distribution of pumas showed high similarity between the Atlantic Forest and remaining areas of the Neotropical region, whereas the puma diet in both the Atlantic Forest alone and the entire Neotropics differed from that in North America. The puma diet in North America had a higher share of large-sized prey, high mean weight of prey, and narrower niche breadth (Fig. 4).

Forest cover effects

The proportion of small-sized prey in the puma diet significantly increased with deforestation ($R^2 = 0.31$, p < 0.01, slope = -2.75), while the opposite was observed for the large-sized prey ($R^2 = 0.27$, p = 0.06, slope = 2.03), with marginal statistical support (Fig. 5 a and c). The relationship was not significant for medium-sized prey ($R^2 = 0.11$, p = 0.25, slope = 0.95) (Fig. 5b). None of the prey groups presented significant relationships with forest cover, although the proportion of mammals in the puma diet increased with increasing forest cover ($R^2 = 0.19$, p = 0.16, slope = 1.54), while bird consumption was favored by deforestation, with marginal statistical support ($R^2 = 0.28$, p = 0.08, slope = -2.37) (Fig. 6a). Ungulates presented a positive significant relationship with forest cover ($R^2 = 0.48$, p = 0.02, slope = 3.22), while the reverse was observed for small rodents, with marginal statistical support ($R^2 = 0.28$, p = 0.08, slope = -2.16) (Fig. 6b). No

Table 1Prey items consumed bypumas (Puma concolor) in thelargest continuous Atlantic Forestremnant, state of São Paulo,Brazil, depicting the prey meanbody mass (in kg) and thepercentage of occurrence fromsmall to large-sized prey

Taxon	Body mass	Percentage of occurrence		
		CEP (24)	NSV (16)	Total (40)
Large-sized (> 15 kg)	_	0.48	0.67	0.57
Hydrochoerus hydrochaeris	50.00	_	0.11	0.05
Mazama spp.	18.00	0.16	0.06	0.12
Pecari tajacu	25.00	0.16	0.06	0.12
Tayassu pecari	35.00	0.16	0.44	0.28
Medium-sized (1 to 15 kg)	_	0.48	0.22	0.37
Cabassous tatouay	5.35	0.08	_	0.05
Coendou spinosus	1.80	_	0.06	0.02
Cuniculus paca	9.30	0.16	0.11	0.14
Dasypodidae n.i.	3.65	0.04	_	0.02
Dasyprocta leporina	5.50	_	0.06	0.02
Dasypus novemcinctus	3.65	0.04	_	0.02
Euphractus sexcinctus	5.40	0.04	_	0.02
Galictis cuja	2.00	0.04	_	0.02
Herpailurus yagouaroundi	4.50	0.04	_	0.02
Tamandua tetradactyla	5.20	0.04	_	0.02
Small-sized (< 1 kg)	_	0.04	0.11	0.07
Birds n.i.	_	0.04	0.06	0.05
Reptiles n.i.	_	_	0.06	0.02

The numbers in brackets indicate the number of fecal samples analyzed per locality. *CEP* Corredor Ecológico de Paranapiacaba, *NSV* Núcleo Santa Virgínia, *n.i.* non-identified

other mammalian order presented significant relationships with forest cover. The MWMP significantly increased with increasing forest cover ($R^2 = 0.23$, p < 0.001, slope = 1.38) (Fig. 5d), and niche breadth was not influenced by it ($R^2 < 0.001$, p = 0.95, slope = 0.06) (Fig. 5e).

Discussion

Pumas presented high variation in all diet parameters (percentage of occurrence, MWMP, and niche breadth) across the Atlantic Forest, although larger prey (> 1 kg) was more consumed in preserved areas and smaller prey (< 1 kg) was more consumed in HMLs. Large forest remnants maintain more sensitive species, especially large mammals (Magioli et al. 2015; Bogoni et al. 2020), which are preferred by pumas, resulting in high MWMPs in preserved areas. Mammals were the bulk of the puma diet in both systems but were more consumed in preserved areas (89% vs 68% in HMLs), while the reverse was observed for small birds in HMLs (26% vs 5% in preserved areas). Considering the relative contribution of various mammalian prey, ungulates, large rodents, and armadillos were most consumed in preserved areas, while small rodents were consumed to a greater degree than any other mammal in HMLs. The proportion of small-sized prey in the diet of pumas increased and the MWMP decreased with deforestation, thus evidencing the loss of large-sized species and biomass collapse in HMLs (Galetti et al. 2017). This pattern was further confirmed by the increase in predation on ungulates with increasing forest cover, which are prey species with the highest mean body mass and high susceptibility to deforestation (Ripple et al. 2015), and the increase in the proportion of small-sized rodents and birds with decreasing forest cover. The diet parameters of pumas in the Atlantic Forest and Neotropics were similar, whereas the parameters of both of these areas differed from that in North America, where pumas consumed more large-sized prey (> 15 kg).

Puma diet in a deforestation gradient

When comparing the diet parameters of pumas in a deforestation gradient across the Atlantic Forest, we observed that the proportion of small-sized prey increased with forest loss. In HMLs, the remaining large-sized species occurred at low abundances and were rare or locally extinct (Bogoni et al. 2020), such as large herbivores, which tend to disappear with habitat loss and hunting (Ripple et al. 2015). Conversely, small-sized prey, such as some rodent species (e.g., *Oligoryzomys* sp., *Akodon* sp.), are common, abundant, and thrive in HMLs (Bovendorp et al. 2017), thus becoming more



Fig. 1 Proportion of vertebrate prey in the diet of pumas (*Puma concolor*) in preserved areas (blue dots) and human-modified landscapes (HMLs; red dots) of the Atlantic Forest, Brazil, and the mean weight of mammalian prey (MWMP; in kg) (black symbols) for each study sites. Prey items were classified as small- (yellow), medium- (green), and large-sized (blue). 1, De Azevedo (2008); 2, Golec (2012); 3, Magezi (2013); 4,

Leite and Galvão (2002); 5, Vidolin (2004); 6, Nakano-Oliveira (2006); 7, Martins et al. (2008); 8, Corredor Ecológico de Paranapiacaba (CEP, this study); 9, Röhe (2002); 10, Núcleo Santa Virgínia (NSV, this study); 11, Brito (2000); 12, Rocha-Mendes et al. (2010); 13, Gheler-Costa et al. (2018); 14, Rongetta (2014); 15, Magioli et al. (2014); 16, Santos et al. (2014)

available for pumas. This availability of small-sized prey (small-sized birds and rodents) is reflected in the puma diet

with increasing deforestation, thus supporting our first hypothesis.



Fig. 2 Differences in the (**a**) percentage of occurrence from small- to large-sized prey, the (**b**) mean weight of mammalian prey (MWMP; in kg), and the (**c**) standardized niche breadth of pumas (*Puma concolor*)

between preserved areas (green) and human-modified landscapes (HMLs; purple) of the Atlantic Forest, Brazil. Boxplots show means (diamonds), medians, quartiles, and outliers. *p < 0.05



Fig. 3 (a) Percentage of occurrence of prey groups consumed by pumas (*Puma concolor*) between preserved areas (green) and human-modified landscapes (HMLs; purple) of the Atlantic Forest, Brazil. (b) Percentage

of occurrence of mammal orders consumed by pumas between preserved areas and HMLs. Boxplots show means (diamonds), medians, quartiles, and outliers. *p < 0.05

Medium- and large-sized prey were more consumed in preserved areas (53% and 28%, respectively) compared to HMLs (31% and 12%, respectively), and these groups are more abundant in large forest remnants, especially forestdwelling species, such as peccaries, deer, and primates (Chiarello 1999; Lima et al. 2017). Nonetheless, the contribution of these groups to the puma diet in response to forest cover was lower than expected, partially refuting our first hypothesis for these groups. This unexpected variation may indicate bias in the criteria we used to classify the study localities (i.e., percentage of forest cover). For example, three areas that presented average levels of forest cover (i.e., Brito 2000; Röhe 2002; Golec 2012; see Table S1 in Online Resource) are structurally connected to large and/or continuous forest blocks, which increase the odds of having larger prey available for pumas, as shown by the composition of the puma diet in these areas.

Since we created buffers around the center of the sampling areas to calculate forest cover, the real extent of connected forest habitat might be underestimated, thereby influencing our results.

Additionally, the low effect of forest cover on puma prey size can also be explained by the persistence of some larger species in HMLs, particularly medium-sized generalists and those tolerant to modified habitats (Magioli et al. 2019), which include important prey to pumas, such as armadillos (e.g., *Dasypus novemcinctus*), South American coati (*Nasua nasua*), and paca (*Cuniculus paca*) (e.g., Magioli et al. 2016; Bovo et al. 2018). Some large-sized species also thrive in HMLs, especially in landscapes dominated by agricultural uses, such as capybara (*Hydrochoerus hydrochaeris*) (de Bovo et al. 2016), which becomes abundant and represents important prey for pumas (e.g., 19% of diet in Magioli et al. (2014) and 43% Magioli et al. (unpublished data)).



Fig. 4. (a) Comparison of percentage of occurrence (small- to large-sized prey), (b) mean weight of prey, and (c) niche breadth of pumas (*Puma concolor*) among Atlantic Forest, Neotropical region, and North America.

Boxplots show means (diamonds), medians, quartiles, and outliers. $\ast p < 0.05$



Fig. 5 Relationships of forest cover with the (a-c) percentage of occurrence of prey (small- to large-sized), (d) the mean weight of mammalian prey (MWMP; in kg), and (e) the standardized niche

breadth of pumas (*Puma concolor*) in the Atlantic Forest, Brazil. Values in red indicate relationships with statistical support; shaded areas show the 95% confidence intervals of the regressions

Considering the relative contribution of different prey in the puma diet, mammals were predominant, with rodents (small and large) accounting for one-third of all prey consumed in the Atlantic Forest. Rodents are an important prey type for pumas in the Neotropics, as also shown by other studies in parts of Central and South America (Emmons 1987; Branch et al. 1996; Pacheco et al. 2004; Moreno et al. 2006; Foster et al. 2010). In preserved areas of the Atlantic Forest, the proportion of mammals in the diet was more pronounced and slightly increased with forest cover augmentation. Ungulates, large rodents, and armadillos were important prey in preserved areas, but only ungulate predation increased with increasing forest cover, and it was virtually restricted to large forest remnants. In HMLs, small rodents and birds were



the main prey, accounting for 55% of all items in the puma diet, with the consumption of both groups increasing with deforestation. In addition to being a driver of the loss of species and their functions (Magioli et al. 2015), deforestation also affects the prey range available for pumas, as largesized prey become rarer in highly deforested landscapes.

The range of MWMP was wide across the Atlantic Forest (0.40 to 49.8 kg) within and between study systems but higher in preserved areas (18 vs 4.7 kg in HMLs). This pattern was further confirmed by the augmentation in MWMP values with increasing forest cover, thus supporting our second hypothesis. The variation in MWMP values in the Atlantic Forest was similar to that in other parts of the Neotropics (Iriarte et al. 1990; Oliveira 2002), and both were lower than those in North America (Iriarte et al. 1990, 1991; Núñez et al. 2000; Polisar et al. 2003; Monroy-Vilchis et al. 2009). In North America, pumas have less variability in their diets, and few prey species are compared with that in tropical areas, most of which are large-sized (mean 76.6%), resulting in high mean weight of prey and low niche breadth (Iriarte et al. 1990; Oliveira 2002). This pattern was reversed in the Atlantic Forest and across the Neotropics, with high variation in the number of prey consumed, especially small- and medium-sized prey, which resulted in more variation in niche breadth, indicating the existence of individuals with specialized and more generalist diets and decreasing the mean weight of prey (Iriarte et al. 1990; Oliveira 2002; Monroy-Vilchis et al. 2009).

We conclude that deforestation led to an increase in the consumption of small-sized prey by pumas, resulting in a reduction in the mean weight of prey in landscapes with low forest cover (< 40%). This change in the diet composition of pumas reflects the loss of large-sized species and biomass collapse in response to habitat loss and fragmentation across the Atlantic Forest, which is consistent with previous studies (Galetti et al. 2017; Bogoni et al. 2020). Although mediumand large-sized prey were more consumed in preserved areas (> 40% of forest cover), some of these localities showed pumas consuming high proportions of smaller prey, thus highlighting that human interference and hunting may have already reduced or even extirpated large-sized species in large forest remnants (Galetti et al. 2017). Our data present some limitations regarding the number of studies used for analysis and the sample size in certain studies. Nonetheless, the patterns we found are supported by the literature, which indicates that puma feeding patterns are context-dependent, i.e., they consume prey that are more common, available, and vulnerable (e.g., Sunquist and Sunquist 2002; Nielsen et al. 2015). Increasing the number of studies, especially in HMLs, and the number of fecal samples analyzed per study (\geq 50 samples; see Zanin et al. 2020) would strengthen the results found here.

Finally, our findings show the important role of some small forest remnants in HMLs for wildlife survival, including puma. Although pumas are widely distributed across HMLs of the Atlantic Forest, estimates indicate that their effective population size in the biome is below 1000 individuals (de Azevedo et al. 2013) and that the species depends on large forest remnants to thrive (Azevedo et al. 2020). This situation stresses the need to improve the quality of small remnants in HMLs and to increase their connectivity with larger remnants to support the puma prey base, including larger species and forest-dwelling animals and to reduce the negative impacts of urban and agricultural expansion.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-021-00556-9.

Acknowledgements We are grateful to the Forest Science Department ("Luiz de Queiroz" College of Agriculture, University of São Paulo), the Interdisciplinary Graduate Program in Applied Ecology (PPGI-EA), and the Wildlife Ecology, Management and Conservation Lab (LEMaC). We thank Alex A.A. Bovo, Juliano A. Bogoni, Ronaldo G. Morato, Krzysztof Schmidt, and two anonymous reviewers for comments and suggestions on an early version of this manuscript.

Code availability Not applicable

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Funding acquisition: Katia M. P. M. B. Ferraz

Funding This study was funded by São Paulo Research Foundation (FAPESP; grant numbers #2014/09300-0 and #2014/10192-7), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, Fundação Grupo Boticário de Proteção à Natureza (#2014-10014 and #1097_20171), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant numbers #308503/2014-7 and #308632/2018-4).

Data availability All data used for analysis is cited in the text and available as Supplementary Material.

Declarations

Ethics approvalNot applicableConsent to participateNot applicableConsent for publicationNot applicable

Conflict of interest The authors declare no competing interests.

References

Abra FD, Granziera BM, Huijser MP, Ferraz KMPMB, Haddad CM, Paolino RM (2019) Pay or prevent? Human safety, costs to society and legal perspectives on animal-vehicle collisions in São Paulo state, Brazil. PLoS One 14:e0215152 Azevedo FC, Lemos FG, Freitas-Junior MC, et al (2020) The importance of forests for an apex predator: spatial ecology and habitat selection by pumas in an agroecosystem. Anim Conserv. https://doi.org/10. 1111/acv.12659.

Bogoni JA, Peres CA, Ferraz KMPMB (2020) Extent, intensity and drivers of mammal defaunation: a continental-scale analysis across the Neotropics. Sci Rep 10:14750. https://doi.org/10.1038/s41598-020-72010-w

Bovendorp RS, Villar N, de Abreu-Junior EF, Bello C, Regolin AL, Percequillo AR, Galetti M (2017) Atlantic small-mammal: a dataset of communities of rodents and marsupials of the Atlantic forests of South America. Ecology 98:2226. https://doi.org/10.1002/ecy.1893

Bovo AAA, Magioli M, Percequillo AR et al (2018) Human-modified landscape acts as refuge for mammals in Atlantic Forest. Biota Neotrop 18:e20170395. https://doi.org/10.1590/1676-0611-BN-2017-0395

Branch LC, Pessino M, Villarreal D (1996) Response of pumas to a population decline of the plains Vizcacha. J Mammal 77:1132–1140. https://doi.org/10.2307/1382795

Brito BFA (2000) Ecologia alimentar da onça parda Puma concolor na Mata Atlântica de Linhares, Espírito Santo. Universidade de Brasília, Brasil

Chiarello AG (1999) Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol Conserv 89:71–82. https://doi.org/10.1016/S0006-3207(98)00130-X

De Azevedo FCC (2008) Food habits and livestock depredation of sympatric jaguars and pumas in the Iguaçu National Park Area, South Brazil. Biotropica 40:494–500. https://doi.org/10.1111/j.1744-7429.2008.00404.x

de Azevedo FC, Lemos FG, de Almeida LB et al (2013) Avaliação do risco de extinção da onça-parda Puma concolor (Linnaeus, 1771) no Brasil. Biodiversidade Bras 3:107–121

de Bovo AA, KMPMB F, Verdade LM, Moreira JR (2016) 11. Capybaras (Hydrochoerus hydrochaeris) in anthropogenic environments: challenges and conflicts. In: Gheler-Costa C, Lyra-Jorge MC, Verdade LM (eds) Biodiversity in agricultural landscapes of southeastern Brazil. De Gruyter, Berlin, Boston, pp 178–189

Dirzo R, Young HS, Galetti M et al (2014) Defaunation in the Anthropocene. Science (80-) 345:401–406. https://doi.org/10. 1126/science.1251817

Emmons LH (1987) Comparative feeding ecology of felids in a neotropical rainforest. Behav Ecol Sociobiol 20:271–283. https://doi.org/ 10.1007/BF00292180

Estes JA, Terborgh J, Brashares JS et al (2011) Trophic downgrading of planet earth. Science (80-) 333:301–306. https://doi.org/10.1126/ science.1205106

Foster RJ, Harmsen BJ, Valdes B, Pomilla C, Doncaster CP (2010) Food habits of sympatric jaguars and pumas across a gradient of human disturbance. J Zool 280:309–318. https://doi.org/10.1111/j.1469-7998.2009.00663.x

Galetti M, Eizirik E, Beisiegel B et al (2013) Atlantic rainforest's jaguars in decline. Science (80-) 342:930 LP–930930. https://doi.org/10. 1126/science.342.6161.930-a

Galetti M, Brocardo CR, Begotti RA, Hortenci L, Rocha-Mendes F, Bernardo CSS, Bueno RS, Nobre R, Bovendorp RS, Marques RM, Meirelles F, Gobbo SK, Beca G, Schmaedecke G, Siqueira T (2017) Defaunation and biomass collapse of mammals in the largest Atlantic forest remnant. Anim Conserv 20:270–281. https://doi.org/ 10.1111/acv.12311

Gheler-costa C, Botero GP, Reia L et al (2018) Ecologia trófica de onçaparda (Puma concolor) em paisagem agrícola. Rev em Agronegócio e Meio Ambient 11:203–225. https://doi.org/10.17765/2176-9168. 2018v11n1p203-225

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc Natl Acad Sci 107:16732–16737. https://doi.org/10.1073/pnas. 0910275107

Golec C (2012) Dieta de cinco espécies simpátricas de felídeos: Puma concolor (Linnaeus 1771), Puma yagouaroundi (E. Geoffroy, 1803), Leopardus pardalis (Linnaeus 1758), Leopardus wiedii (Schinz, 1821) e Leopardus tigrinus (Schreber, 1775). Universidade Estadual do Paraná, Paranavaí

Hurlbert SH (1978) The measurement of niche overlap and some relatives. Ecology 59:67–77. https://doi.org/10.2307/1936632

ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade (2018) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume II – Mamíferos. Instituto Chico Mendes de Conservação da Biodiversidade. Ministério do Meio Ambiente, Brasília

Iriarte JA, Franklin WL, Johnson WE, Redford KH (1990) Biogeographic variation of food habits and body size of the America puma. Oecologia 85:185–190. https://doi.org/10.1007/ BF00319400

Iriarte JA, Johnson WE, Franklin WL (1991) Feeding ecology of the Patagonia puma in southernmost Chile. Rev Chil Hist Nat 64:145–156

Jaksic FM (1983) The trophic structure of sympatric assemblages of diurnal and nocturnal birds of prey. Am Midl Nat 109:152–162. https://doi.org/10.2307/2425525

Korschgen LJ (1980) Procedures for food-habits analyses. In: Schamnitz SD (ed) Wildlife management techniques manual. The Wildlife Society, Washington, pp 113–127

Leite MRP, Galvão F (2002) El jaguar, el puma y el hombre en tres áreas protegidas del bosque atlántico costero de Paraná, Brasil. In: Medellín RA, Equihua C, Chetkiewicz CLB et al (eds) El jaguar en el nuevo milenio. Universidad Autónoma de México, Wildlife Conservation Society, Mexico, DF, Fondo de Cultura Económica, pp 237–250

Levins R (1968) Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton

Lima F, Beca G, Muylaert RL, Jenkins CN, Perilli MLL, Paschoal AMO, Massara RL, Paglia AP, Chiarello AG, Graipel ME, Cherem JJ, Regolin AL, Oliveira Santos LGR, Brocardo CR, Paviolo A, di Bitetti MS, Scoss LM, Rocha FL, Fusco-Costa R, Rosa CA, da Silva MX, Hufnagell L, Santos PM, Duarte GT, Guimarães LN, Bailey LL, Rodrigues FHG, Cunha HM, Fantacini FM, Batista GO, Bogoni JA, Tortato MA, Luiz MR, Peroni N, de Castilho PV, Maccarini TB, Filho VP, Angelo CD, Cruz P, Quiroga V, Iezzi ME, Varela D, Cavalcanti SMC, Martensen AC, Maggiorini EV, Keesen FF, Nunes AV, Lessa GM, Cordeiro-Estrela P, Beltrão MG, de Albuquerque ACF, Ingberman B, Cassano CR, Junior LC, Ribeiro MC, Galetti M (2017) ATLANTIC-CAMTRAPS: a dataset of medium and large terrestrial mammal communities in the Atlantic Forest of South America. Ecology 98:2979. https://doi.org/10. 1002/ecy.1998

Maehr DS, Brady JR (1986) Food habits of bobcats in Florida. J Mammal 67:133–138. https://doi.org/10.2307/1381009

Magezi G (2013) Dieta de felídeos silvestres em áreas de Floresta Atlântica Costeira, litoral Norte do Estado do Paraná. Universidade Federal do Paraná, Paranavaí

Magioli M, Moreira MZ, Ferraz KMB, Miotto RA, de Camargo PB, Rodrigues MG, da Silva Canhoto MC, Setz EF (2014) Stable isotope evidence of puma concolor (felidae) feeding patterns in agricultural landscapes in southeastern brazil. Biotropica 46:451–460. https://doi.org/10.1111/btp.12115

- Magioli M, Ribeiro MC, Ferraz KMPMB, Rodrigues MG (2015) Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Anim Conserv 18:499–511. https://doi.org/10.1111/acv.12201
- Magioli M, Ferraz KMPMB, Setz EZF et al (2016) Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. Eur J Wildl Res 62:431–446. https://doi. org/10.1007/s10344-016-1017-x
- Magioli M, Moreira MZ, Fonseca RCB, Ribeiro MC, Rodrigues MG, KMPM F (2019) Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proc Natl Acad Sci 116:18466–18472. https://doi.org/10.1073/pnas.1904384116
- Projeto MapBiomas (2020) Coleção 5 da série anual de mapas de cobertura e uso de solo do Brasil. https://mapbiomas.org/en/colecoes-mapbiomas-1?cama set language=en. Accessed 8 Sep 2020
- Marchini S, Crawshaw PG (2015) Human–wildlife conflicts in Brazil: a fast-growing issue. Hum Dimens Wildl 20:323–328. https://doi.org/ 10.1080/10871209.2015.1004145
- Martins R, Quadros J, Mazzolli M (2008) Hábito alimentar e interferência antrópica na atividade de marcação territorial do *Puma concolor* e *Leopardus pardalis* (Carnivora: Felidae) e outros carnívoros na Estação Ecológica de Juréia-Itatins, São Paulo. Brasil Rev Bras Zool 25:427–435
- Miotto RA, Cervini M, Kajin M, Begotti RA, Galetti PM Jr (2014) Estimating puma Puma concolor population size in a humandisturbed landscape in Brazil, using DNA mark-recapture data. Oryx 48:250-257. DOI. https://doi.org/10.1017/ S0030605312000841
- Miranda GHB, Rodrigues FHG, Paglia AP (2014) Guia de identificação de pelos de mamíferos brasileiros. Editora Ciências Forenses, Brasília
- Monroy-Vilchis O, Gómez Y, Janczur M, Urios V (2009) Food niche of Puma concolor in Central Mexico. Wildl Biol 15:97–105. https:// doi.org/10.2981/07-054
- Moreno RS, Kays RW, Samudio R Jr (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. J Mammal 87:808–816. https:// doi.org/10.1644/05-MAMM-A-360R2.1
- Nakano-Oliveira E (2006) Ecologia e conservação de mamíferos carnívoros de Mata Atlântica na região do complexo estuarino lagunar de Cananeia. Universidade Estadual de Campinas, Campinas
- Nielsen C, Thompson D, Kelly M, Lopez-Gonzalez CA (2015) Puma concolor. (errata version published in 2016) The IUCN Red List of Threatened Species 2015: e.T18868A97216466. https://doi.org/10. 2305/IUCN.UK.2015-4.RLTS.T18868A50663436.en. Accessed Dec 2020
- Núñez R, Miller B, Lindzey F (2000) Food habits of jaguars and purnas in Jalisco, Mexico. J Zool 252:373–379. https://doi.org/10.1111/j. 1469-7998.2000.tb00632.x
- Oliveira TG (2002) Comparative feeding ecology of jaguar and puma in the Neotropics. In: Medellín RA, Equihua C, Chetkiewicz CLB et al (eds) El jaguar en el nuevo milenio. Universidad Autónoma de México, Wildlife Conservation Society, Fondo de Cultura Económica, pp 265–288
- Oliveira T, Cassaro K (2006) Guia de campo dos felinos do Brasil. Instituto Pró-Carnívoros; Fundação do Parque Zoológico de São Paulo. Sociedade de Zoológicos do Brasil, Pró-Vida Brasil, São Paulo
- Pacheco LF, Lucero A, Villca M (2004) Dieta del puma (*Puma concolor*) en el Parque Nacional Sajama, Bolivia y su conflicto con la ganadería. Ecol Boliv 39:75–83

- Paglia AP, da Fonseca GAB, Rylands AB et al (2012) Lista Anotada dos Mamíferos do Brasil 2ª Edição. Occas Pap Conserv Biol 6:76
- Paviolo A, De Angelo C, Ferraz KMPMB et al (2016) A biodiversity hotspot losing its top predator: the challenge of jaguar conservation in the Atlantic Forest of South America. Sci Rep 6:37147. https:// doi.org/10.1038/srep37147
- Polisar J, Maxit I, Scognamillo D, Farrell L, Sunquist ME, Eisenberg JF (2003) Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biol Conserv 109: 297–310. https://doi.org/10.1016/S0006-3207(02)00157-X
- Quadros J (2002) Identificação microscópica de pelos de mamíferos e sua aplicação no estudo da dieta de carnívoros. Universidade Federal do Paraná, Curitiba
- R Core Team (2020) R: A Language and Environment for Statistical Computing (Version 4.0.3, R Foundation for Statistical Computing, Vienna, Austria, 2020) Electronic Database. http:// www.R-project.org/. Accessed Dec 2020
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142: 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021
- Ripple WJ, Estes JA, Beschta RL et al (2014) Status and ecological effects of the world's largest carnivores. Science (80-) 343: 1241484. https://doi.org/10.1126/science.1241484
- Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GIH, Levi T, Lindsey PA, Macdonald DW, Malhi Y, Painter LE, Sandom CJ, Terborgh J, van Valkenburgh B (2015) Collapse of the world's largest herbivores. Sci Adv 1: e1400103. https://doi.org/10.1126/sciadv.1400103
- Rocha-Mendes F, Mikich SB, Quadros J, Pedro WA (2010) Feeding ecology of carnivores (Mammalia, Carnivora) in Atlantic Forest remnants, Southern Brazil. Biota Neotrop 10:21–30
- Röhe F (2002) Hábitos alimentares da su uarana (*Puma concolor*) (Linnaeus 1771) em Mosaico de Floresta Secundária e reflorestamento de Eucaliptus saligna. Mata Atlântica, no Município de Pilar do Sul-SP. Universidade Estadual de Campinas, Campinas
- Rongetta A (2014) Dieta alimentar da onça-parda, Puma concolor (Linnaeus, 1771), em uma unidade de manejo florestal em Borebi-SP. Universidade Estadual Paulista "Júlio de Mesquita Filho", São Paulo
- RStudio Team (2020) RStudio: integrated development for R
- Sanderson EW, Redford KH, Chetkiewicz C-LB, Medellin RA, Rabinowitz AR, Robinson JG, Taber AB (2002) Planning to save a species: the jaguar as a model. Conserv Biol 16:58–72. https://doi. org/10.1046/j.1523-1739.2002.00352.x
- Santos JL, Paschoal AMO, Massara RL, Chiarello AG (2014) High consumption of primates by pumas and ocelots in a remnant of the Brazilian Atlantic Forest. Braz J Biol 74:632–641
- Sunquist M, Sunquist F (2002) Wild cats of the world. University of Chicago Press, Chicago
- Vidolin G (2004) Aspectos bio-ecológicos de Puma concolor (Linnaeus, 1771), Leopardus pardalis (Linnaeus, 1758) e Leopardus tigrinus (Schreber, 1775) na Reserva Natural Salto Morato, Guaraqueçaba, Paraná, Brasil. Universidade Federal do Paraná, Curitiba
- Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer International Publishing, New York
- Zanin M, Adrados B, de Foletto VC et al (2020) What should I eat: feeding behaviour of puma in a Brazilian protected semi-arid area, Hystrix. Ital J Mammal 31:21–25. https://doi.org/10.4404/hystrix-00265-2019

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