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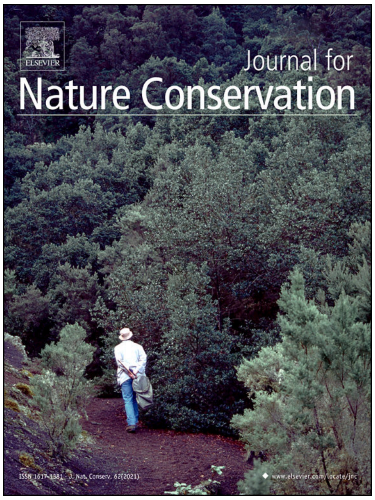

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Physical geography trumps legal protection in driving the perceived sustainability of game hunting in Amazonian local communities

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Introduction

Tropical forests are the most biodiverse terrestrial ecosystems, shelter two-third of all species globally, and are facing unprecedented anthropogenic pressures (Gardner et al., 2010). The most successful strategy to protect this biodiversity is to avoid deforestation through the establishment of Protected Areas (hereafter PAs; Andam et al., 2008; Rodrigues et al., 2004). Sustainable Use Reserves (hereafter, SURs; that we assumed fiting within IUCN Categories V and VI) comprise a considerable proportion of the

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aggregate protected acreage across the tropics (or 40% of the territory, (Schmitt et al., 2009) and Amazonia (Peres, 2011). While IUCN category V aims to safeguard the integrity of the interactions among local people and natural ecosystems, category VI aims to protect natural ecosystems and ecological processes, and promote the sustainable use of natural resources (Dudley et al., 2010).

Forest cover assessments often fail to capture the most cryptic sub-canopy impacts on biodiversity induced by the extraction of a wide spectrum of nontimber forest products for either subsistence or commerce (Peres et al., 2006). These activities typically precede more predatory forms of land use and can impact sites in tropical forests with seemingly intact forest cover (Ingram et al., 2021; Peres & Lake, 2003). The frequently escalating demographic impacts of nontimber resource harvesting calls into question the effectiveness of SURs in serving the long-term interests of biodiversity conservation (Peres, 2011; Terborgh & Peres, 2017), though low-level, well-managed resource-extraction can be achieved sustainably (Hernández-Barrios et al., 2015; Ribeiro et al., 2014; Ticktin, 2004).

Hunting of terrestrial and arboreal vertebrates is widely considered the most widespread form of anthropogenic disturbance in tropical forests (Benítez-López et al., 2019). Hunting alters the populations of game species (Benítez-López et al., 2019; Harrison, 2011; Milner-Gulland et al., 2003), and disrupts effective seed dispersal and forest carbon storage (Bello et al., 2015; Muller-Landau, 2007; Peres et al., 2016). The consumption of wildmeat is, however, an essential component of the subsistence economy of tropical forest dwellers, and a growing concern in the food security of indigenous and traditional communities (Nasi et al., 2011; Nunes et al., 2019).

Lowland Amazonia hosts the largest contiguous tracts of tropical forest on Earth, including many PAs established over the last 35 years (Jenkins & Joppa, 2009).

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Brazil accounts for three-quarters of this territory, but >60% of the total PA area (excluding officially recognized Indigenous Lands) consists of SURs that are legally human-occupied (Brasil, 2020). The total area of SURs covers 775,600 km^2, approximately 77% of which entirely lack a management plan and a clear mandate to implement natural resource management regulations (Brasil, 2020).

Despite incipient but positive cases of community-based game management initiatives within some SURs (Oliveira & Calouro, 2019; Vieira et al., 2015), conservation strategies to promote their sustainable management have been entirely neglected by the Brazilian government (Antunes et al., 2019). This reinforces concerns that multiple-use tropical forest reserves will become “paper parks” that fail to protect human-biodiversity interactions as well the sustainability of subsistence hunting. However, our understanding of the extent to which and how hunting intensity truly depletes game vertebrate populations under different landscape and human geography contexts remains unclear.

The magnitude of impacts of overhunting depends on several local to regional scale factors, including human settlement size and settlement age (Beirne et al., 2019; Jerozolimski & Peres, 2003; Parry & Peres, 2015; Stafford et al., 2017), the availability of alternative animal protein for local human populations (Endo et al., 2016; Parry & Peres, 2015) and the distance to urban centers and physical accessibility of catchment areas (Abrahams et al., 2017; Benítez-López et al., 2017; Parry & Peres, 2015; Peres & Lake, 2003). Compared to formally unprotected areas, it is widely recognized that all categories of tropical PAs inhibit the worst impacts of overhunting (Benítez-López et al., 2017), but we have scant information about how the mitigation of hunting pressure potentially exerted by SURs compares with their surrounding areas.

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In this paper, we examine the Local Ecological Knowledge (hereafter, LEK) of 211 long-term subsistence hunters inhabiting 93 local communities within and immediately outside nine sustainable-use reserves of the central-western Brazilian Amazon. Specifically, LEK can be defined as all the personal empirical experience that local people acquired through years of interactions with natural environments, which are transmitted to their communities (Brook & McLachlan, 2008; Charnley et al., 2007). LEK has been successfully used to assess the hunting effects on game local population (Braga-Pereira et al., 2021; Parry & Peres, 2015; Zayonc & Coomes, 2021).

We tested the general hypothesis that the semi-subsistence human settlements located far from protected areas will exhibit greater overall hunting pressure within village catchment areas than those located inside SURs. We also expected that larger and older settlements, particularly those near urban centers that are surrounded by lesser extents of seasonally-flooded forests and water bodies, which are good proxies of aquatic animal protein availability, exert higher pressure on forest game vertebrates. Specifically, we examined how local perceptions of hunting pressure and game stocks relate to (1) distance to reserve boundaries, (2) settlement size and age, (3) distance to urban areas, and (4) the extent of neighbouring floodplain areas. To do so, we quantified reported perceptions of prey availability changes over time, the species composition of the most consumed terrestrial vertebrate prey, and their perceived levels of local depletion.

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Methods

Study area

We collected LEK data in the central-western portion of the Brazilian Amazon during two stages. In the first stage, between 2013 and 2015, we collected data in the regions of the middle Juruá and Uatumã rivers (Fig. 1A and B), as described by Abrahams et al., (2017). In the second stage, during 2018 and 2019, we implemented new data acquisition in the regions of upper Juruá and upper Purus rivers basins (Fig. 1C, D, E).

In the middle Juruá region, we obtained data at both local communities and urban neighbourhoods (hereafter, *communities*) located within and immediately outside two adjacent SURs, the Uacari Sustainable Development Reserve (UacR) and the Médio Juruá Extractive Reserve (MJR), located near the towns of Carauari and Itamarati in the state of Amazonas (hereafter, Médio Juruá Reserves; JR). This landscape is comprised of a mix of unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests, as well as permanent water bodies. In the Uatumã region, we collected data within and immediately outside the Uatumã Sustainable Development Reserve (UatR), located near the towns of São Sebastião do Uatumã and Itapiranga in the state of Amazonas. The landscape is comprised mainly of *terra firme* and a small portion of seasonally-flooded forests, locally referred to as *igapó*, and permanent water bodies. We deliberately bolstered the generalization power to this study by including regions drained by both nutrient-rich white-water (Juruá-Purus) and nutrient-poor black-waters (Uatumã), thereby capturing nearly the full gradient of soil fertility of central-western Amazonia.

In the upper Juruá and Purus regions, we interviewed local inhabitants living both within and immediately outside SURs in three subregions: (1) Cazumbá-Iracema (CIR; Caeté and Macauã rivers) and Arapixi (AR; Purus river) Extractive Reserves (Fig. 1C); (2) Riozinho da Liberdade Extractive Reserve (RLR; Liberdade river), Liberdade State Forest (LF; Liberdade river), Mogno State Forest (MF; Liberdade river), hereafter Liberdade Reserves (LR; Fig. 1D); and the (3) Médio Purus Extractive Reserve (MPR; Purus river; Fig. 3E). All communities at Cazumbá-Iracema and some communities at Arapixi are located near the town of Sena Madureira (state of Acre), while the other

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Arapixi communities are located near the city of Boca do Acre (state of Amazonas). The two cities nearest the communities of LR are Cruzeiro do Sul (Acre) and Ipixuna (Amazonas). Local communities at MPR are nearest the cities of Pauini and Lábrea (Amazonas). The landscapes of CIR and LR are predominantly comprised of *terra firme* forests and to a minor extent, flooded forest, while the landscape at AR and MPR consist primarily of *terra firme* forests, although *várzea* forests are important elements of the landscape.

Regions encompassing all of these reserves are inhabited by *ribeirinhos*, former rubber-tappers living in semi-subsistence communities of mixed-descent. These local residents practice terrestrial subsistence hunting using firearms, mainly 24- and 36-gauge shotguns, with no reported use of snares and gun-traps. Sites in western Amazonia encompass highly productive white-water floodplain ecosystems (Fig. 1A, C, D, E), while those in Central Amazonia (Fig. 1B) encompasses much lower productivity black-water rivers (Junk et al., 2015), potentially resulting in lower faunal biomass density (Emmons, 1984).

Local interviews

This study was conducted under ethical approval from the University of East Anglia Ethical Review Board and the University of São Paulo Ethics Committee. We obtained explicit permission to conduct interviews from all participating local communities and informants. We interviewed experienced subsistence hunters, who were willing informants and had been indicated to us using a snow-balling approach within these communities. MIA conducted all the interview in middle Juruá and Uatumã rivers and RS conducted all the interview in the upper Juruá and Purus rivers basins. All interviews were conducted in Portuguese.

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We applied semi-structured questionnaires to 211 subsistence hunters, 69% and 31% of whom were carried out with local people living inside and outside the nine SURs examined here, respectively. Most of these interviews were conducted in the region of CIR and AR (34%), with the remaining interviews as following: LR (23%), JR (24%), MPR (12%) and UatR (8%). We interviewed between 1 and 12 resident hunters per community (2.23 ± 2.30 informants, mean ± SD), amounting to 93 local communities.

We used a semi-structured questionnaire to obtain data on (1) hunters' perceptions of change in game abundance within the catchment areas near their communities over the previous 10 years (i.e. "worse now"; "no change"; and "better now); (2) their currently available prey profile, i.e. the three most-hunted and most-consumed prey species, ranked by the hunter's own perception of the number of individuals of each species that had been consumed; (3) the perception of local depletion for each of 16 game species hunted in central-western Amazonia (Table 1), expressed by the distance they would be required to travel from their households to detect direct or indirect signs of each species, and; (4) the age of each community, defined as the number of years since the community had been officially established. Hunters were also asked about their age and how frequently they accessed the forests around their communities as part of their regular year-round activities.

We used the biological traits of all reported prey species (see Table 1) to create two indices calculated from the prey profile responses of each hunter. We calculated the (1) mean body size and the (2) reproductive rate of each reported prey profile, using (1) the mean body mass (kg) and (2) the mean finite intrinsic rate of natural increase (λ_{max}) of each prey profile. These traits have been widely used to determine the demographic consequences of hunting in tropical forests (Fa et al., 2002).

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Based on the assumption that the gradient of depletion of hunted species radiates from individual households into inland forests (as for all central-place foragers; (Sirén et al., 2004), a proxy of species depletion can be obtained by the perceptions of local residents about the minimum distance (km) travelled to detect any signs of each game species, including sightings, tracks, scats, bark scratches, vocalizations and carcasses. We derived these travel distances from the known georeferenced household of each interviewee to the nearest locality where signs of each of the 16 focal species could be detected.

We calculated these travel distances as the amount of time that each interviewee estimated would be required to travel from their household to reach the nearest site at which any given species (or signs thereof) could normally be encountered, multiplied this time estimate by the mean hunter travel velocity, considering the mode of transport they reportedly used (see details in Abrahams et al., 2017). We excluded from this analysis travel distance data for grey brocket deer (*Mazama nemorivaga*) at CIR and woolly monkeys (*Lagothrix* spp.) at CIR, LR and UatR, since most interviewees in these regions reported long-term natural absences of these species in the vicinities of their communities. We then truncated outlier values of the detection travel distance data to 30 km, given that the mean radial day range of Amazonian central-place hunters is 5-6 km (Sirén et al., 2004). Moreover, several of our interviewees reported they seasonally used temporary hunting camps located up to 24 km from their communities and could hunt as far as 6 km from these camps. These camps were used to hunt more desirable species that are difficult to catch near their communities.

We then used these travel distances as a proxy of perceived degree of local prey depletion, except for travel distances for three rarely consumed species (puma [*Puma concolor*], jaguar [*Panthera onca*] and giant anteater [*Myrmecophaga tridactyla*]). We

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divided the mean body mass of the remaining 13 species by their respective local detection distances to calculate the mean body mass detected per km per hunter (kg/km). In addition, we calculated the mean detection travel distance for all prey species as estimated by each hunter (All.spp).

Explanatory spatial variables

We derived all spatial variables using QGIS 3.14 (QGIS, 2021). We digitized every household within 10 km of the central-point of each community, through supervised mapping of Bing Maps aerial photographs using the Open-layers plugin (1:2000) (see Table 2). We performed this mapping using 2019 aerial photographs for the middle Juruá and Uatumã datasets. We assumed that no major positional change in human settlements had taken place since our field sampling (2013-2015). For the upper Juruá-Purus dataset we performed supervised mapping using 2018 aerial photographs. We defined the size of each community studied as the total number of households around 1, 5 and 10-km of the community centroid

To represent the effect of protection level afforded by PAs on local communities, we calculated the Euclidean distance (km) between each community and the nearest boundary of the SUR in each region. Reserves within either the Juruá river (Fig. 1A) or the Liberdade river regions (Fig. 1D) are adjacent to each other and therefore we merged their perimeters into a single polygon. In order to capture the reserve protection effect, we assumed positive or negative values for distances to communities located either inside or outside each SUR polygon, respectively.

We estimated the access distance from each human settlement to the nearest urban center by digitizing rivers and roads (paved and unpaved) that residents reportedly used. These access distances can vary seasonally since some unpaved roads

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are only usable during the dry season while some river channels become navigable only during the wet season, reducing travel time and distance to the nearest city. Given this seasonal variation, we calculated the mean access distance to the nearest city for each human settlement by averaging estimates from both the dry and wet seasons.

We assumed that the available aquatic protein is comprised mostly of fish and to a lesser degree aquatic reptile species (caiman and aquatic turtles and their eggs). We also assumed that the availability of aquatic animal protein to local people is directly related to the local amount of suitable habitat for exploited aquatic and semi-aquatic species. Thus, we created a proxy of local aquatic animal protein availability using the proportional area around each community comprised of seasonally and permanently flooded areas (hereafter, *flooded area*). We calculated this metric by aggregating, within 5-km of the centroid of any given community, the total area of permanent water bodies (e.g. river channels, oxbow lakes), plus all forests that become seasonally flooded, divided by the total 5-km buffer area. We extracted these data from a raster file described in (Hess et al., 2015).

Statistical analysis

Our five explanatory variables are summarized in Table 2. We performed all statistical analyses using R 4.0.4. software (R.Core.Team, 2021). Prior to analyses we checked data distributions and relationships among response and predictor variables using dispersion plots and we log- or sqrt-transformed data whenever necessary, following (Zuur et al., 2010). We also explored correlations (Pearson value > |0.7|) and collinearity (Variance Inflation Factor > 3) among explanatory variables (R base and USDM package; Naimi et al., 2014). We rescaled variables (mean = 0 and SD = 1) to enable model convergence and variable effect size comparisons (Harrison et al., 2018).

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Our three community sizes (1, 5 and 10km) were positively correlated ($P > 0.7$) and we also investigated if these sizes were correlated with our metric of access distance to nearest urban area, since rural human population density in Amazon is higher near urban areas (Parry et al., 2010), however we did not find any correlative association among them. We therefore decided to use the number of households within 1km of the community centroid as our metric of community size.

We used mixed-effects models (see Bolker et al., 2009) to evaluate the effects of (1) community size and (2) age, (3) distance to reserve boundaries, (4) distance to urban areas, and (5) the extent of neighbouring floodplain areas had on (a) the perceived change in local game abundance, (b) the species composition of the three most consumed terrestrial vertebrate prey (in reported prey profiles); and (c) their perceived levels of local depletion, expressed by the detection travel distance to different game species (Table 2). We accounted for spatial dependence among informants by specifying "community" as a random effect, since we interviewed more than one informant in each community. We opted to show only the effects of the global models, since minimal adequate models can overestimate the effect size of significant predictors (Harrison et al., 2018) and global models better indicate the direction and intensity of the effects of explanatory variables.

Since local perceptions of game stocks in forest areas near settlements are ordinal ("declining"; "no change"; "increasing"), we examined these using cumulative link mixed models (CLMM function; Ordinal package; Christensen, 2018). Prey profile metrics and local depletion data were analyzed using either Gamma (GLMM) or Gaussian (LMM) Generalized Linear Mixed Models (glmer and lmer functions of the lme4 package; (Bates et al., 2015). GLMMs were more parsimonious (lower AIC value)

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than LMMs, but since all our GLMMs were overdispersed (Harrison et al., 2018), we decided to retain the use of LMMs.

In order to increase the credibility of the inferential power of the effect sizes of all of our models, we used the function *bootstrap_parameters* of the *parameters* R package (Lüdecke et al., 2020), with 5,000 model iterations based on resamples (with replacements) to create a distribution of coefficients for each variable, as well as their respective confidence intervals.

Results

The mean age of local hunters interviewed was 45.03 (±14.80) years, and 64% of all respondents entered into the forest at least once a week, 26% at least once a month and 8% once a year.

Nineteen taxa of terrestrial bird and mammals were described as regularly consumed by our interviewees (Table 1) with lowland paca (*Cuniculus paca*), collared peccary (*Dicotyles tajacu*), red brocket deer (*Mazama americana*) and agouti (*Dasyprocta* spp.) encompassing over 55% of aggregated prey rankings.

Local perceptions about changes in local game abundance showed that most of the interviewed hunters (69%) perceived an overall ‘worsening’ situation, whereas 16% stated that no change had occurred, and 15% perceived that the overall game availability situation had ‘improved’. Hunters living in communities surrounded by a higher fraction of seasonally-flooded forest, farther from urban centers and inside the boundaries of Protected Areas experienced a significant perceived positive temporal change in overall game abundance (Fig. 2A, B, C and B).

The mean body mass (per hunter) of the three most hunted game species ranged from 1.23 to 74.0 kg (22.63 ± 19.5 kg, mean ± SD) and none of our explanatory

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variables significantly affected the body mass distribution of reported prey profiles (Fig. 3A). The mean species reproductive rate (λ_{max}) within reported prey profiles (per hunter) ranged from 1.35 to 3.0 (1.90 ± 0.32, mean ± SD), and hunters farther from urban areas and residents of communities adjacent to larger areas of seasonally-flooded habitat harvested low-fecundity prey species more frequently (Fig. 3B and C).

Detection travel distances per hunter for any of the 16 game species considered here (Table 2) ranged from 0.15 to 30 km (6.98 ± 9.86 km, mean ± SD). Hunters living farther into core areas of SURs reported shorter detection distances of nine species, but these effects were not significant, with exception of pumas, that showed a marginal positive effect (Fig. 4A). Hunters living in older communities reported longer detection travel distances to yellow- or red-footed tortoises (*Chelonoidis* spp.) and marginally to woolly monkeys and all species in aggregate (All spp.; Fig. 4B). Hunters in larger communities reported longer detection distances to any signs of jaguar, collared peccary and spider monkey (*Ateles* spp.), and marginally so for puma. Although hunters in large communities reported an overall smaller size structure of desirable prey detected per distance travelled (kg/km), this effect was only marginally significant (Fig. 4C).

Hunters living farther from urban centers experienced shorter detection travel distances for all species in aggregate (All spp.) and higher overall prey biomass per distance travelled (Kg/km; Fig. 4D). The positive effect of urban access distance on detection distances were also seen for the majority of species (14 species), where three of them showed significant effects (namely, large tinamou [*Tinamus* spp.], howler monkey [*Alouatta* spp.], white lipped peccary [*Tayassu pecari*]), and five harvest-sensitive taxa also showed marginal effects of city access distance (spider monkey, footed tortoise, curassow [*Mitu* or *Crax* spp.], giant armadillo [*Priodontes maximus*] and woolly monkey; Fig. 4D).

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Hunters living in communities surrounded by larger areas of adjacent floodplains reported significantly longer detection travel distances for giant armadillo, collared peccary and large tinamous, and marginally farther distances for lowland paca, grey brocket deer and puma (Fig. 4E). Conversely, these hunters reported significantly shorter detection distances for all species when these were pooled together (All spp.), as well as for spider monkey and curassow (Fig. 4E).

Discussion

Most of the hunters we interviewed reported a decline in local game abundance in the forests surrounding their communities over the previous 10 years. In the context of our study local communities (N = 93) and interviewees (N = 211), our modest sample size suggests that at the landscape scale, hunting as currently practiced is perceived to detrimentally impact local game assemblages and local livelihoods within and around the nine SURs examined here. Contrary to our expectations, however, the positive effects of legal protection of PAs per se were seen only in the changes of perceived overall local game abundance. Our study also demonstrates that Amazonian rural communities enjoying greater access to extensive floodplain areas and located farther from urban centers, were more likely to perceive that local game hunting was sustainable over time. High-fecundity terrestrial species, such as agouti, lowland paca, collared peccary, and red brocket deer, were the most locally consumed species overall. Low-lambda species, on the other hand, were only frequently consumed farther from urban centers and within communities surrounded by extensive floodplains where most of the wild animal protein requirements was presumably met by local fisheries. Likewise, community demographic configuration (settlement age and size), only impacted the depletion of a few select species compared to the other predictors.

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Sustainability of game hunting is modulated by settlement geography

Local hunters living in communities sited in core reserve areas were more likely to perceive hunting to be sustainable, considering changes of perceived local game abundance over time. Despite the fact that nine game species showed signals of reduced depletion in human communities inside SURs, none of them were significant and only puma showed marginal effect. Within these reserves, human pressure on biodiversity is expected to be lower due to restrictions in land use and management actions (Gray et al., 2016). Many Amazonian reserves are also less physically accessible via their river and road networks than unprotected forests elsewhere (Peres & Lake, 2003), and illegal hunting is less likely to occur in more inaccessible sites, including remote Amazonian protected areas (Kauano et al., 2017). However, the positive reported effects of SURs in mitigating hunting pressure may have been influenced by a social desirability bias (Bogner & Landrock, 2016), whereby hunters living inside protected areas can perceive that interviewers expect positive narratives about game abundance.

As previously shown elsewhere (Parry & Peres, 2015), our results indicate that physical accessibility to floodplains, and hence accessibility to more abundant sources of aquatic animal protein, was associated with a generally higher perception that local game hunting was sustainable, which is reinforced by higher offtakes of low-lambda prey species within these catchments. We infer that aquatic resources, wherever they are available, largely meet local animal protein needs, reducing local dependency on terrestrial animal protein via compensatory effects at different timescales, thereby alleviating hunting pressure on terrestrial game stocks. A similar aquatic-terrestrial protein relationship has been observed at much larger scales in West Africa, where the reduction of marine fish stocks resulted in higher rates of game depletion in inland

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protected areas (Brashares et al., 2004). This compensatory effect can also be seen in western Amazonia. For example, rural Amazonians in general, and riverine communities in particular, tend to consume more fish than game meat, but game meat consumption increases when fish stocks become less seasonally available (Endo et al., 2016).

Moreover, local communities at RDA and RMJ (Juruá River) and RMP (Purus River) have been conducting community-based management of arapaima fish (*Arapaima gigas*) within floodplain oxbow lakes, which further increases the local availability of aquatic protein (Campos-Silva & Peres, 2016; Campos-Silva et al., 2018). It is reasonable to surmise that wise resource management of the local availability of aquatic protein can promote a reduction in local pressure on terrestrial game species and, consequently, a more favourable perception of higher hunting sustainability.

The reduced depletion of harvest-sensitive taxa in community catchment areas embedded in a larger proportion of floodplain areas can be interpreted as a consequence of reduced game meat dependence by the hunters in these communities. This pattern was seen in the perceived depletion of spider monkey and curassow. Shorter travel distances to signs of all game species (All.spp) may also be seen as further indication that, in general, the high availability of aquatic animal protein reduces the size of the spatial depletion envelope induced by central-place terrestrial hunting.

Nevertheless, for some species, the counterintuitive relationship we found between the extent of seasonally-flooded habitats near communities and their perceived wildlife depletion could be better explained by habitat associations. Species such as giant armadillo, collared peccary, lowland paca, grey brocket deer, puma and tinamou, show higher habitat preference for unflooded than flooded forests (Alvarenga et al.,

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2018; Haugaasen & Peres, 2007). Accordingly, these species were typically detected farther from riverine and lacustrine communities near river channels, which were therefore farther removed from upland forest areas, particularly considering that floodplain areas in some of our study areas could be as extensive as 25-30 km wide on both banks of the river (middle Juruá and Purus rivers).

Travel distance to the nearest town or city was the most important predictor of the mean fecundity rate of the most consumed game species across all 93 communities examined here. Hunters in more remote communities clearly perceived hunting to be generally more sustainable. Hunters living farther from urban areas also reported higher biomass of prey species detected (kg/km) in the vicinities of their communities and shorter detection distances for all species. This pattern was statistically significantly for three exploited species (large tinamou, howler monkey and white-lipped peccary), and marginally so for five other harvest-sensitive species (spider monkey, tortoise, curassow, giant armadillo and woolly monkey).

Overall, these results are consistent with previous studies in that many tropical cities can drain wild meat for both local consumption and trade, and low-fecundity species are typically depleted in peri-urban areas (Parry & Peres, 2015). Urban proximity is the most important negative driver of population abundance in tropical forest game species (Benítez-López et al., 2017) and, although wild meat trade is illegal in Brazil (Antunes et al., 2019), urban consumption of wild meat is both prevalent and widespread throughout the Amazon (Chaves et al., 2017; Parry et al., 2014). This is especially the case of small market towns, such as those spatially related to our communities, where local people still enjoy eating wild terrestrial vertebrates while relying on a steady supply of domestic protein (el Bizri et al., 2020). However,

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additional effects caused by higher rural human population densities near cities (Parry et al., 2010) can contribute to higher game depletion near urban areas.

Household geography and hunting sustainability

Only some game species were meaningfully affected by the demographic profile of the communities we studied. Older communities significantly perceived local depletion only for yellow- and red-footed tortoises, whereas this effect was uninformative for woolly monkeys. These illustrate cases of highly harvest-sensitive and preferred game species that have been depleted in many overhunted portions of Amazonia (Peres & Palacios, 2007). Community size (numbers of consumers) significantly impacted only jaguars, collared peccaries and spider monkeys and marginally impacted only pumas. Although the age and size of local communities may strongly influence local depletion of Amazonian game vertebrates (Jerozolimski & Peres, 2003), this is not substantiated by at least some studies (Abrahams et al., 2017; Stafford et al., 2017). Given the spatial configuration of our study settlements, it is possible that the landscape scale effect size of urban centers and local availability of aquatic protein override the additional impacts of local community demographics.

The mean body mass of prey species is generally lower in overhunted catchment areas in the Amazon (Jerozolimski & Peres, 2003), not least because large-bodied vertebrates are often both preferred target species and more sensitive to hunting (Bodmer et al., 1994; Bogoni et al., 2020). Our measure of body size of the most consumed species was, however, not influenced by any of our predictors. In previously depleted Amazonian forests, subsistence hunters can respond by simply travelling farther to pursue larger-bodied prey wherever these are still available (Alvard, 1993; Levi et al., 2011), and this is likely occurring well beyond the most depleted areas

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around our study communities. In our study reserves in Acre (LR and CIR), for example, local hunters frequently erected and maintained temporary hunting camps farther than 10 km away from their villages, where they seasonally pursued the most preferred game species. These camps effectively overcome even large species-specific depletion envelopes to ensure ready access to under-harvested populations of even the most desirable species, but this option can only work under contexts of relatively low village densities and vast tracts of undisturbed forests.

Conservation implications

In summary, our interviews revealed clear signs of negative impacts of subsistence hunting within and around human-occupied protected areas of the Brazilian Amazon. Yet, local availability of alternative aquatic protein near community settlements and greater travel distances to urban centers contributed to an overall perception of more sustainable game hunting. This study aims to contribute to the design of evidence-based conservation strategies that can enhance natural resource management in sustainable-use tropical forest reserves.

Regional resource management policies should include strategies that can reduce the urban-centric depletion of game species, especially low-lambda species. This should include more efficient surveillance and deterrence of commercial hunting and urban bushmeat trade, as well as providing alternative inexpensive sources of animal protein for urban consumption, including wild fisheries and small domestic livestock.

Community-based management of natural resources has been considered the best available option for the local protection and/or recovery of native biodiversity, in addition to socioeconomic gains in enhancing the living standards of rural populations (Campos-Silva & Peres, 2016; Constantino et al., 2012). Community-based

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management of aquatic resources can potentially reduce excessive reliance on terrestrial game species and should be prioritized and subsidized in communities located on extensive floodplain areas of the Amazon and elsewhere in the tropics. However, for local communities that lack access to sources of aquatic protein, the best alternative to mitigate the inherent impact of overhunting on terrestrial game species should be the management of subsistence offtakes, with a focus on stringent quotas protecting the most vulnerable low-fecundity species. Given the importance of wild meat to the rural poor (Nunes et al., 2019), these can be seen as 'win-win' management strategies in protecting both local livelihoods and wild game stocks.

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Tables

Table 1 – A checklist of species that were the subject of semi-structured interviews, ordered by the reportedly most to least hunted and consumed prey species (expressed as a percentage of the aggregated prey rankings of all respondents (P %), their body mass (kg) and finite rate of natural population increase (λ_{max}). Species codes are given for the subset of species for which perceived depletion was analyzed (expressed as the reported travel distance to the nearest locality where they had been detected).

English name	Species name	Species code	P (%)	kg[1]	λ_{max}[1]
Lowland paca*	*Cuniculus paca*	Cuni.pa	17.8	9.5	1.95
Collared peccary*	*Dicotyles tajacu*	Dico.ta	16.6	25.0	2.01
Red brocket deer*	*Mazama americana*	Maza.am	11.5	30.0	1.42
Agouti	*Dasyprocta* spp.	-	9.5	4.5	3.00
White lipped peccary*	*Tayassu pecari*	Taya.pe	7.6	32.0	1.58
Large tinamou*	*Tinamus* spp.	Tina.sp	6.6	1.2	1.50
Small armadillo	Nonspecific small cingulata	-	6.4	6.0	1.91
Grey brocket deer*	*Mazama nemorivaga*	Maza.ne	6.2	18.0	1.61
Curassow*	*Mitu* sp. or *Crax* sp.	Mitu.Crax	4.9	3.0	1.47
Brazilian tapir*	*Tapirus terrestris*	Tapi.te	4.1	160.0	1.22
Spix's guan	*Penelope jacquacu*	-	2.3	1.3	1.49
Howler monkey*	*Alouatta* spp.	Alou.sp	1.9	6.5	1.17
South American red squirrel	*Hadrosciurus spadiceus*	-	1.2	1.2	3.50
Woolly monkey*	*Lagothrix* spp.	Lago.sp	0.7	8.7	1.12
Trumpeter	*Psophia* spp.	-	0.5	1.2	1.30
Capybara	*Hydrochoerus hydrochaeris*	-	0.5	31.5	1.99

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Red/yellow footed tortoise*	*Chelonoidis* spp.	Chel.sp	0.5	4.6	2.50
Large-headed capuchin	*Sapajus macrocephalus*	-	0.4	3.4	1.15
South American coati	*Nasua nasua*	-	0.1	5.1	1.26
Spider monkey*	*Ateles* spp.	Atel.sp	0	9.0	1.08
Jaguar	*Panthera onca*	Pant.on	0	80.0	1.60
Puma	*Puma concolor*	Puma.co	0	45.0	1.36
Giant armadillo*	*Priodontes maximus*	Prio.ma	0	30.0	1.80
Giant anteater	*Myrmecophaga tridactyla*	Myrm.tr	0	30.5	1.70

1 - Abrahams et al., (2017). * Species included in the two metrics of local game depletion (kg/km; All.spp; see Methods section).

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Table 2 – Description of the selected independent variables used in mixed-effects models, applied to data collected at 93 local communities. For each explanatory variable we report the predicted impact on the perceived local game abundance (GA), the mean body size and reproductive rate of the reported prey profile (PP) and the reported travel distance to the nearest location where each prey species could be detected (TDD).

Independent variables	Code	Unit of measure	GA and PP	TDD
Population size of community	SIZE	Number of households ($\log_{10}$)	Negative	Positive
Age of community	AGE	Years	Negative	Positive
Travel distance to urban centers	CITY	Sqrt (km)	Positive	Negative
Distance to Protected Area boundaries	PROTE	km	Positive	Negative
Extent of surrounding flooded areas	FLOOD	Proportion	Positive	Negative

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Figures captions

Fig. 1 – Geographic locations of the five study regions (panels A-E) within lowland Amazonia (green portion of the upper left panel), Brazil. (A) Médio Juruá Extractive Reserve (MJR) and Uacari Sustainable-Use Reserve (UacR); (B) Uatumã Sustainable-Use Reserve region; (C) Cazumbá-Iracema Extractive Reserve (CIR) and Arapixi Extractive Reserve (AR); (D) Riozinho da Liberdade Extractive Reserve (RLR), Liberdade State Forest (LF) and Mogno State Forest (MF); and (E) Médio Purus Extractive Reserve. The 93 local communities surveyed here, their nearest urban centers, the Protected Area boundaries, and main rivers are shown as white dots, red dots, orange polygons and blue lines, respectively.

Fig. 2 – Panels synthesizing results of Cumulative Link Mixed Models of perceived game abundance. Panel A shows the magnitude and direction of the effects (bootstrapped coefficients ± 90% and 95% confidence intervals) of independent variables. (FLOOD = Extent of adjacent flooded area; PROTE = Distance to protected area boundaries; CITY = Travel distance to urban centers, SIZE = Population size of the community; AGE = Age of the community) on the perception of local game abundance, ordered from the most positive to the most negative effect. Panels B, C and D show the estimated probability (± 95% confidence interval) of the proportions of responses over the perceived local game abundance ("declining" in red, "no change" in black; and "increasing" in blue) according to the extent of adjacent flooded areas, travel distance to urban centers, and distance to protected area boundaries, respectively.

Fig. 3 – Panels synthesizing results of Generalized Linear Mixed Models showing the magnitude and direction of effects (standardized coefficients ± 90% and 95%

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confidence intervals) of independent variables (FLOOD = Extent of adjacent flooded area; PROTE = Distance to protected area boundaries; CITY = Travel distance to urban centers, SIZE = Population size of the community; AGE = Age of the community) on the prey profile indices of average body size (A) and fecundity rate (B) for the three reportedly most hunted species. Panel C shows the relationships between prey profile metrics of fecundity rate, travel distance to urban centers and extent of adjacent flooded area (Flood). The estimated fecundity rate of prey profiles and 95% confidence interval are represented by a black line with a grey border, while the extent of adjacent flooded area is represented by the green to blue colour gradient of the data points.

Fig. 4 – Panels synthesizing results of Generalized Linear Mixed Models showing the magnitude and direction of effects (bootstrapped coefficients ± 90% and 95% confidence intervals) of five independent predictors on reported travel distances exercised by hunters to detect 16 forest vertebrate taxa, prey biomass per distance travelled (kg/km) and mean distance to detect an aggregate pool of 13 hunted species (All.spp).

Highlights

- Tropical forest sustainable-use reserves attempt to reconcile human needs and biodiversity conservation.
- Availability of aquatic protein and distance to urban areas increase the perceived sustainability of hunting.
- Availability of aquatic protein and distance to urban areas also affected consumption and depletion of harvest-sensitive species.

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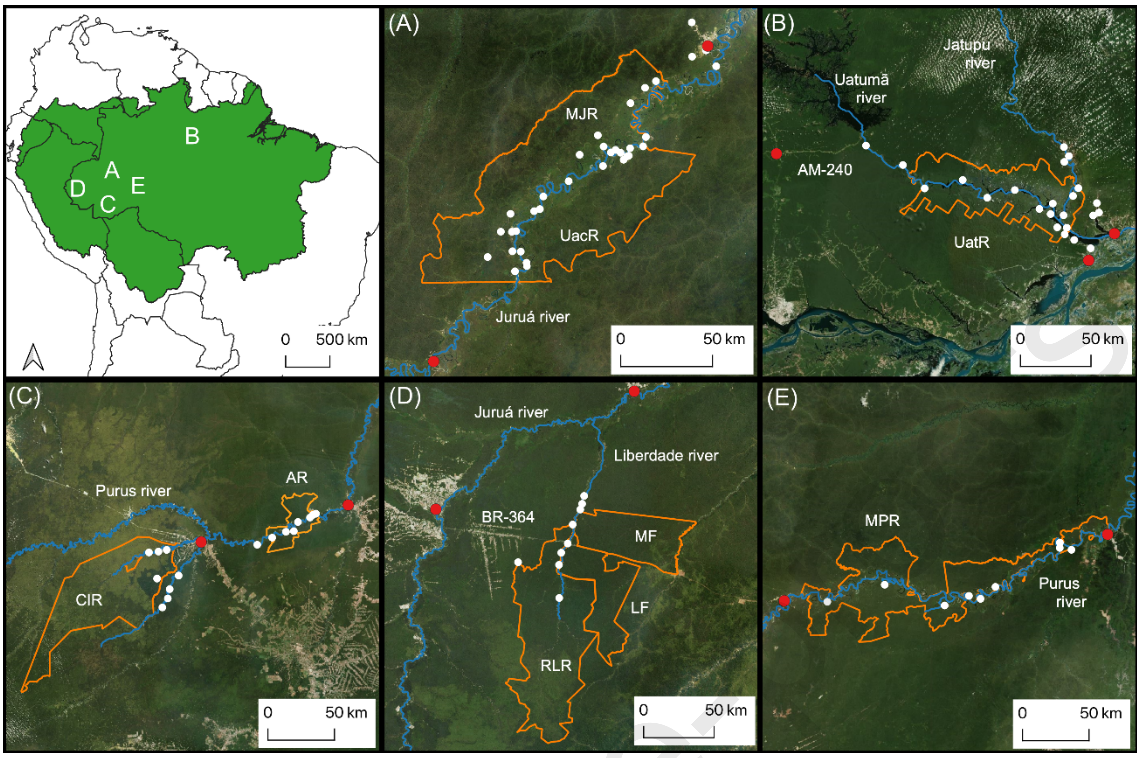

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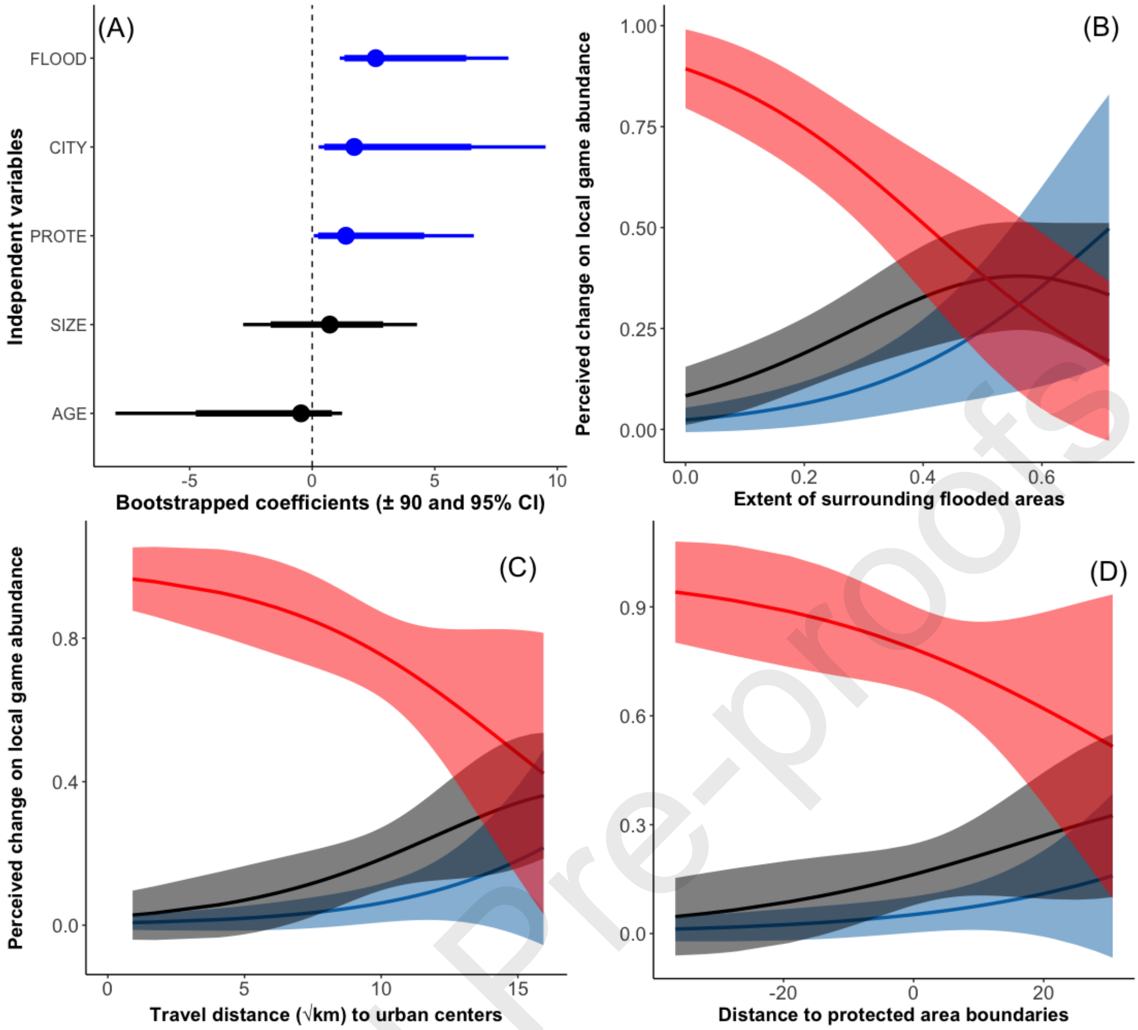

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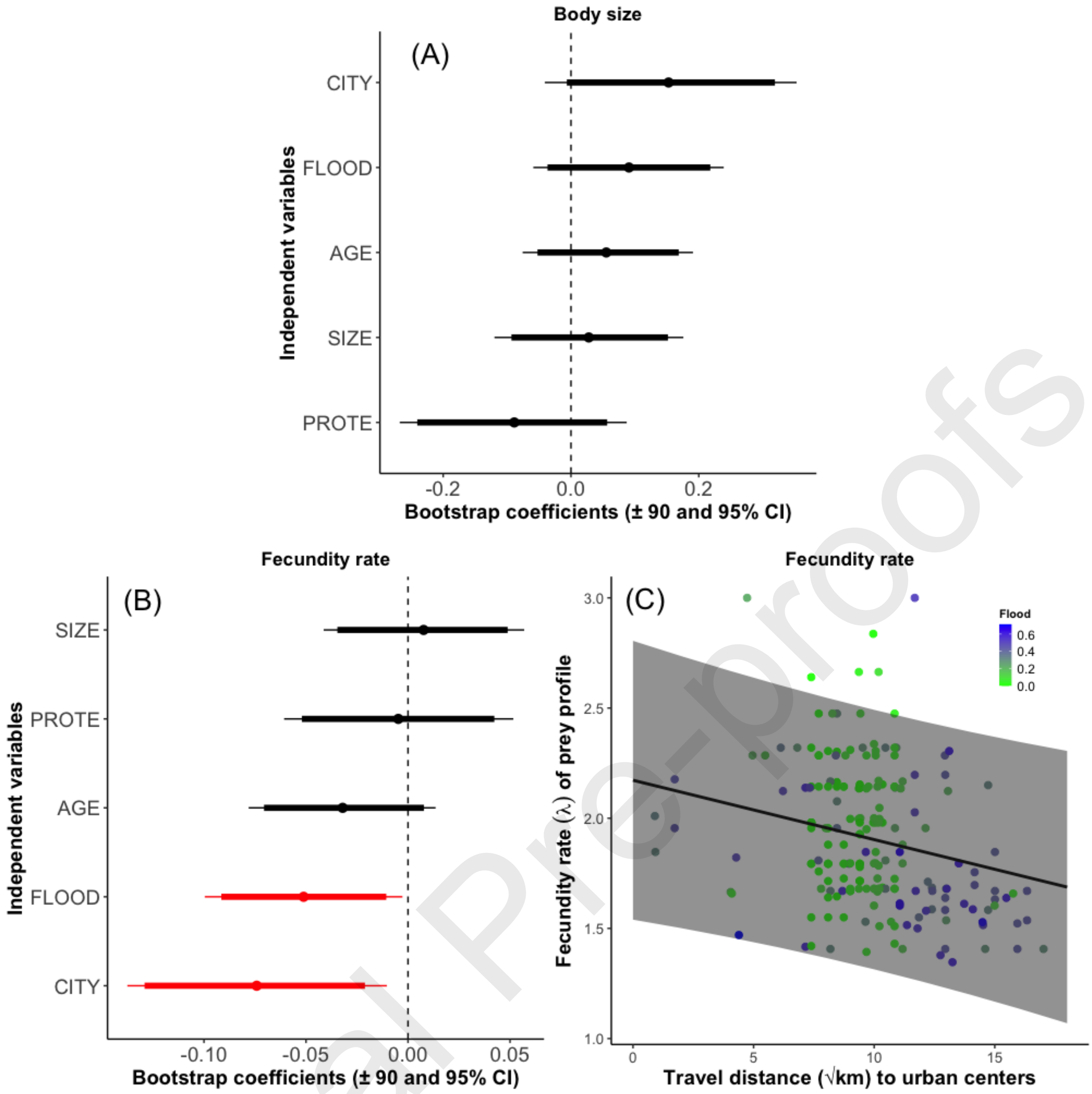

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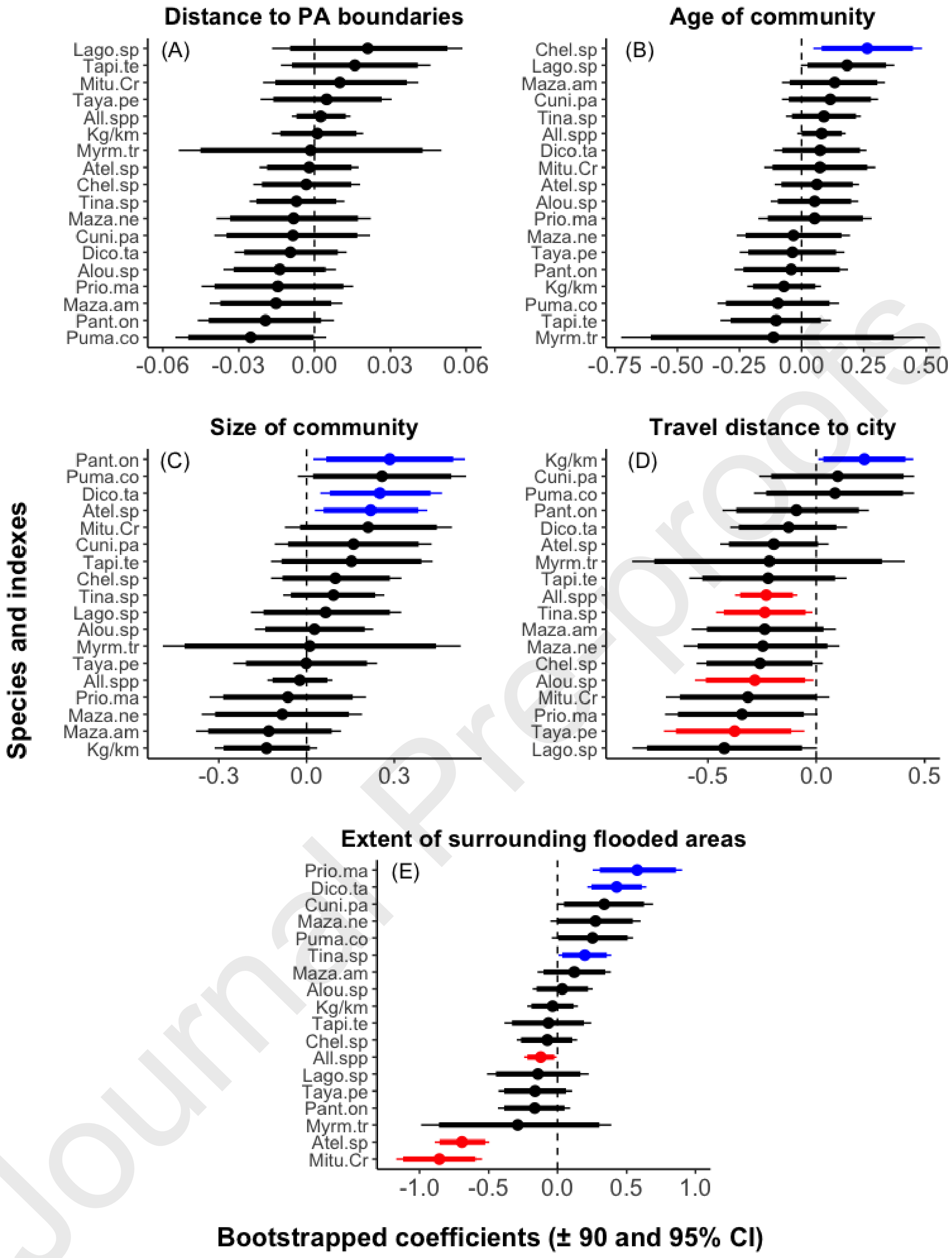

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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