Habitat use patterns suggest that climate-driven vegetation changes will negatively impact mammal communities in the Amazon

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Abstract

Climate change will affect species persistence and distribution, particularly in high-diversity ecosystems like the Amazon. Studies predict that as temperature and deforestation increase and precipitation patterns change in the Amazon, areas along its southern and eastern borders will suffer large-scale savannization, the conversion of tropical forest to degraded savannah-like vegetation. Here, we aim to identify the terrestrial mammal species potentially most at risk from savannization by studying their use of natural forest and savannah habitats within four protected areas, using camera-trap surveys and community occupancy models. We grouped species into categories according to the overlap of their global distributions with the Amazon and Cerrado biome (Amazon, Cerrado and generalist species) and investigated the effect on their space use of savannah cover within a 100-m buffer, and of the immediate habitat type (continuous forest, riparian forest and savannah) at the camera trap. Both savannah cover and savannah habitat type affected space use of most Amazon and generalist species strongly negatively. Only Cerrado species ever showed strong positive responses to savannah cover. These results suggest that most of the terrestrial mammal community is potentially vulnerable to savannization, including several species typically considered habitat generalists. Negative effects of disturbed savannah-like habitats are likely even stronger than effects of natural savannah reported here. Although less favorable than continuous forest, riparian forest had a strong negative effect for only a small fraction of species, indicating that effects of savannization may be buffered to some extent by riparian forests. Our results suggest that climate change-induced vegetation changes may reduce the ability of protected areas in the southern Brazilian Amazon to safeguard populations of terrestrial mammals and should be considered when assessing potential climate-change effects on these species.

Introduction

Climate change is a threat to biodiversity worldwide, increasing extinction risk by exposing one-sixth of species to climate-driven range contractions, with South America being the most affected continent (Urban, 2015). In the largest tropical forest on Earth, the Amazon, rising temperatures and lengthening of droughts alone, could jeopardize ecosystem integrity and lead to expansion of tropical savannahs (Salazar, Nobre, & Oyama, 2007; Nobre et al., 2016). The harmful effects of climate change occur in concert with, and are amplified by, anthropogenic disturbances such as deforestation, fires or invasive species, which further benefit the expansion of degraded savannah-like vegetation (Cox et al., 2000; Cramer et al., 2001; Nobre et al., 2016), a process called savannization. These derived savannahs are impoverished in native plant species diversity, fire-prone and often under direct anthropogenic influence (Veldman, 2016; Veldman & Putz, 2011).

The southern border of the Amazon marks the transition zone between the Amazon forest and the Brazilian savannah (Cerrado) and is the world's largest forest–savannah ecotone (Marques et al., 2020). At the intersection of two highly biodiverse biomes, this ecotone is particularly threatened by climate-driven vegetation changes (Nobre et al., 2016). First, the forests in the southern Amazon region experience the

longest dry season in the biome and therefore are more susceptible to the dryer and warmer conditions predicted for the region (Levine et al., 2016). Second, modeling studies predict that if temperature increases by 4°C or deforestation in the Amazon exceeds 40% (or even less), most areas along its southern (as well as eastern) border may suffer large-scale savannization (Nobre et al., 2016; Lovejoy & Nobre, 2018). This region has already suffered severe habitat loss, with c. 224 000 of its 613 261 km^2 (36.5%) being converted to anthropogenic use in the past three decades (Marques et al., 2020).

The predicted climate and vegetation changes associated with savannization are expected to have significant impacts on species distributions, interactions and habitat relationships, which may disrupt community composition and function (Lawler et al., 2009). Impacts of climate change on plant communities in the southern Brazilian Amazon, characterized by the increase in drought-tolerant species, have been well documented (Nepstad et al., 2007; Brando et al., 2014). However, impacts on the faunal community remain less studied. Modeling studies predict climate change will likely cause reduction, fragmentation and displacement of Amazonian mammal species' distributions (Sales, Galetti, & Pires, 2020a; Sales et al., 2020b). These effects are expected to be particularly severe for Amazon-endemic mammals or species with low dispersal ability (Ribeiro et al., 2016; Sales et al., 2020a, 2020b). The savannization process alone is expected to reduce suitable areas for Amazonian forest-specialist mammals by nearly 50%, while savannah species may gain distribution (Sales et al., 2020a, 2020b).

These modeling studies, however, are based on coarse patterns of range-wide climate and habitat associations. But, species can exhibit flexibility in habitat use depending on local context, particularly in ecotonal regions (Lidicker, 1999; Kark, 2013). The existence of natural savannah and forest vegetation in close proximity along the Amazon-Cerrado ecotone provides another avenue to anticipate future effects of savannization on species distributions and faunal communities: The region is home to wildlife species from both biomes, with varying habitat associations and likely also varying levels of plasticity in habitat use. Investigating how these species use forest and savannah habitat in areas where they have access to both could indicate which species will be impacted negatively or positively by savannization.

We aim to identify the terrestrial mammal species potentially most at risk from savannization in southern Amazonia by studying their use of natural forest and savannah habitats within four protected areas. Owing to the mobility of the target species, we expect that most species make use to some degree of both types of habitats, but that marked differences in use of savannah exist among species. Specifically, we expect that species predominantly associated with the Amazon biome will be negatively associated with savannah vegetation, and thus most at risk of savannization. Species associated with the Cerrado biome will be positively associated with savannah habitat. Finally, species distributed across both biomes will be intermediate in their response to savannah. Our results contribute to our ability to predict climate-change effects on the terrestrial mammal community in a region that is extremely biodiverse (Barbosa et al., 2007), at high risk due to the combined effects of deforestation and climate change (Nepstad et al., 2001; Marques et al., 2020) and severely understudied (Carvalho & Mustin, 2017).

Materials and methods

Study area

Our study region was located in the southern Brazilian Amazon (7°23′24″S/65°41′24″W; 13°33′0″S/60°25′12″W), in the transition zone between the central Brazilian savannah (Cerrado) and the Amazon forest. We surveyed four restricted-access protected areas that have natural forest and savannah habitats: Campos Amazônicos National Park (CANP), Mapinguari National Park (MNP), Guaporé Biological Reserve (GBR) and Corumbiara State Park (CSP) (Figure 1). CANP and MNP are located in the northern part of our study region, at the borders of the Brazilian states of Amazonas and Rondônia, while CSP and GBR are in the south of the study region, at the borders of Brazil and Bolivia. The protected areas in the south are strongly influenced by the Guaporé River flooding regime that inundates extensive areas, usually between January and May (MA-IBDF, 1984; SPVS, 1995). All four protected areas cover a mix of open, dense and alluvial ombrophilous Amazonian forest, as well as semideciduous forest, transitional forest, savannah and savannah–steppe habitats, with the total proportion of savannah habitat ranging from 7% in MNP to 50% in CSP (Appendix S1) (ICMBio, 2011; Perigolo, de Medeiros, & Simon, 2017; MMA, 2018). The climate in the region is tropical humid, with average monthly temperatures between 25 and 28°C. Average annual precipitation between 1991 and 2021 was 2216 mm (climate-data.org), with a rainy season from November to April and a dry season from May to October (Bastos & Diniz, 1982).

Camera-trap survey

To assess habitat use of terrestrial medium and large-bodied mammals (hereafter just mammals), we conducted five camera-trap surveys, two in CANP and one each in MNP, CSP and GBR, between January 2016 and September 2020. Within each area, we aimed for approximately equal coverage of forest and savannah habitat. To make surveys logistically viable, camera-trap placement was based on access information provided by the protected area managers, such as presence of rivers, roads and terrain features that limit walking incursion. In each survey, we deployed 58–78 camera traps (models PC800 Hyperfire, Reconyx or HD Essential/Aggressor, Bushnell; randomly assigned to sites) in continuous forest and savannah habitat. In the latter, we deployed cameras both in riparian forest and open savannah (Figure 1, Appendix S1). Average camera-trap spacing was 3025 m in continuous forest, 2154 m in riparian forest and 2886 m in savannah. We set up camera traps along game trails c. 30 cm above the ground, operating 24 h day^{-1} for
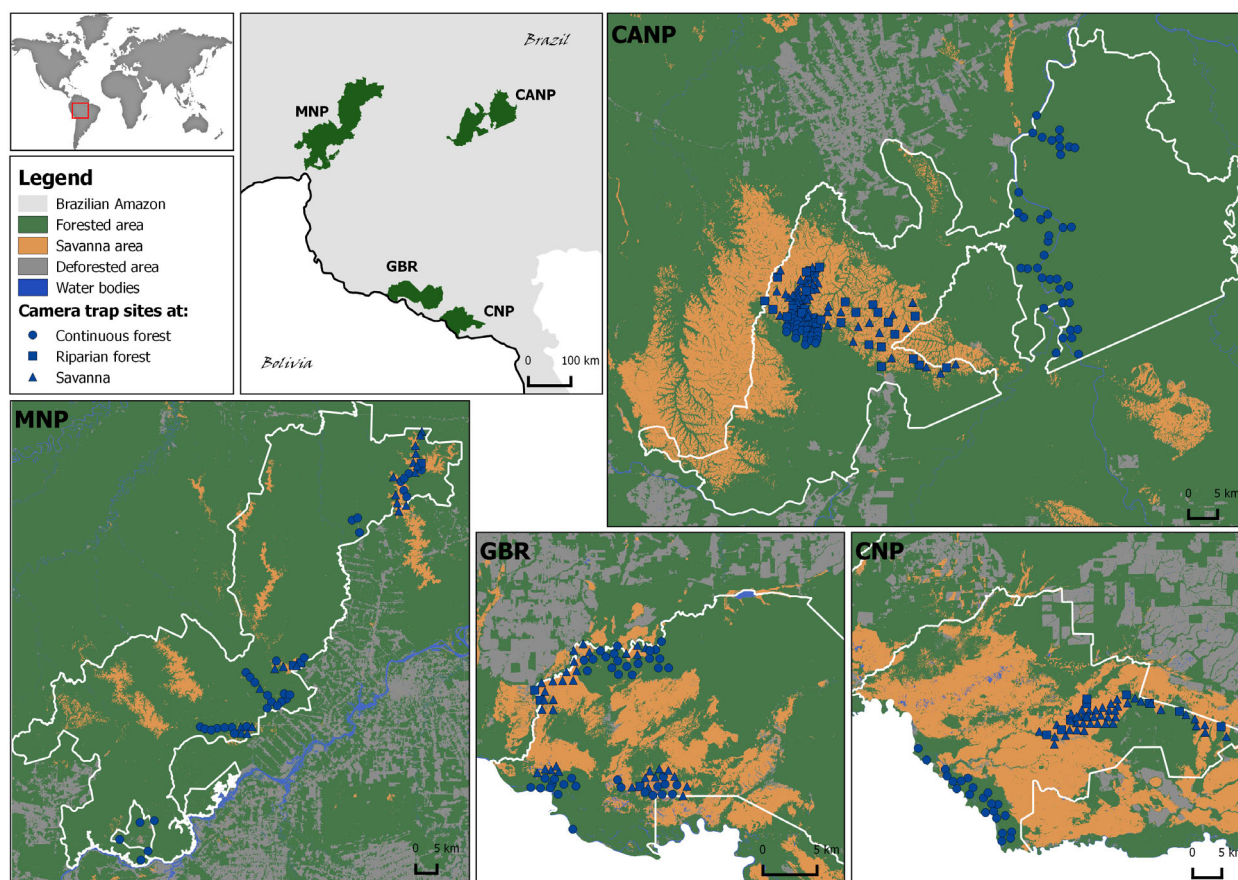
Figure 1 Map of the study region in the southern Brazilian Amazon with camera-trap locations, land cover features and surveyed protected areas (CANP, Campos Amazônicos National Park; MNP, Mapinguari National Park GBR; Guaporé Biological Reserve and CSP; Corumbiara State Park). As there were two surveys at CANP, camera-trap locations of the second survey are in light blue.

at least 30 days (unless malfunctioning occurred), with no delay between subsequent triggers and without bait.

We visually identified all pictures of mammals to species, except for pictures of nine-banded armadillo *Dasypus novemcinctus* and greater long-nosed armadillo *D. kappleri*, which we grouped into *Dasypus* spp. because the two species are difficult to distinguish from photographs and they are ecologically similar. For our analysis, we included mammal species that are mainly terrestrial (i.e. arboreal species such as monkeys and squirrels, and riverine specialists such as otters were excluded) and with average adult body mass above 0.5 kg. We classified these species into three categories according to their range-wide distribution, using IUCN Red List range maps (IUCN, 2021): (1) Amazon-associated species, whose distributions are predominantly constrained to the Amazon basin, (2) Cerrado-associated or tolerant species, whose distributions are predominantly located south of the Amazon basin and include the Cerrado biome (Cerrado species for brevity), and (3) generalist species, whose distributions include both the Cerrado and the Amazon basin (and possibly other biomes/regions). For community occupancy modeling (see Section 2.3), we used species records from

the five camera-trap surveys to create detection histories (a site-by-occasion-by-species array with entries of 0 for nondetection and 1 for detection) using 7-day sampling occasions.

Community occupancy model

We applied community occupancy models (Dorazio & Royle, 2005; Gelfand *et al.*, 2005), which use repeated species detection/nondetection data of a community of species across multiple sampling locations to estimate species occurrence while accounting for imperfect detection.

Specifically, the model estimates occurrence of species at a sampling location as a Bernoulli random variable with success probability ψ (occupancy probability), which can be a function of site-level covariates. Binary detection data across multiple sampling occasions are also modeled as Bernoulli random variables with success probability = detection probability P, which can be modeled as a function of site and occasion-level covariates. Species-specific parameters are modeled as coming from a common distribution governed by hyperparameters that are shared by the community. A form

of information sharing among species, this model structure can improve parameter estimates for species with sparse data and simultaneously allows for inference on the community and species level (Zipkin *et al.*, 2010; Kéry & Royle, 2016). Occupancy models assume that the occupancy state is 'closed' to changes, that is that a site is either occupied or unoccupied during a survey. For point-based sampling methods such as camera trapping, mobile species like mammals can move in and out of a sampling unit; in this scenario, occupancy probability should be interpreted as the probability of use of a site (MacKenzie, 2006). We adopt this interpretation and use the terms 'space use' and 'occupancy' interchangeably.

To investigate how mammal space use was affected by savannah habitat, we considered savannah cover and local habitat type as covariates on occupancy probability (ψ). We calculated savannah cover as the per cent of savannah within a 100-m buffer around each camera trap, using the Brazilian Annual Land Use and Land Cover Mapping Project (Collection 5, MapBiomas, 2021) 2018 layers (representing the midpoint of our surveys) at 1 arc-second (*c.* 30 m) resolution. Because sampling locations were in protected areas, we do not expect habitat to change over the years of our surveys. MapBiomas layers distinguish five major classes: forest, open savannah-like vegetation, farming, nonvegetated anthropogenic areas and water. Because savannah and forest were the two dominant habitat types, cover values for both habitats were highly correlated; moreover, as our camera sites were within protected areas, the amount of farming and anthropogenic areas was insignificant. Therefore, we did not consider other habitat types as predictors. We also did not consider other buffer sizes to calculate savannah cover, as we were primarily interested in how local conditions affect species space use; savannah cover for other radii was highly correlated with cover at the 100-m scale (Appendix S1). Local habitat type was recorded in the field as a categorical covariate with three levels: continuous forest, riparian forest and savannah.

To model detection probability, we included effort as the number of days the camera trap was active in a 7-day sampling occasion. Furthermore, we used habitat openness as a binary covariate on detection probability. It is easier to identify wildlife trails in forested habitat, and it is possible that in savannah habitat, we occasionally mis-identified accidental vegetation structure as a trail; moreover, we presume that wildlife is less bound to move along trails in open savannah habitat. Both of these factors can lead to higher detection probability in forest, and we therefore grouped continuous and riparian forest into closed habitat and considered savannah as open habitat.

With these covariates, we built two complementary models. In the first model, we investigated the absolute effect of savannah cover on mammal occupancy. Because local habitat type and savannah cover were strongly correlated (Appendix S1), we did not include habitat type in the first model. We included a quadratic effect of savannah cover and modeled both coefficients as species and region (north or south) random effects. This model allowed each species to

respond differently to savannah cover in the two study regions to accommodate possible differences in vegetation structure and the ecological role of savannah, owing to the seasonal flooding in the south. We included a quadratic effect of savannah cover to investigate potential optimum responses. We scaled values of savannah cover across all camera-trap locations.

In the second model, we investigated the effect of local habitat type and its interaction with savannah cover on mammal occupancy. We considered this an important additional model because we expected local habitat type to affect how species use this landscape, and because habitat specialist species may react differently to savannah cover depending on whether they are locally in forest or savannah habitat. The second model included local habitat type as a covariate on occupancy, with continuous forest being the reference category, and habitat-specific responses to savannah cover for each species. To deal with the correlation between habitat type and savannah cover, we scaled savannah cover independently for each habitat type. Thus, this second model estimated the effect of deviation in savannah cover from the habitat-specific mean; the habitat type effect includes any possible effect of differing mean savannah cover among habitat types. Because differences in response to savannah cover between regions, and quadratic effects of savannah cover, were weak (see Figure 2), we did not model region-specific responses in this model and used only a linear effect.

A single community-wide hyperdistribution may mask responses specific to groups within the community (Pacifici *et al.*, 2014). Comparing species coefficients for savannah cover and habitat from simplified models with and without separate hyper-means for Amazon, generalist and Cerrado species, we found that such group structure was important for responses to savannah habitat (Appendix S2). In model 2, we therefore allowed each species group to have its own hyper-mean for species response to savannah habitat. We maintained the community-wide hyperdistribution for response to savannah cover in both models; to quantify group-level response to savannah cover, we calculated the mean coefficient of all species within each group. We did not include species never detected in a region (model 1) or habitat type (model 2) in these calculations, as estimates for these species are very close to the community mean and would bias the group mean estimates. We performed these calculations on all posterior samples of parameters to obtain full posterior distributions.

In both models, we modeled occupancy and detection intercepts as species and survey-specific random effects, to account for potential variation due to seasonality and unmeasured local factors. Both models also used both detection covariates, where the effect of effort was modeled as a fixed effect (i.e. constant across species), and the effect of habitat openness (0 = closed and 1 = open habitat) as species-specific. We calculated Bayesian *P*-values as a measure of model fit (Gelman, 2003) based on Freeman–Tukey residuals, aggregating species and location-specific detections across occasions (Kéry & Royle, 2021). These suggested that
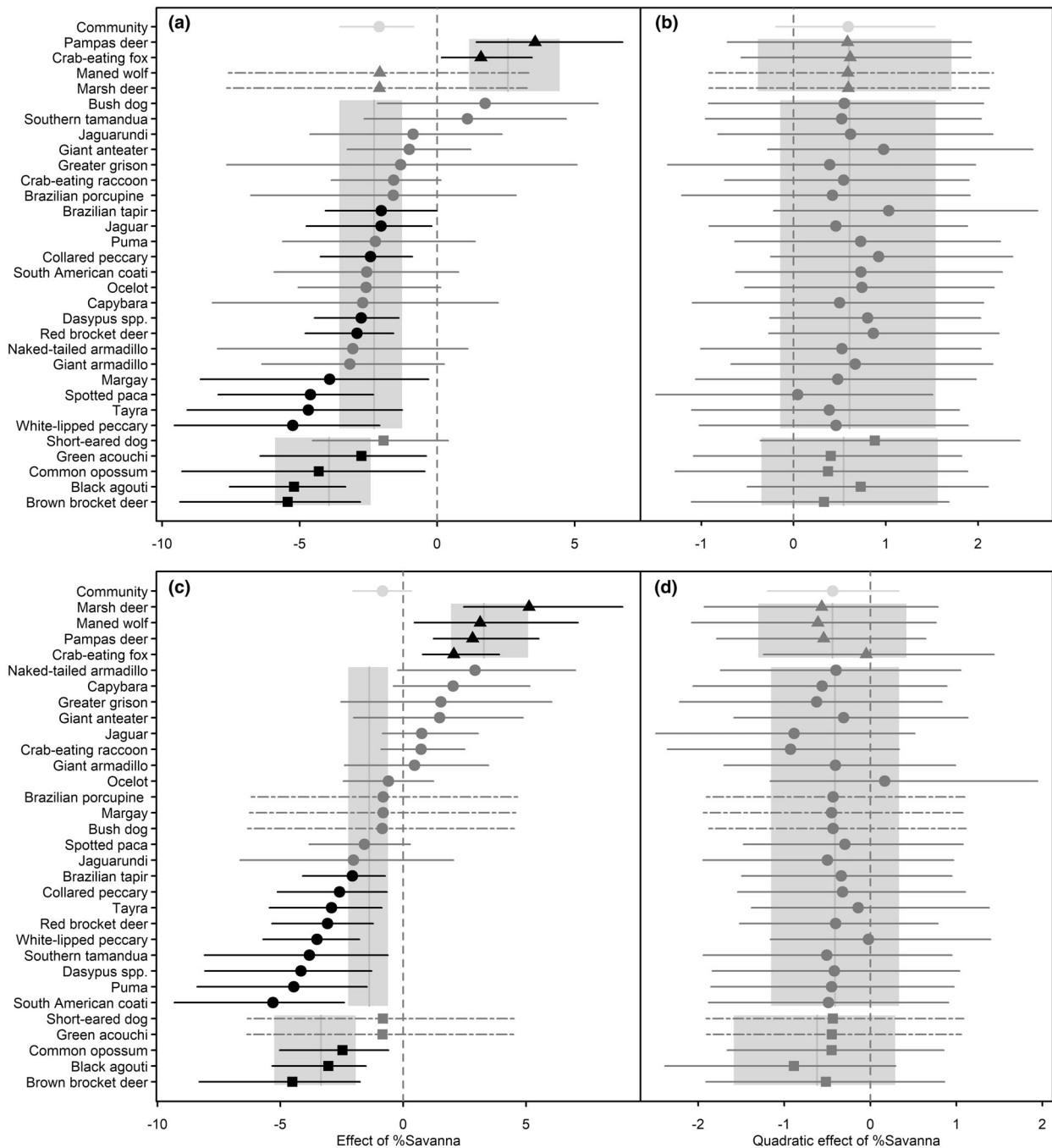
Figure 2 Linear (a, c) and quadratic (b, d) effect of per cent of savannah cover (average percentage of savannah across 30-m pixels in a 0.1-km radius around each camera trap) on occupancy of three groups of mammal species whose global distributions are associated with the Amazon (squares), the Cerrado (triangles) or both biomes (dots), estimated with a Bayesian community occupancy model fit to camera-trap data from four protected areas in the southern Brazilian Amazon collected between January 2016 and September 2020. Top row: effects in the northern region of our study area; bottom row: effects in the southern region. Symbols represent posterior means and horizontal lines 90% Bayesian Credible Intervals (BCI). Strong effects (whose 90% BCI do not overlap zero, vertical dashed gray line) are in black. Dashed horizontal lines are species not detected in the specific region. Top light-gray dots/horizontal lines represent community posterior means with 90% BCI. Vertical gray lines and shaded areas are group-specific mean responses with 90% BC, calculated post hoc excluding species never detected in a given region.

detection covariates were insufficient to capture variability in P. We added a normally distributed species and location-specific error term to the detection model, which made the model fit the data.

We implemented the models using Bayesian Markov chain Monte Carlo (MCMC) methods with the package NIMBLE v.0.9.1 (de Valpine *et al.*, 2017) in R v. 4.0.5 (R Core Team, 2021). We used vague uniform and normal priors for all parameters (for full specification, see model code in Appendix S5). We ran three chains of 150 000 (model 1) and 300 000 (model 2) iterations, discarding 100 000 and 250 000, respectively, as burn-in, thinning the rest by 10. We checked chain convergence by inspecting trace plots and R-hat statistics (Gelman & Rubin, 1992). We present parameter estimates as posterior means with posterior standard deviation (SD) and 90% Bayesian Credible Intervals (90% BCI), which tend to have more stable posterior distributions than the commonly used 95% BCI (McElreath, 2018). We considered covariate effects strong when 90% BCI did not overlap 0.

Results

The five camera-trap surveys yielded 5516 records of 31 terrestrial mammals (Appendix S1), with a sampling effort of 14 781 camera-trap days. Based on IUCN Red List range maps (IUCN, 2021), most species recorded (22 out of 31 species, 70%) were generalists. Five species were considered Amazon-associated; four species were considered Cerrado species (Appendix S1).

Results from our first model, investigating the absolute effects of savannah cover for the northern and southern parts of the study region, showed that savannah cover had a strong negative linear effect on community occupancy for the northern region and a weak negative linear effect for the southern region. In both regions, group-average responses were strong and negative for Amazon and generalist species, and strong and positive for Cerrado species (Figure 2). As expected, the intensity and direction of the linear effect of savannah cover varied among species: It was strongly negative for 13 species in the north and for 12 species in the south (all Amazon or generalist species), with nine of these species showing strong negative effects in both regions. The linear effect was strongly positive for two species in the north and four species in the south (all Cerrado species), with two species showing strong positive effects in both regions (the other two species were recorded only in the south). The quadratic effect of savannah was weak for all species, groups and the community in both regions (Figure 2b, d). The difference between the regions in the effect of savannah cover was weak for the community and most species; only three species that occurred in both regions showed strong differences in the coefficient (Appendix S3).

Results from the second model, investigating the effect of local habitat type and its interaction with savannah cover, indicated a strong effect of local habitat type on species space use (Figure 3a, b). Relative to continuous forest (the reference category), savannah had a strong negative effect on

group-level occupancy for generalist and Amazon species, and on species-level occupancy of 16 species from these two groups. All Cerrado species, as a group and individually, showed weak positive responses to savannah habitat. Only Amazon species showed a strong negative group-level response to riparian forest; nine species (four Amazon and five generalist species) showed strong negative species-level responses.

The effect of savannah cover scaled by habitat type (i.e. the deviation from the habitat-specific mean) was strongest in savannah habitat (Figure 3c–e). Both the Amazon and generalist species groups showed strong negative responses, as did 14 species from these two groups, and the community as a whole. Cerrado species responses were variable and weak. In riparian forest, the effect of savannah cover was weak for the community and all groups and strong and negative only for two Amazon species. In continuous forest habitat, only the generalist group showed a strong negative average response to savannah cover, as did five species (four generalists and one Amazon species).

Results for the detection component of both models are in Appendix S3 (Figures A3.2 and A3.3).

To test whether the overwhelmingly negative response to savannah habitat could have been caused by higher levels of anthropogenic pressure at savannah sampling locations, we compiled five variables associated with anthropogenic pressure, compared their averages and ranges across the three habitat types, and ran simplified models for two of the variables – the proportion of agricultural habitat and average human footprint index (HFI) in a 5-km buffer – that tended to have higher values at savannah sampling locations (Appendix S4). Results suggested that higher proportions of agriculture may have contributed to negative responses to savannah habitat, but strong responses to agriculture were less common than to savannah habitat.

Discussion

Even though the terrestrial mammal community in the southern Brazilian Amazon was dominated by species associated with both the Amazon and Cerrado biomes, the majority of species responded negatively in their space use to savannah at the immediate local and 100-m scale. Only Cerrado-associated or tolerant species responded positively or neutrally to savannah. The importance of savannah cover as a driver of mammal space use depended on the immediate local habitat context: increasing amounts of savannah reduced space use most strongly at sites located in savannah habitat for most Amazon and generalist species, which made up 87% of the analyzed community. This suggests that the majority of the terrestrial mammal community in the southern Brazilian Amazon is potentially vulnerable to the predicted climate change-induced savannization, including several species typically considered habitat generalists.

Models suggest that a changing climate alone (Salazar *et al.*, 2007; Hirota *et al.*, 2019) could cause replacement of Amazon forest by tropical savannahs. Increasing temperature and a disruption of rainfall patterns can favor drought-
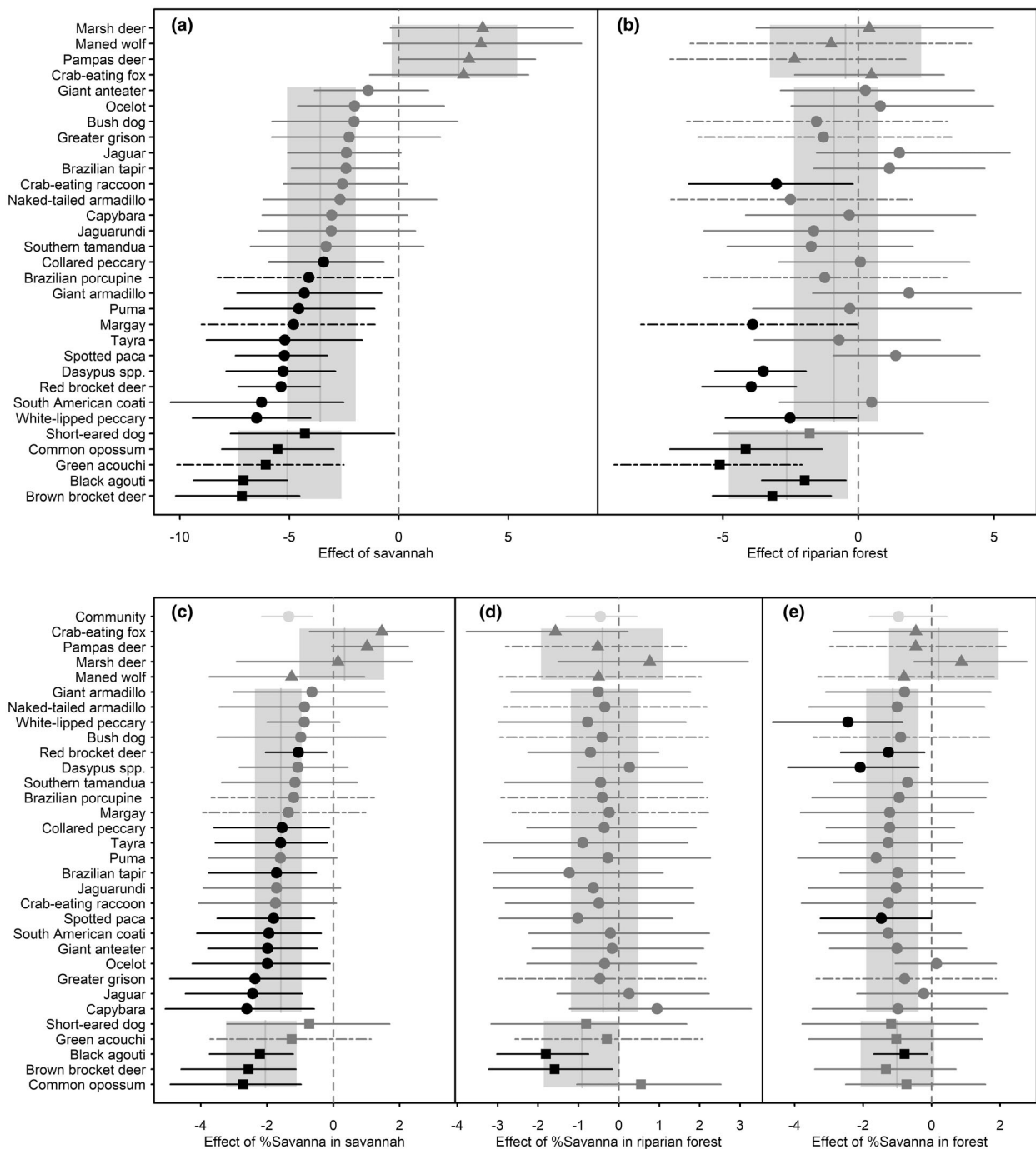
Figure 3 Effect of local habitat type (a, b) and interaction with per cent savannah cover (scaled independently for each habitat type; c–e) on occupancy of three groups of mammal species whose global distributions are associated with the Amazon (squares), the Cerrado (triangles) or both biomes (dots), estimated with a Bayesian community occupancy model fit to camera-trap data collected in four protected areas in the southern Brazilian Amazon from January 2016 to September 2020. Symbols represent posterior means and horizontal lines 90% Bayesian Credible Intervals (BCI). Strong effects (whose 90% BCI do not overlap zero, vertical dashed gray line) are in black. Dashed horizontal lines are species not detected in the specific habitat type. Top light-gray dots/horizontal lines in c-e represent community posterior means with 90% BCI. Vertical gray lines and shaded areas are group-specific mean responses with 90% BC, estimated within the model (a, b) or calculated post hoc excluding species never detected in a given habitat type (c–e).

tolerant plant species and progressively shift vegetation structure away from dense tropical forest (Nepstad *et al.*, 2007). Thus, even in areas relatively protected from other forms of anthropogenic degradation (e.g. burning and logging), much of the terrestrial mammal community may suffer negative effects of climate change-induced shifts to drier, open vegetation forms. As deforestation outside of protected areas continues, a decline in preferred forested habitat inside protected areas is a troubling prospect for regional species conservation. Moreover, land use change outside of protected areas can affect wildlife inside protected areas (Hansen & DeFries, 2007). We observed some evidence that wildlife space use was negatively associated with the proportion of agriculture at a 5-km scale (though effects were mostly weak), which was generally low (<5%) but had a tendency to be higher for locations in savannah habitat. This may contribute to the observed negative associations of many species with savannah habitat and illustrates that even inside protected areas, both climate change and other anthropogenic pressures contribute to savannization and its impact on wildlife.

The threat of savannization is further magnified, where climate change directly acts in synergy with other anthropogenic pressures favoring the expansion of degraded savannah-like habitat (Veldman, 2016). The resulting derived savannahs are dominated by bamboo and exotic grasses, often under direct anthropogenic influences such as cattle grazing (Veldman & Putz, 2011), and are unlikely to provide the same resources that occur in natural savannah areas (Veldman, 2016) such as the ones we surveyed. Moreover, anthropogenic processes like burning and logging create degraded savannah-like habitat on a much shorter time scale than climate change alone (past climate-driven rainforest–savannah dynamics along the Amazon border have taken place over millennia, e.g. Mayle *et al.*, 2007), leaving local wildlife no time to adjust to changing habitat conditions. It is likely, therefore, that the negative effects of savannization on species space use and distribution outside of protected areas will be stronger than observed in our study, mirroring both a change in vegetation form and increased direct anthropogenic pressure.

Contrary to most map representations with a sharp line between the two biomes, the transitional zone between the Amazon and Cerrado is broad and complex (Marques *et al.*, 2020). As expected in such an ecotone region, our study recorded a rich community of terrestrial mammals. Dominated by habitat generalists, this community could be expected to show considerable use of both forest and savannah habitat, and indeed, most species used savannah to some extent. Nonetheless, we found that while Amazon species as a group showed the strongest negative response to savannah, the negative responses of generalist species – both as a group and on the species level – were similar in magnitude at both of the considered scales. Thus, contrary to Sales *et al.* (2020a, 2020b), who predicted that generalist species will expand their ranges under savannization, our study suggests that they are locally vulnerable to savannization. For these widely distributed species, savannization along the southern Brazilian Amazon is unlikely to constitute a threat to their global distribution or status. Moreover, these species may be flexible enough to shift habitat use toward savannah habitat under savannization and thus may not lose as much suitable habitat as strict forest specialists. Still, our results suggest they will lose access to their locally preferred habitat (i.e. forest), which can translate into physiological stress, disruption of reproductive dynamics and decline in fitness and population sizes (Tewksbury, Huey, & Deutsch, 2008; Huey *et al.*, 2012; Cruz-Mcdonnell & Wolf, 2016).

Even though the study areas were located in regions with different ecologies, differences in species response to savannah cover were mostly minor. The absence of important quadratic effects of savannah cover suggests that species either favored or disfavored savannah. But, results on which species were strongly affected by savannah habitat differed to some degree between the two models. Cerrado species had strong positive responses to savannah cover in the first model, but weak-positive responses to savannah habitat, and weak mixed responses to savannah cover (and riparian forest habitat) in model 2. It is likely that the larger number of parameters in model 2 increased parameter uncertainty, especially for this small group of species with two members with few detections. The clear tendency toward a positive response to savannah habitat, compared with mixed responses to savannah cover, suggests that Cerrado species responded more strongly in their space use to the immediate habitat type.

Fifteen Amazon and generalist species showed strong negative responses to savannah habitat or cover across models. These included most large herbivores (tapir, red and brown brocket deer, white-lipped and collared peccary), both large carnivores (jaguar, puma) and several smaller species (e.g. tayra, *Dasypus* spp., black agouti). In general, large-bodied mammals are more susceptible to negative effects of climate change (Mccain & King, 2014). Large herbivores and carnivores perform key trophic processes relevant to the maintenance of the structure and function of terrestrial ecosystem (e.g. seed dispersal, seed predation and prey population control) and are therefore indicators of habitat integrity and of conservation concern (Jorge *et al.*, 2013). Severe reduction in distribution of these species in the study region due to savannization could jeopardize the integrity of remaining forest and the ecotonal ecosystem as a whole, even inside protected areas. This is especially concerning when combined with expected reductions in other mammal orders that play crucial ecological roles and that have been shown to be vulnerable to climate change, such as Primates and Chiroptera (Ribeiro *et al.*, 2016; Sales *et al.*, 2020a, 2020b). Moreover, large ungulates are also the species most affected by forest loss and fragmentation outside of protected areas in this region (Rocha, 2021). Decimated by hunting and loss of natural habitat throughout the Neotropics (Bogoni, Peres, & Ferraz, 2020), they are likely particularly dependent on protected areas (e.g. Ferreira *et al.*, 2020). Our results suggest that climate change-induced vegetation changes may reduce the ability of protected areas in the southern Brazilian Amazon to safeguard populations of these species, adding to the

understanding that Amazonian protected areas are likely insufficient to buffer mammals against climate-change effects (Ribeiro *et al.*, 2016).

Savannah was the least used local habitat type for Amazon and generalist species groups and for the large majority of species within these groups. Although less favorable than continuous forest, riparian forest only had a strong negative effect for the Amazon species group and some generalist species. Moreover, the amount of savannah cover in the surroundings was less important for most species if they were in forest. This indicates that negative effects of savannization may be buffered to some extent by riparian forests, though we caution that the lower number of camera traps in riparian forest (Appendix S1) may have reduced our ability to detect strong effects. Riparian forests are widespread in most tropical savannahs and contribute to landscape heterogeneity and species diversity (Naiman, Decamps, & McClain, 2005). They provide habitat for forest-dwelling species within savannah landscapes (Redford & Fonseca, 1986) and can function as dispersal corridors (Johnson, Saraiva, & Coelho, 1999). Because of their general access to ample water (Silva *et al.*, 2008), riparian forests are less sensitive to changing climates. Our results suggest that riparian forest may mitigate some of the negative impacts of climate change on terrestrial wildlife in protected areas affected by savannization in the Amazon.

We interpret the strong negative responses in space use to savannah habitat by the majority of the terrestrial mammal community as evidence that much of this community is at risk to suffer negative effects of savannization in the changing landscape of the southern Brazilian Amazon. But, there are several caveats to this interpretation. First, some species may be able to cope with savannization, despite their current local preference for forested areas. Particularly, several generalist species are known to prefer or select for open habitats in other parts of their range (e.g. Bertassoni & Ribeiro, 2019 for giant anteaters rangewide; Scognamillo *et al.*, 2003 for pumas in the Llanos; Vynne *et al.*, 2011, for giant armadillos, giant anteaters and pumas in the Cerrado). Second, ecotonal populations can be more resilient to changes (Kark, 2013), potentially alleviating the negative effects of savannization, at least within protected areas where direct anthropogenic impacts are minimized. On the contrary, the often extreme effects estimated in this study, owing to the stark differences in space use between savannah and forest habitats, pose numerical challenges and likely caused some of the very wide credible intervals, complicating the identification of important effects. This is further compounded by sparse detection data for some species, and small numbers of species in some species groups. Finally, our results should not be misunderstood as diminishing the conservation value of Amazonian savannahs. These unique ecosystems with endemic species are understudied and underprotected (Carvalho & Mustin, 2017). Rather, our results point to increasing challenges for protected areas in the southern Brazilian Amazon to safeguard all their biodiversity in the face of climate change and continuing deforestation.

There is a growing body of literature showing the different ways in which climate change negatively affects biodiversity, such as reducing species distributions, exposing species to nonanalog climates or causing climate niche mismatch and physiological stress (Huey *et al.*, 2012; Ribeiro *et al.*, 2016; Pacifici, Visconti, & Rondinini, 2018; Miranda, Imperatriz-Fonseca, & Giannini, 2019; Menéndez-Guerrero, Green, & Davies, 2020). There is also an increasing understanding of the complex interactions between climate and land use change effects on biodiversity and faunal communities (Malhi *et al.*, 2008; Brodie, 2016; Karp *et al.*, 2018). By contrast, climate-driven changes in natural habitat remain understudied, particularly for faunal communities. Using in situ data of species habitat use, our study suggests that effects of savannization may be more widespread in the medium to large-bodied terrestrial mammal community of the southern Brazilian Amazon than previously thought (Sales *et al.*, 2020a, 2020b). This is concerning beyond this taxonomic group, as these species are highly mobile and therefore typically more able to deal with landscape changes than other taxa (e.g. primates and amphibians) (Menéndez-Guerrero *et al.*, 2020; Sales *et al.*, 2020a, 2020b). Our study therefore highlights the need to incorporate climate-driven habitat changes into assessments of climate-change effects on wildlife.

Author contributions

DGR and RS conceived the ideas, designed methodology and analyzed the data. DGR collected the data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data and code for the presented analyses can be downloaded from Dryad at https://doi.org/10.25338/B84060.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Additional information on study areas, sampling effort, and data.

Appendix S2. Determining group structure in the community occupancy model.

Appendix S3. Additional community occupancy model results.

Appendix S4. Potential confounding effects on occupancy probability.

Appendix S5. Nimble model code for two main models presented in main text.