GATHER ROUND THE TREE: WOODY ABOVEGROUND BIOMASS INCREASES ANIMAL PRESENCE AND SPECIES RICHNESS IN A TROPICAL FOREST-SAVANNA ECOTONE

by

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A thesis

submitted in partial fulfillment

of the requirements for the degree of

Master of Science in Biology

Boise State University

December 2021

BOISE STATE UNIVERSITY GRADUATE COLLEGE

DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

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Thesis Title: Gather Round the Tree: Woody Aboveground Biomass Increases Animal Presence and Species Richness in a Tropical Forest-Savanna Ecotone.

Date of Final Oral Examination: 22 October 2021

The following individuals read and discussed the thesis submitted by student Merry Vanessa Marshall Davidson, and they evaluated the student's presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

The culmination of this work is dedicated to my God, and every teacher I have had in my educational pursuits, my ancestors, family, and friends. Thank you all who have guided each step of my journey thus far, believed in my potential, and encouraged me to follow my passion.

ACKNOWLEDGMENTS

To my advisor, committee members, mentor, and collaborator: Thank you for the support and for cheering me on continually. Sometimes y'all were ahead of me and I didn't realize the support/advice I was given until I was going through it. Advisor (Dr. Trevor Caughlin) Committee (Dr. Jodi Brandt & Dr. Jennifer Forbey) Mentor (Dr. Anand Roopsind) Collaborator (Dr. Matt Hallett)

Science Computing Department: Thank you for the technological innovation, that is, the camera trap interface! The project ran more efficiently because of y'all. Kyle S. Shannon, and Jason Watt

To my fellow classmates: Thank you for your support because we were all going through this together!! Thank you to those listed here who helped me strengthen my computational skills (R and GEE). Also thank you for your help at one point or another during the development of my project. Nick Kolarik, Brent Clark, Caughlin Lab (including Dr. Juan Miguel, Sandra Velazco, Dr. Cristina Barber Alvarez-Buylla, Andrii Zaiats, Anna Roser, Peter Olsoy), TSARS Seminar class

To my colleagues: For those who helped on the camera trap tagging, thanks for helping me feel comfortable to run this project by being so nice and knowledgeable. I appreciate your time and input. Arianne Harris, Meshach Pierre (The Three MuskeTEARS!), Huichang Yang (A-Team!) Nick M. Hougaard, Brittany Evans, Malika Singh

Boise State Biology Department: Thank you for your help with poster printing, trip coordinating, and admin! Y'all were so friendly, and I never felt like I was bothering y'all. Nicole Terrayago, Brittany Archuleta, Adil Refaey

To the Graduate Student Success Center: Thank you for the guidance with every aspect of my journey through this program. The 3 Minute Thesis was a formative experience. Wayne Cochrane, Lynzi Cooper

To my family: I wasn't always around, and I never mastered a work-life balance. For that I say sorry and thank you for your patience and support, nonetheless. Davidson's: Bill/Fish, Rain, Tré, and Linda. Marshall's: James, and Marie Paz, Darrah, Amapola Antonio, Linda and Dorothy

To my friends from all stages of life. Thanks for your encouragement, and at times, distraction from school. Madison Preston, Rebecca Donaldson, Katia Mendoza, Kendra Luna

Thank you for the funding that allowed me to focus on school and see my study region firsthand: Teaching Assistantship (Anatomy and Physiology) and Dan Montgomery Graduate Student Award (2019)

ABSTRACT

Boundaries between ecosystems are often biodiversity hotspots with relatively high vulnerability to global change. The boundary between tropical rainforest and savanna ecosystems in the Amazon presents an ecotone that is undergoing a shift in ecosystem structure, as a warming climate promotes the expansion of grassland. How animal communities in the Amazon will respond to changes in ecosystem structure is a crucial unanswered question with implications for the many ecosystem services that animals provide, from a food source for Indigenous people to seed dispersal for vulnerable tree populations. Recent modeling work has forecasted that faunal savannization will occur in the Amazon, as savanna-dwelling animals replace forest specialists. However, empirical data to test these forecasts has remained scarce, due to the need for large-scale data across local and regional forest-savanna gradients. To overcome this difficulty, we quantified associations between terrestrial vertebrates and ecosystem structure using replicated camera traps across a forest-savanna ecotone in central Guyana. To capture continuous gradients in woody biomass across the ecotone, we paired radar-derived measurements of aboveground biomass from Phased Array-type L-band Synthetic Aperture Radar (PALSAR) with animal species presence at camera trap sites, including >54,000 individual photos. We hypothesized that different animal species communities would emerge in sites with different levels of aboveground biomass, representing forest and savanna specialists. We tested this hypothesis with hierarchical

Bayesian models for animal species detection and species richness across our study landscapes. Our results did not support the hypothesis that there is a guild of savanna specialists with increased presence in sites with low aboveground biomass. Instead, nearly all (54 out of 56) species showed increased probability of detection in sites with higher aboveground biomass. Consequently, overall species richness was significantly related to aboveground biomass, including a median proportional increase in species richness of 90.0% (CI: 21.57 to 200.0%) for every kiloton of biomass at a site. These results suggest that woody structure plays a critical role in supporting animal species richness at the Amazonian forest-savanna ecotone, including non-forest tree cover such as bush islands, gallery forest, and isolated trees. Ongoing declines in tree cover will likely have detrimental impacts across most groups of animal species. Without landscape conservation strategies to maintain tree cover at the forest-savanna boundary, climate change could have severe consequences for Amazonian animal populations.

Keywords: animal community, boundary composition and gradient, camera trap, animal faunal savannization, landscape conservation, tropical rainforest, woody aboveground biomass.

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AGB	Woody aboveground biomass
kt	Kilotons

INTRODUCTION

Transitional zones, where ecological communities coincide from distinct ecosystems, are critical for biodiversity conservation (Kark, 2017). Transitional zones, or ecotones, typically have high species richness due to species spillover from different ecosystems as well as the occurrence of unique ecotonal species (Cáceres et al., 2007; Jähnig et al., 2018; Kent et al., 1997; Odum, 1953; Widiana et al., 2020). Ecotones are often highly dynamic, with boundaries that shift in space and time, resulting in cascading impacts on biodiversity (Kent et al., 1997). The dynamic nature of ecotonal regions makes them particularly susceptible to anthropogenic and climate driven change. Threats to biodiversity, including climate change, altered fire regimes, and over-extraction of resources, are especially prevalent in forest-savanna ecotones. Woody plant encroachment into savanna ecosystems, due to fire suppression, can reduce plant and animal diversity with implications for the ecosystem services savannas provide (Stevens et al., 2017; Venter et al., 2018). On the other hand, declines in woody biomass at the forest-savanna ecotone, due to increased wildfires, result in degradation of forest patches that support biodiversity and store carbon (Flores & Holmgren, 2021). Understanding species distributions at forest-savanna boundaries is necessary to inform biodiversity conservation in some of Earth's most threatened ecosystems.

Forest-savanna ecotones in the Amazon are a hotspot for biodiversity (Erds et al., 2017; Smith et al., 1997) and are increasingly threatened by global change. Deforestation and increased fire frequency and extent have led to a decrease in forest area extent (Cardoso et al., 2021), much of which is being replaced by savanna (Armenteras et al., 2021; Silvério et al., 2013). These changes are exacerbated by climate change, as the regional climate grows hotter and drier, promoting savanna vegetation at the expense of tropical rainforest (Coe et al., 2013; Laurance & Williamson, 2001; Sales et al., 2020). The loss of forest is likely to intensify regional drought, as tropical forests regulate the Amazon's water cycle, including increasing atmospheric moisture in the dry season via evapotranspiration (Zemp et al., 2017) . These ecosystem-level changes are paralleled by changing plant species composition, including an increase in plants that tolerate warmer temperatures and increased precipitation, and reduced tree cover (K. J. Feeley et al., 2020; Hirota et al., 2010).

A relatively unknown component of ongoing ecosystem changes at the forest-savanna ecotone in the Amazon is how animal communities will respond to increases in savanna replacing tropical rainforest. Data on animal community composition at the forest-savanna ecotone will be essential to forecasting survival prospects of animal species under a changing climate. However, these data are currently scarce, leading to uncertainty in predictions of animal habitat use and specialization. If habitat specialization constrains animal populations, we might expect to see declines in species that are forest specialists. A recent modeling effort, based on ecological niche models and dispersal simulations, has raised the alarm over "savannization" of faunal communities, including the expected loss of nearly 50% of suitable range for forest specialist species (Sales et al., 2020). However, other studies have indicated that Amazonian animal species may be resilient to ecosystem structure change (*e.g.,* Roopsind et al., 2017). Even if forest specialization is relatively common, animals may be able to adapt to changing habitat structure by dispersal into favorable patches (Ramos Pereira et al., 2013). The important roles that Amazonian animals play in maintaining tropical tree diversity (Terborgh et al., 2008), nutrient cycles (Feeley, 2005), and supporting human nutrition through Indigenous hunting (Read et al., 2010), point to an urgent need for data on animal habitat specialization in Amazonian ecotones.

Assessing habitat structure at forest-savanna ecotones, including whether animal species are associated with a particular habitat type, is complicated by the gradual transitions between forest and savanna habitat. Quantifying habitat at the scale of animal habitat use (often hundreds to thousands of meters) creates logistical barriers for direct measurements of plant species composition in field plots. An alternate approach is the use of remotely sensed metrics of vegetation, including vegetation indices (Daldegan et al., 2019) and land cover classification (Marques et al., 2020). Both of these approaches have limitations. Vegetation indices lack a physical interpretation that can be easily linked to forest structure on the ground. Land cover classifications are straightforward to interpret but may not be appropriate for habitats where forest structure changes gradually (Caughlin et al., 2016; Toniol et al., 2017). Active remote sensing technologies, including radar and lidar, may provide a solution by providing continuous measurements of forest structure that relate to animal habitat use (Davies & Asner, 2014; Palminteri et al., 2012). However, whether remotely-sensed metrics of habitat type correlate with animal habitat use at forest-savanna ecotone remains an open question (Deere et al., 2020).

In this study, we test how the distribution of woody aboveground biomass at the forest-savanna ecotone impacts occurrence and richness of animal communities. To assess how ongoing and predicted change in vegetation may impact animal communities, we leverage 54,357 camera trap photos along a forest-savanna boundary located in Southern Guyana. This savanna-forest boundary is of high conservation value as it encompasses an area that represents the mixing of species between the tropical forests of the Guiana Shield ecoregion and the grasslands of the Amazon Basin (Watkins et al., 2010; Jansen-Jacobs & ter Steege, 2000). We used woody aboveground biomass, as a proxy of habitat structural complexity, to couple with the camera trap detections of large and medium size vertebrates (Map 1). We then implemented hierarchical Bayesian models to assess the effects of vegetation characteristics on animal species presence and species richness. We hypothesize that:

(1) Remotely sensed woody biomass is related to ground-truthed habitat categories that describe heterogeneous patterns of tree cover
(2) Radar-derived woody aboveground biomass metrics are correlated with animal species detection
(3) Forest specialists are most sensitive to spatial differences in woody aboveground biomass across the ecotone
(4) Animal species richness is positively associated with woody aboveground biomass

METHODS

Study Area

The Rupununi region is located in southwestern Guyana and covers approximately 48,000 km^2 (Read et al., 2010). The region receives annual rainfall of 1,500- 2,000 mm with a main rainy season during May-August, that results in the flooding of a majority of the landscape and the mixing of waters between the Guiana Shield and the Amazonian river basins (Jansen-Jacobs & ter Steege, 2000; Mistry et al., 2008; Pos et al., 2016). The Rupununi is divided into a northern and southern range by the Kanuku Mountains and is an extension of the larger Rio Branco savannas of Brazil (Jansen-Jacobs & ter Steege, 2000; Montambault & Massa, 2002).

The dominant vegetation in the Rupununi savannas belong to the following grass genera: *Trachypogon, Paspalum, Axonopus and Andropogon* with dispersed trees primarily *Curatella americana, Byrsonima crassifolia, and B. verbascifolia* (Fanshawe, 1952; Jansen-Jacobs & ter Steege, 2000; Myers, 1936). These trees occur in clumps that vary in size within the grassland savannas as two distinct forest islands known as bush islands and gallery forests (Jansen-Jacobs & ter Steege, 2000). Bush islands stands have tree heights of up to 10 m, typically have thick corky bark, and broad leaves (Eiten, 1972; Jansen-Jacobs & ter Steege, 2000). In addition to these bush islands, gallery forests occur in standing water alongside rivers and creeks and lowland and montane forests closer to the Kanuku mountains (da Silva Meneses et al., 2013).

The Rupununi is considered a biodiversity hotspot due to the co-occurrence of Guiana Shield species (e.g. red bellied piranha) and Amazonian species (e.g. black caimans) that arise from the confluence of the Amazon river basin and Guiana shield watershed during the rainy season (de Souza et al., 2020). Documented species include 643 birds, 191 mammals, 103 reptiles and 67 amphibians (Watkins et al., 2010). Approximately 70 percent of mammals, 53 percent of birds, and 26 per cent of plant species recorded in Guyana are found in the Kanuku Mountains and the associated savannas (Montambault & Massa, 2002). In addition to its biodiversity, the region is also home to several Indigenous tribes, that include the Wapishana and Macushi peoples who have occupied these forests and savannas for millennia (Read et al., 2010).

Camera Trap Data

Camera trap data collection used best practices for animal detection, outlined in Karanth & Nichols (1998) and Silver (2004). Camera trap stations were set out based on previous studies for logging and hunting (Hallett et al., 2019). Sites included information for distance from trails, cattle, and hunting (Hallett et al., 2019). "Images were collected using Bushnell Trophy Cam #119447C, #119734C, #119736C, and #119837C; Bushnell®, KS, USA, spaced 2 - 3 km apart, 30 - 40 cm above ground, and without the use of lures or scents," (Hallett et al., 2019). Camera trap stations were defined by placement of a single camera trap in an area; camera trap sites were defined by a collection of camera trap stations in a defined area (Map 1). Date and time were recorded with each image, and only 1 camera was deployed per station. After deployment, the cameras were active 24 hours daily. Cameras were triggered by motion to take a burst of 3 images, with a 1 second delay between bursts, until the cameras were no longer triggered. Camera trap stations in our study ranged between 2013 and 2017, contained within 5 sites, and located on the edges of the Rupununi savanna and Iwokrama forest (Map 1). Stations in our dataset were included based on location along the forest-savanna ecotone (away from the interiors of savannas and forests).

From the 96 total species detected in the raw data refer to Appendix Table (Table A1), our subset included 56 total species focused on terrestrial vertebrates. All viable photos were included in our dataset based on the species we selected. We aggregated raw observations by present/absent per camera trap site and included them into our logistic model as the dependent variable (Table 1).

Once the camera trap photos were in digital form (Figure 1), we used cloud computing to streamline the process of labeling the images. We developed a web interface to tag images, reducing the amount of data entry to zero, and replaced it with an efficient point and click tagging system. This interface allowed multiple users to process photos simultaneously, increasing the efficiency of image labeling, and ultimately enabling labeling of animals across >50,000 individual photos.

Habitat Categories

Our camera trap sites were identified by habitat type during the set-up of camera trap sites (Table A2), (Hallett et al., 2019). Habitat types included: savanna, gallery, bush island, low-land, and montane. Savanna is dominated by grasses. Gallery habitats are patches of trees found near water or in standing water. Bush island habitats are clumps of trees that are dispersed within the savanna (away from water). Low-land habitats are tropical forests found in lower elevation (below 500 m). Montane habitat (or upland forests) is located in higher elevations (500-1500 m) (ter Steege, 2000). Each camera trap site may be classified as a mixture of habitat types, due to the nature of the boundary. To classify a site to one category will inevitably result in a loss of information, and not capture the complexity of each site. Instead, we sought to represent woody biomass variation as a continuous variable (Cushman, Gutzweiler, et al., 2010; Mcgarigal et al., 2009) across these habitats. In our study woody aboveground biomass is defined as aboveground biomass of trees, and the term is synonymous with tree cover and forest cover on the landscape scale.

Woody Aboveground Biomass

To represent heterogeneous patterns of tree cover across the landscape, we estimated the woody aboveground biomass (AGB) at each camera trap location. AGB includes the stem, bark, branches, and twigs of the woody components of vegetation (Zimbres et al., 2020). AGB data is derived from a globally available, 100 m resolution remotely sensed data product, Phased Array-type L-band Synthetic Aperture Radar (PALSAR) (Santoro & Cartus, 2021). Synthetic aperture radar (SAR) backscatter to is used to gather AGB data, that aligns with the majority of the camera trap field data collection (Santoro & Cartus, 2021). The ability to detect the nuances of tree cover in the landscape is possible through the 100 m resolution this product provides, which surpasses its predecessors with 1000 m resolution (Santoro & Cartus, 2021). Global raster layer datasets of biomass are available for the years 2010, 2017, and 2018 through the GlobBiomass platform (Santoro, 2018). Imagery from year 2018 was used in our study. For each camera trap location, we created a 100 m buffer polygon and summed the AGB within the polygon kilotons/hectare (kilotons (furthermore defined as kt). To evaluate how the AGB raster represented landscape features on the ground, we tested for correlations between AGB, and habitat type recorded for each camera trap station using linear regression (Figure 2). As we expect that point estimates of habitat type at a camera trap would never be perfectly correlated with landscape-level AGB, we focused on statistical significance as an indicator of relationships between AGB and habitat type.

Multi-Animal Species Logistic Model

Presence or absence of each animal species was determined at each camera trap site (Forrester et al., 2016; Shannon et al., 2014). Presence was determined if the animal was detected at least once during the duration of the camera trap survey. To understand the relationship between tree cover and the presence on animals, we analyzed data with a generalized linear mixed-effects model (GLMM) using a Bayesian approach. In this model, animal species was the binomial response variable, and AGB was the continuous independent variable. We used this type of model to test for differences in the effect on both the overall animal community (fixed effect) and animal species (random effect), depending on the tree cover continuous variable. By incorporating landscape and camera trap sites as varying intercepts (random effects) in the model, we considered spatial dependence based on camera trap regions. This model allowed us to infer if specific animal species were more likely to be detected in one gradient of tree cover over another. We represented animal species as a binomial response variable and included a random intercept and slope for species identity and random intercepts for both landscape and camera trap site identity.

Animal Species Richness Model

To model species richness, we counted the total number of species observed at each camera trap site. We then modeled species richness using a negative binomial GLMM, including biomass as a predictor variable and landscape as a random intercept.

GLMM analyses were conducted in R (R Core Team, 2020), using the Hamiltonian Monte Carlo algorithm in the stan_glmer function, part of the *rstanarm* package (Muth et al., 2018). For each of our two models, we ran four chains (2000 iterations) with a warm up of 1000 iterations. Weakly conservative priors were used, the default in this package. We assessed model convergence visually with the *shinystan* package as well as with the R-hat and neff criteria for convergence of HMC chains (Brooks & Gelman, 1997).

RESULTS

Camera Trap Data

This study garnered 12,052 hours (SD 108.190) of camera trap images all between 2013 and 2017 (one camera trap site was deployed in 2013, the rest between 2015-2017). Camera trap hours are underestimated due to a date malfunction at one camera trap site. There were 66 camera trap stations contained within five camera trap sites in this region, with the following number of camera traps at each site: Dadanawa (DAD)-(12), Rupununi (RUP)-(14), Saddle Mountain (SM)-(8), Shulinab (SH)-(18), and Yupukari (YUP)-(14). Across all trap sites, there were 96 animal species detected. Detections were defined by number of species (not individuals) accounted for in all images within the dataset.

Animal Presence

The camera trap station with the most animal detections, 26 species, was categorized as montane forest with a relatively high biomass of 0.458 kt/hectare (Table 1). Three camera trap stations with one species detected were categorized as savanna habitats with relatively low biomass (6.27E-05 to 0.196 kt/hectare) (Table 1). The camera trap station with the most animals present, was categorized as montane forest with a biomass of 0.458 kt/hectare. In stations where only one species was detected, biomass was relatively low (6.27E-05 kt/hectare to 0.021 kt/hectare) and both were categorized as savanna habitats (Table 1). See Table 1 for full list of animal detections, by habitat category and biomass. When animal presence was grouped by habitat category (Table 2), gallery forest habitat had the greatest number of animal species present (43) and savanna habitat had the least number of animal species present (20).

The animals detected at the most sites (naive occupancy) were red rumped agouti *(Dasyprocta leporina)* (37 sites), Ocelot *(Leopardus pardalis)* (33), Black Curassow *(Crax alector)* (32), Crab eating fox *(Cerdocyon thous)* (31), (Table A1). There were 11 sites where only one animal was detected, (Table A2) which included birds, reptiles and amphibians such as the red footed tortoise *(Chelonoidis carbonarius)* and undulated tinamou *(Crypturellus undulatus)*.

Habitat Categories and Woody Aboveground Biomass

During the installation of camera traps, habitat was categorized into land classifications (Hallett et al., 2019) (for full habitat category description (see Table A3)), which we used to compare to the AGB gradient (Table 1). AGB of zero suggests little to no forest tree cover, indicative of savanna landscape, while higher ranges of AGB are analogous to a closed canopy forest. The range of AGB from all sites was (0 kt/hectare) - (1.39 kt/hectare). A linear regression revealed significant correlations between habitat categories and AGB ($F_{4, 61}$ = 5.703, p-value = 0.0005754), Multiple R-squared = 0.272. Our linear model had an R^2 value of 27.2%, indicating that a large proportion of variability in AGB remained unexplained by habitat categories. Gallery forest habitat had the highest aboveground biomass and savanna had the least amount (Figure 2). We ran a grouping statistical analysis in R (package *agricolae*), which illustrates that there are two distinct groups and overlap from the third group (Figure 3). Altogether, these results indicate that aboveground biomass reflects on-the-ground differences in tree cover across the forest-savanna ecotone, but that amount of AGB varies considerably within habitat categories.

Multi-Animal Species Logistic Model

Our Bayesian GLMM revealed that increasing AGB significantly increased the probability of camera trap detection. For an average animal species in an average site, an increase from the minimum to the maximum value of AGB observed in the data resulted in a median increase in probability of presence of 15.05% (95% CI: 5.06 to 31.53%). This community-level parameter represents the effect of biomass across all animal species and was highly certain, including a >99.99% probability that biomass increased the probability of species presence (Figure 4). Refer to appendix figure (Figure B. 1), for effects of all species in entire dataset.

Species-specific results suggest that nearly all species responded positively to aboveground biomass. Out of 56 species, only two (crab-eating fox and domestic cows) showed a median decline in probability of presence in an average site with maximum biomass compared to minimum biomass (Figure 5). While these two animal species were the only species with a significantly different response to biomass from the average species, there were 21 total species with a higher than 50% probability of being different from the average response. Slightly more than half of these species, 12 out of 21, exhibited a positive response to biomass. The two species with the strongest positive response to biomass were lowland paca and ocelot (Figure 1). When comparing an average site with minimum biomass to the same site with maximum biomass, the probability of detecting lowland paca was predicted to increase by 66.94% (95% CI: 38.53 to 84.12%), while the probability of detecting ocelots was predicted to increase by 57.62% (95% CI: 24.23 to 79.00%). Altogether, our GLMMs suggest that the majority of species respond similarly to lowland paca and ocelots, with a positive probability of detection within increasing biomass.

Animal Species Richness Model

Biomass had a strong positive impact on species richness (Figure 6). Our negative binomial GLMM predicted that, for an average landscape, an increase from minimum to maximum AGB would increase species richness by a median of 9.71 species (CI: 2.47 to 20.66 species). For every kiloton of aboveground biomass, the GLMM predicted a median proportional increase in species richness of 90.0% (CI: 21.57 to 200.0%). Our model indicated high certainty that the effect of biomass was positive, including a 99.68% probability that biomass increased species richness.

DISCUSSION

We combined animal detections from camera trap photos and remotely sensed data derived from radar to relate AGB to animal species composition across an Amazonian ecotone. Our site is representative of the forest-savanna ecotone across the Amazon, where climate change and deforestation are resulting in declining AGB and an increase in the extent of grassland habitat (Feeley et al., 2020; Hirota et al., 2010). We hypothesized that our data would reveal two distinct groups of terrestrial vertebrates, forest specialists, with increased detection in sites with high AGB, and savanna specialists, with increased detection in sites with lower AGB (Sales et al. 2020). However, our results did not support this hypothesis. Instead, AGB had a positive correlation with species detection across nearly all species in our dataset. Consequently, species richness was significantly related to AGB, with higher species richness in sites with higher AGB. Our results suggest that terrestrial vertebrates in the forest-savanna boundary preferentially use habitats with tree cover. Dichotomous characterization of species and sites as either forest or savanna likely overlooks heterogeneous patches of tree cover that animal species rely on for habitat.

We found surprisingly little variability in species response to AGB, relative to previous studies that suggest a high degree in specialization between terrestrial vertebrate species (Sales et al. 2020). Of the fifty-six species in our dataset (Figure B1), only four species had a significantly different response to AGB, relative to the average species (Figure 4). The lack of habitat specialization could be related to methodological limitations, including low number of individual detections. Another likely reason for the near-universal relationship between species detection and AGB is that our AGB metric captured continuous variation in habitat cover, including heterogeneous patterns of non-forest tree cover essential for animal. Non-forest tree cover includes a variety of habitats from gallery forest to bush islands (Figure 2). Altogether, we predict that a decrease in trees at the forest-savanna ecotone, particularly bush islands and gallery forests, would have a negative impact on the animal community.

Our community-level models support previous species-level patterns of occupancy from the same region (Hallett et al., 2019). For example, we found that lowland paca, a rodent species that is an important food source for Indigenous people, had one of the strongest positive relationships to AGB, in concurrence with previous studies that have reported this species in sites with closed canopies (Bizri et al., 2016; El Bizri et al., 2018). We also found that crab-eating foxes were the only native species associated with low AGB sites, in agreement with previous literature on this species (Chirat et al., 2014; Hallett et al., 2019). However, there were also species in our dataset that did not show results similar to previous studies that have classified species as forest vs. savanna specialists. A prime example is ocelots, a key mesopredator in neotropical forests. While we found that ocelot presence was strongly related to AGB, a previous study from the same site indicated that ocelots were not strongly predicted by tree cover (Hallett et al., 2019). Our use of a continuous metric of tree cover, AGB, rather than discrete forest/savanna categories may explain this discrepancy, as ocelots rely on tree cover for shelter even as they hunt and move in grassland sites.

Our results point to the utility of active sensors for detecting continuous variation in habitat structure, with relevance for animal. We found that radar-derived aboveground biomass was significantly related to tree cover types categorized on the ground (Figure 2). However, within a 100 m radius of camera traps, there was wide variation in AGB within each habitat category (Figure 3), revealing landscape heterogeneity. We agree with previous studies that have argued for using biomass information from remotely sensed data as a more accurate metric for tree cover than land cover classification maps (Abbas et al., 2020; Timothy et al., 2016, Hashemi-Beni et al., 2021). These previous studies have argued for the utility of remotely sensed AGB measurements for carbon stock assessments, with relevance for country-level carbon budgets to combat climate change. Our current work demonstrates that radar-derived AGB is also predictive of animal biodiversity in changing landscapes.

The dependence of animal species richness on AGB in our study emphasizes the need to understand threats to tree cover in Amazonian forest-savanna ecotones. Fire is a primary threat to AGB across the Amazon. Although rainforest trees can withstand weak fires, strong fires have the ability to damage these trees to no return (Bond & Parr, 2010). The bush islands that occur in the savannas have high risk of perishing if the intensity of fire consumes the root (Bond & Parr, 2010; Sletto, 2011). If wildfires are not managed, the trees that benefit animal will disappear. For example, in Guyana such fires destroyed large acres in the same area twice in one year (Armenteras et al., 2021; INEWS, 2019; “Major Impact on Wildlife Feared after Huge Rupununi Wildfire,” 2019). Although a portion of fires are started due to natural causes, most are started by humans for hunting and agriculture. Realizing that fires are an integral system to the culture and landscape, finding ways to ensure that fires remain controlled allows people to continue using fires as a tool without endangering nearby the animals and trees. Continuing to study how fire affects the boundary, understanding the compositional nature of the boundary, and being aware of litter fuel loads (Balch et al., 2008), will help the scientific community, and land managers understand the dynamics at boundaries so we may better hone how to handle fire with care.

We argue that a landscape-scale approach with functional metrics of habitat types to conservation will be necessary to maintain the forest-savanna ecotone and dependent species. In contrast to focusing on conservation of a single species (e.g. jaguars or other large carnivores), broad strokes conservation will ensure survival of the ecosystem (Cushman, McKelvey, et al., 2010; Schwenk & Donovan, 2011; Wiens et al., 2008). Large scale efforts can enhance projects that focus on one animal or a species (Schwenk & Donovan, 2011). There are many studies that focus on one animal or a select few species for example (Costa & Zalmon, 2021; Flora et al., 2020; Pérez-Espona, 2021; Smith et al., 2021). Animals that overlap with their focal species may benefit but not for the many other animals that might utilize portions of habitat (Lambeck, 1997). If the animal has a large roaming range and utilizes large swaths of habitat, this umbrella or surrogate model of landscape conservation may be applied (Burdett et al., 2011; Thornton et al., 2016). In Guyana, conserving the trees at the forest-savanna boundary will positively impact many animals in the region, since they rely on the trees during hot dry periods (Lacher & Alho, 2001).

As Guyana gains more visibility from the oil and mining industry, the Rupununi savanna region is not exempt (Hilson & Laing, 2017), it is imperative to enact protective measures to the landscape before destruction goes unchecked. Measures such as wilderness preserves are in place (*Protected Areas*, 2021), but unique hotspots such as the forest-savanna boundaries are only partially protected by way of the Kanuku Mountains Protected area. It is important to have a diversity of habitat (i.e., forests, savannas, and ecotones) included as protected areas, as transitional areas lend themselves to movement across landscape (Vellend, 2010; Smith et al., 1997). In Guyana, the forest-savanna boundary is being threatened by drought, wildfire, and land use. If animal species are not conserved after habitat loss, a decline in animal populations may have feedbacks as tropical trees rely upon animals for seed dispersal and ultimately population abundance (Maciel et al., 2021).

There are several potential additions to the current model that could further our understanding of conservation at the savanna-forest boundaries. Increasing variation of the aboveground biomass by including closed-canopy forest sites will allow us to conclude habitat use better. In this study, forest specialists were categorized in the context of an ecotone, so these landscapes were on the edges of the region. Comparing sites that are in the interior parts of the forest would validate the habitat use of animal species. Including temporal dynamics would enable us to account for the seasonality and breeding behaviors of animal species, which could help explain variability in species presence. Including other landscape variables that impact animal detections like distance to water source, or human presence such as logging or trails, and presence of fruiting trees could explain correlation between woody AGB and animals.

Additional field work to measure the percentage and type of tree species in the region would be a useful complement to our data on animal species composition. A study done in Pakistan (Rajpar et al., 2020) and another in Ghana (Attua & Pabi, 2013) highlighted the diversity of tree species composition (Attua & Pabi, 2013; Rajpar et al., 2020), the increased tree diversity at the edge between forest and agricultural field (Rajpar et al., 2020); and at the forest-savanna ecotone (Attua & Pabi, 2013) and the importance of the diversity of trees for animals (Rajpar et al., 2020). Since animals such as the agouti, tayra, tapir and lowland paca (Camargo-Sanabria & Mendoza, 2016; Galetti et al., 2001) are found feeding on fruiting trees, characterizing the trees as fruiting vs non-fruiting would aid in understanding the causal relationship between animals and trees at the boundary. Investigating an effect between fruiting trees and non-fruiting trees would allow us to infer the functional role of the trees on animal. The positive effect between trees and animal could be due to feeding of fruiting trees or perhaps used as temporary shelter during extreme heat or cover from predators. Quantifying plant-animal interactions will be crucial to improve forecasts of biodiversity in ecotones.

CONCLUSION

Our research highlights the importance of continuous variation in AGB for animal species along an Amazonian forest-savanna boundary. We applied data on AGB derived from satellite-borne radar to predict animal species composition. As these data are globally available, multi-temporal, and free to access, we anticipate that our approach is broadly transferable to regions around the globe. While accounting for continuous variation in AGB improved our statistical modeling approach, we anticipate that recognizing the importance of fine-scale habitat features along the ecotone will also be crucial for landscape conservation efforts.

Tables

Table 1. Habitat categories and statistics of woody aboveground biomass (kilotons/hectare)

Habitat	Number of camera traps	Mean biomass (kilotons/hectare)	SD Biomass
Gallery	26	0.664	0.411
Montane	5	0.539	0.322
Lowland	6	0.411	0.374
Bush Island	16	0.345	0.351
Savanna	13	0.120065762	0.177408

Table 2. Habitat categories and number of animal species detected.

Habitat	Number of species
Gallery	43
Montane	34
Lowland	28
Bush Island	38
Savanna	20

Figures

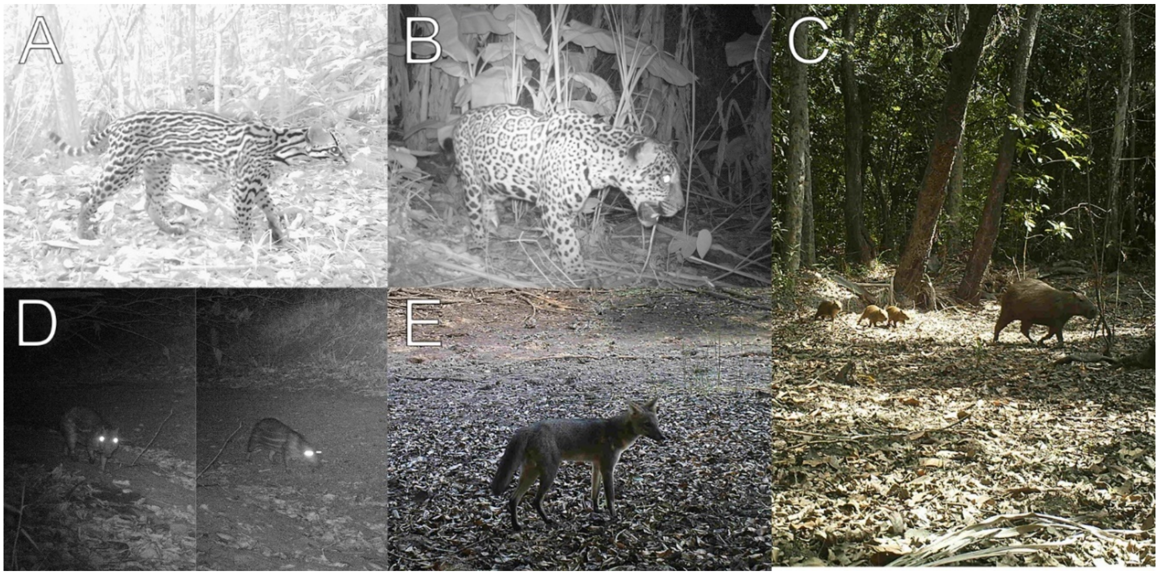


Figure 1. Representative camera trap images from our dataset.

(A) Ocelot *(Leopardus pardalis),* (B) Jaguar *(Panthera onca),* (C) Capybara and pups *(Hydrochoerus hydrochaeris),* (D) Lowland paca *(Cuniculus paca),* (E) Crab-eating fox *(Cerdocyon thous)*

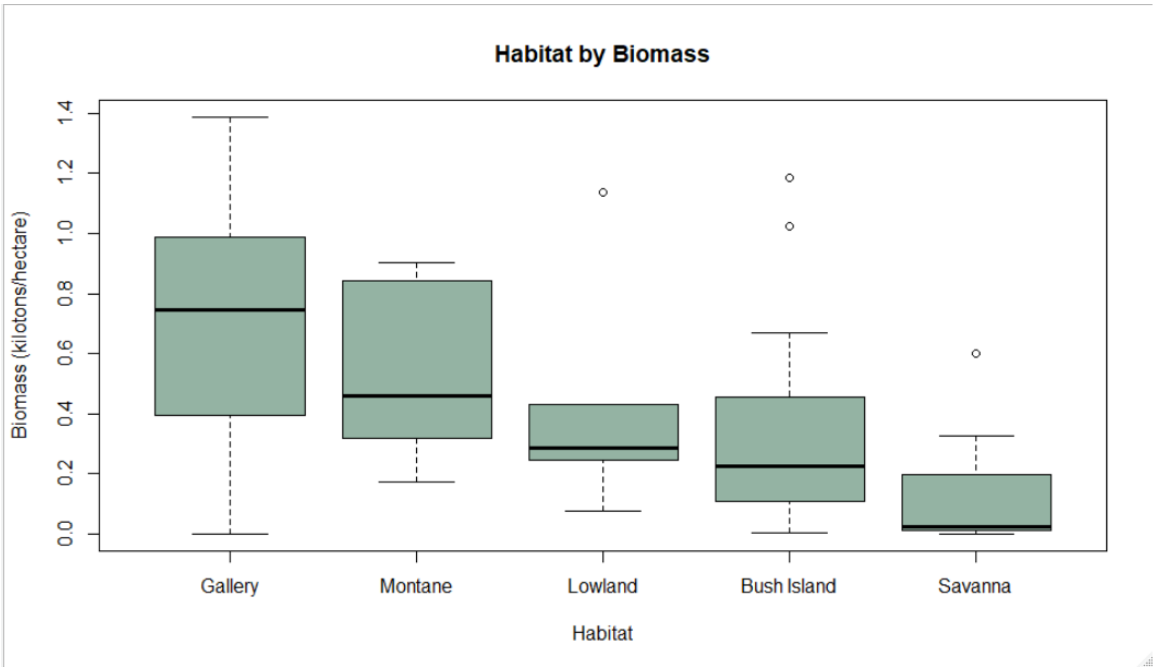


Figure 2. Boxplot of woody aboveground biomass by habitat category

Boxplot of woody aboveground biomass (AGB) (kilotons/hectare) by habitat category. Thick black bar represents the median, while upper and lower boundaries of boxes indicate first and third quartiles. The whiskers represent observations within 1.5 times the upper and lower quartiles, while dots represent outliers outside of the maximum range.

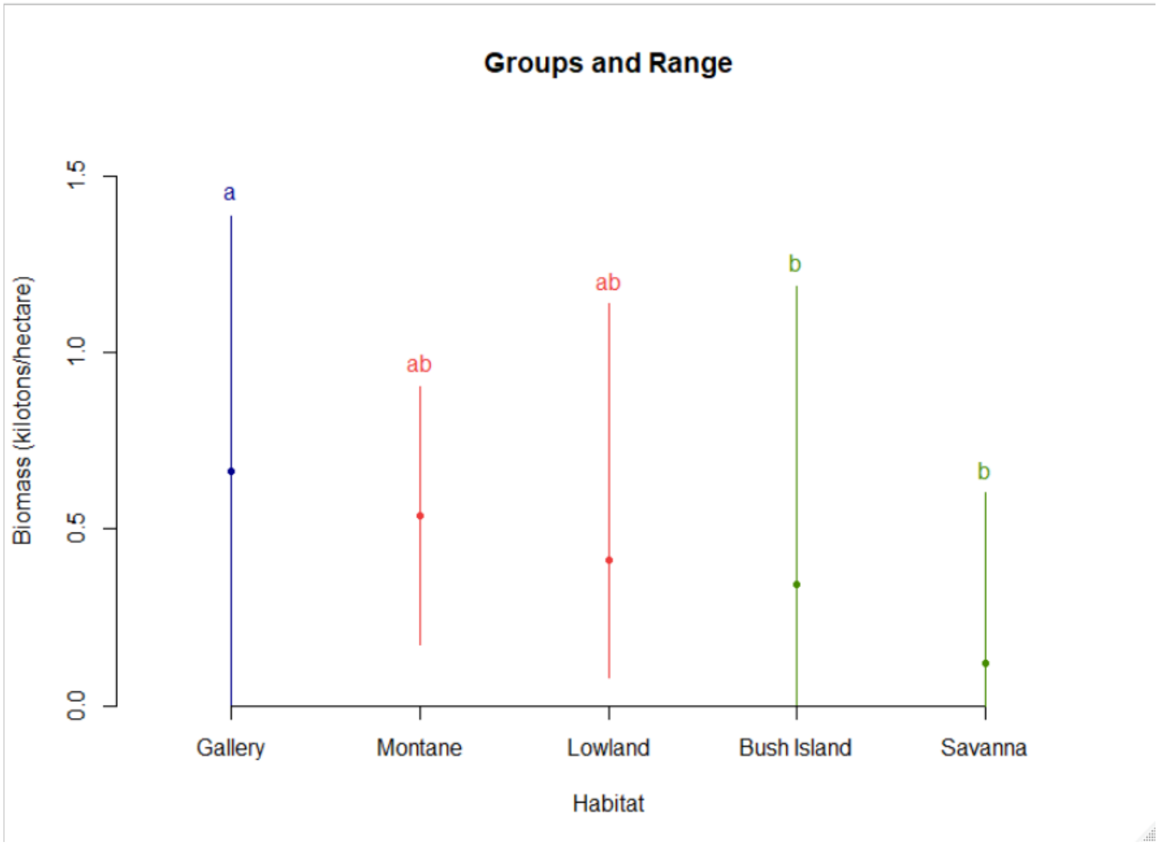


Figure 3. Groups of habitat and range of woody aboveground biomass

Groups of habitat and range of woody aboveground biomass (AGB) plot. Five habitat types with two statistically distinct groups indicated by letters above each line, and one group Montane and Lowland that overlap with the two distinct groups indicated by the overlap in letters (ab). Solid dot represents median of the range of biomass for each habitat type.

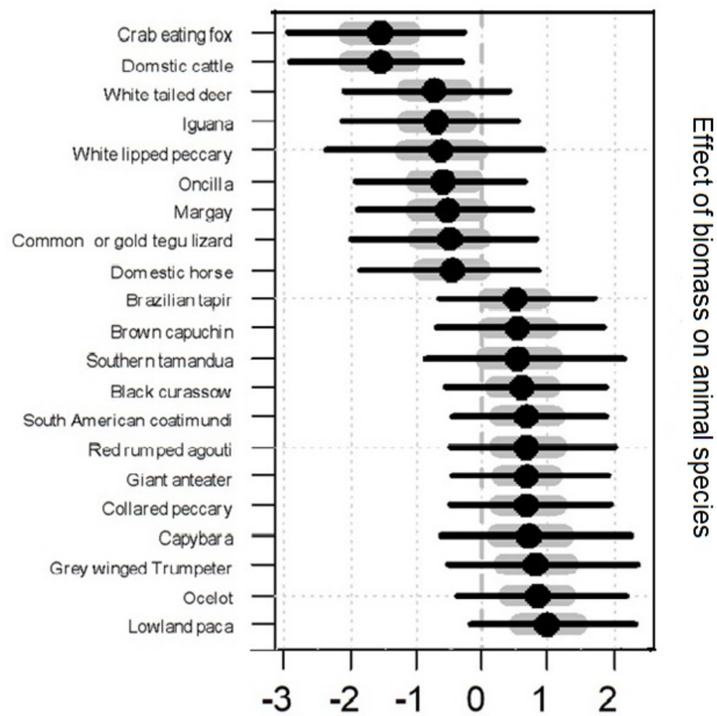


Figure 4. Animal species-level effects of woody aboveground biomass

Animal species-level effects of woody aboveground biomass (AGB). Effect size represents posterior draws from the random slope parameter of the Generalized Linear Mixed Model (GLMM). The thicker horizontal line at zero represents the average across all species. Points below the horizontal line indicate animal species with a more negative relationship to AGB than the average, while points above the horizontal line indicate species with a more positive relationship to AGB than the average species. Black dots represent the median for each species, gray shaded regions are the 50% credible interval (CI), and the black lines are the 95% CI. The height of CI lines indicates relative uncertainty in whether a species was different from the average species. In this figure, only the subset of species with 50% CI that did not overlap zero were included.

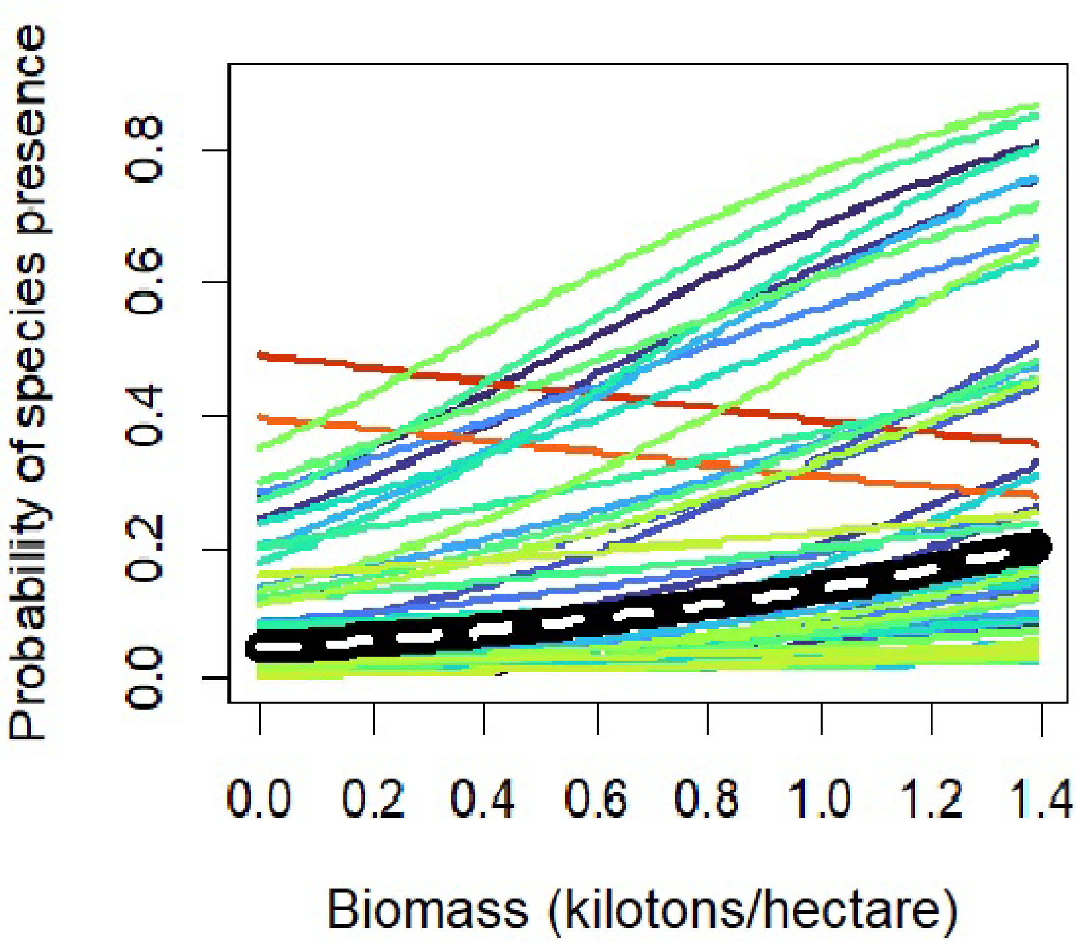


Figure 5. Animal community-level effects of woody aboveground biomass

Woody aboveground biomass (AGB) relative to the detection of animal species. Each line indicates the probability of detection for a particular species of animal at an average camera trap site. The thick black and white dashed line represents predictions for an average species. The two red lines represent the only species with a median negative relationship between AGB and species detection (crab-eating fox and domestic cattle).

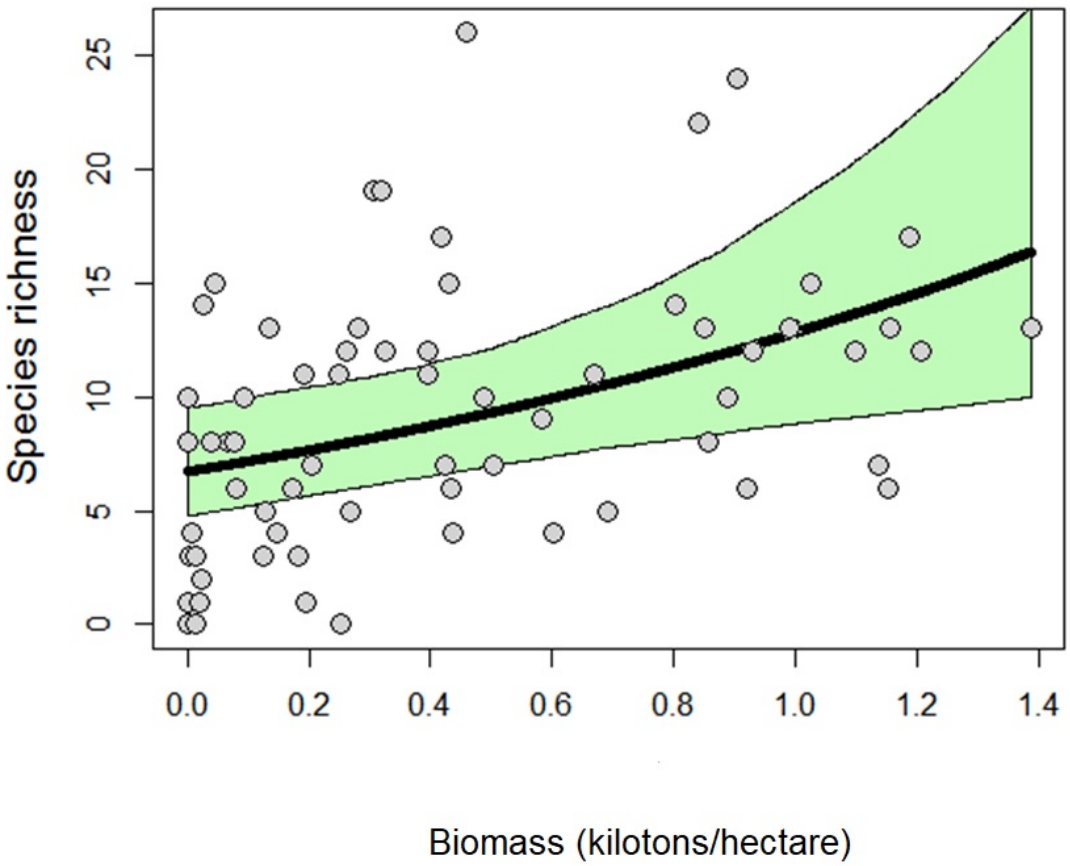
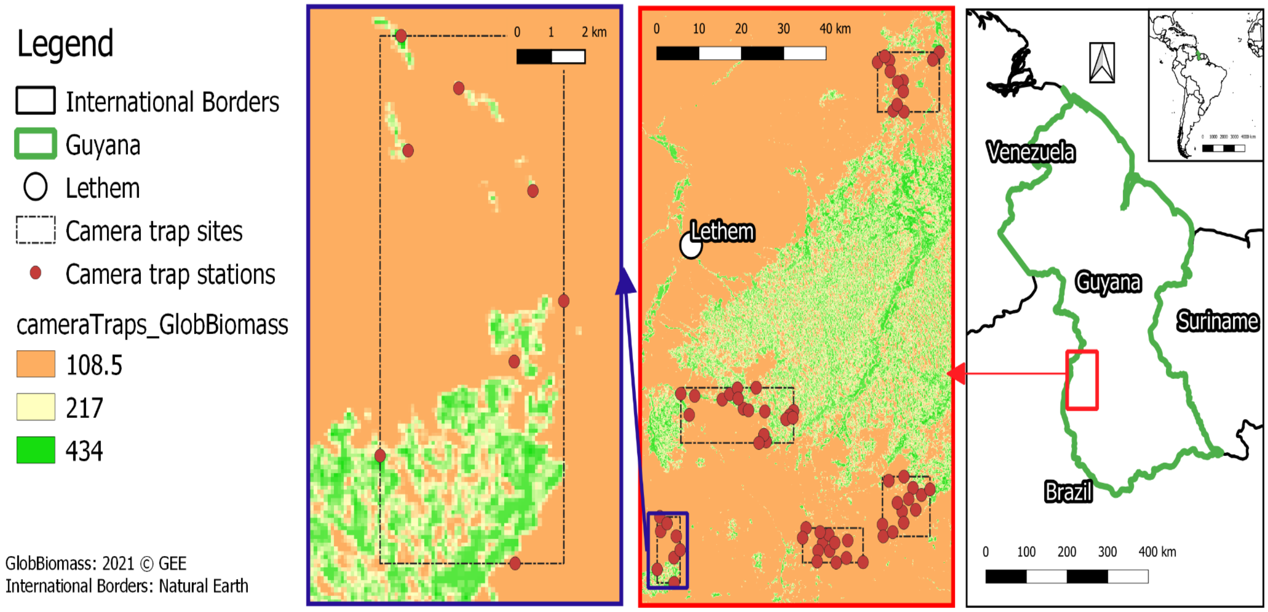


Figure 6. Effect of woody aboveground biomass on species richness

Effect of woody aboveground biomass (AGB) on species richness of the ecotone. This figure shows the relationship between species richness and biomass. Dots represent data for each camera trap station. The black line represents the median predicted effect of AGB on species richness from a generalized linear mixed model (GLMM), and the green shaded region indicates the 95% prediction interval from the GLMM.

Maps



Map 1. Map of study area

Map inlets (right to left). Right-Map of Guyana with insert of Guyana within S. America and study region (indicated by red square). Middle-Map of study region which includes the five camera trap study sites (indicated by dashed lined boxes) within the forest-savanna ecotone region. Right-Map of a single camera trap site (indicated by (indicated by dashed lined boxes) and camera trap stations (indicated by red circles). Green indicates high ranges of woody aboveground biomass (AGB), and orange indicates low ranges of AGB.

REFERENCES

Abbas, S., Wong, M. S., Wu, J., Shahzad, N., & Irteza, S. M. (2020). Approaches of Satellite Remote Sensing for the Assessment of Above-Ground Biomass across Tropical Forests: Pan-tropical to National Scales. *Remote Sensing*, *12*(20), 3351. http://dx.doi.org.libproxy.boisestate.edu/10.3390/rs12203351

Armenteras, D., Dávalos, L. M., Barreto, J. S., Miranda, A., Hernández-Moreno, A., Zamorano-Elgueta, C., González-Delgado, T. M., Meza-Elizalde, M. C., & Retana, J. (2021). Fire-induced loss of the world's most biodiverse forests in Latin America. *Science Advances*, *7*(33), eabd3357. https://doi.org/10.1126/sciadv.abd3357

Attua, E. M., & Pabi, O. (2013). Tree species composition, richness and diversity in the northern forest-savanna ecotone of Ghana. *Journal of Applied Biosciences*, *69*, 5437–5448. https://doi.org/10.4314/jab.v69i0.95069

Balch, J. K., Nepstad, D. C., Brando, P. M., Curran, L. M., PorTELa, O., De CARVALHO JR, O., & Lefebvre, P. (2008). Negative fire feedback in a transitional forest of southeastern Amazonia. *Global Change Biology*, *14*(10), 2276–2287. https://doi.org/10.1111/j.1365-2486.2008.01655.x

Bizri, H. R. E., Araújo, L. W. da S., Araújo, W. da S., Maranhão, L., & Valsecchi, J. (2016). Turning the game around for conservation: Using traditional hunting knowledge to improve the capture efficiency of Amazon lowland pacas. *Wildlife Biology*, *22*(1), 1–6. https://doi.org/10.2981/wlb.00127

Bond, W., & Parr, C. (2010). Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biological Conservation - BIOL CONSERV*, *143*, 2395–2404. https://doi.org/10.1016/j.biocon.2009.12.012

Brooks, S. P., & Gelman, A. (1997). *General Methods for Monitoring Convergence of Iterative Simulations*. 22.

Burdett, C., Theobald, D., Rondinini, C., Di Marco, M., Boitani, L., & K, C. (2011). The Puma as an Umbrella Species for Conserving Western Hemisphere Carnivores. In J. Williams, H. Robinson, & L. Sweanor (Eds.), *Proceedings of the 10th Mountain Lion Workshop* (pp. 112–121). Montana Fish, Wildlife & Parks. https://fwp.mt.gov/binaries/content/assets/fwp/conservation/wildlife-reports/mountain-lion/final-proceedings-ml-workshop-program-8-3-11-smaller.pdf

Cáceres, N. C., Bornschein, M. R., Lopes, W. H., & Percequillo, A. R. (2007). Mammals of the Bodoquena Mountains, southwestern Brazil: An ecological and conservation analysis. *Revista Brasileira de Zoologia*, *24*(2), 426–435. https://doi.org/10.1590/S0101-81752007000200021

Camargo-Sanabria, A. A., & Mendoza, E. (2016). Interactions between terrestrial mammals and the fruits of two neotropical rainforest tree species. *Acta Oecologica*, *73*, 45–52. https://doi.org/10.1016/j.actao.2016.02.005

Cardoso, A. W., Oliveras, I., Abernethy, K. A., Jeffery, K. J., Glover, S., Lehmann, D., Ndong, J. E., White, L. J. T., Bond, W. J., & Malhi, Y. (2021). A distinct ecotonal tree community exists at central African forest–savanna transitions. *Journal of Ecology*, *109*(3), 1170–1183. https://doi.org/10.1111/1365-2745.13549.

Caughlin, T. T., Rifai, S. W., Graves, S. J., Asner, G. P., & Bohlman, S. A. (2016). Integrating LiDAR-derived tree height and Landsat satellite reflectance to estimate forest regrowth in a tropical agricultural landscape. *Remote Sensing in Ecology and Conservation*, *2*(4), 190–203. https://doi.org/10.1002/rse2.33

Chirat, G., Groot, J. C. J., Messad, S., Bocquier, F., & Ickowicz, A. (2014). Instantaneous intake rate of free-grazing cattle as affected by herbage characteristics in heterogeneous tropical agro-pastoral landscapes. *Applied Animal Behaviour Science*, *157*, 48–60. https://doi.org/10.1016/j.applanim.2014.06.003

Coe, M. T., Marthews, T. R., Costa, M. H., Galbraith, D. R., Greenglass, N. L., Imbuzeiro, H. M. A., Levine, N. M., Malhi, Y., Moorcroft, P. R., Muza, M. N., Powell, T. L., Saleska, S. R., Solorzano, L. A., & Wang, J. (2013). Deforestation and climate feedbacks threaten the ecological integrity of south–southeastern Amazonia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1619), 20120155. https://doi.org/10.1098/rstb.2012.0155

Costa, L. L., & Zalmon, I. R. (2021). Macroinvertebrates as umbrella species on sandy beaches. *Biological Conservation*, *253*, 108922. https://doi.org/10.1016/j.biocon.2020.108922

Cushman, S. A., Gutzweiler, K., Evans, J. S., & McGarigal, K. (2010). The Gradient Paradigm: A Conceptual and Analytical Framework for Landscape Ecology. In S. A. Cushman & F. Huettmann (Eds.), *Spatial Complexity, Informatics, and Wildlife Conservation* (pp. 83–108). Springer Japan. https://doi.org/10.1007/978-4-431-87771-4_5

Cushman, S. A., McKELVEY, K. S., Noon, B. R., & McGARIGAL, K. (2010). Use of Abundance of One Species as a Surrogate for Abundance of Others. *Conservation Biology*, *24*(3), 830–840. https://doi.org/10.1111/j.1523-1739.2009.01396.x

da Silva Meneses, M. E. N., da Costa, M. L., & Behling, H. (2013). Late Holocene vegetation and fire dynamics from a savanna-forest ecotone in Roraima state, northern Brazilian Amazon. *Journal of South American Earth Sciences*, *42*, 17–26. https://doi.org/10.1016/j.jsames.2012.10.007

Daldegan, G., Roberts, D., & Ribeiro, F. (2019). Spectral mixture analysis in Google Earth Engine to model and delineate fire scars over a large extent and a long time-series in a rainforest-savanna transition zone. *Remote Sensing of Environment*, *232*. https://doi.org/10.1016/j.rse.2019.111340

Davies, A. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology & Evolution*, *29*(12), 681–691. https://doi.org/10.1016/j.tree.2014.10.005

de Souza, L. S., Armbruster, J. W., & Willink, P. W. (2020). Connectivity of Neotropical River Basins in the Central Guiana Shield Based on Fish Distributions. *Frontiers in Forests and Global Change*, *3*, 8. https://doi.org/10.3389/ffgc.2020.00008

Deere, N. J., Guillera-Arroita, G., Swinfield, T., Milodowski, D. T., Coomes, D. A., Bernard, H., Reynolds, G., Davies, Z. G., & Struebig, M. J. (2020). Maximizing the value of forest restoration for tropical mammals by detecting three-dimensional habitat associations. *Proceedings of the National Academy of Sciences*, 202001823. https://doi.org/10.1073/pnas.2001823117

Eiten, G. (1972). The Cerrado Vegetation of Brazil. *Botanical Review*, *38*(2), 201–341.

El Bizri, H. R., Fa, J. E., Bowler, M., Valsecchi, J., Bodmer, R., & Mayor, P. (2018). Breeding seasonality in the lowland paca (Cuniculus paca) in Amazonia: Interactions with rainfall, fruiting, and sustainable hunting. *Journal of Mammalogy*, *99*(5), 1101–1111. https://doi.org/10.1093/jmammal/gyy102

Erds, L., Tölgyesi, C., Bátori, Z., Semenishchenkov, Y. A., & Magnes, M. (2017). The influence of forest/grassland proportion on the species composition, diversity and natural values of an eastern Austrian forest-steppe. *Russian Journal of Ecology*, *48*(4), 350–357. http://dx.doi.org.libproxy.boisestate.edu/10.1134/S1067413617040063

Fanshawe, D. (1952). The vegetation of Guyana. A preliminary review. *Oxford*, 96.

Feeley, K. (2005). The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake. *Journal of Tropical Ecology*, *21*, 99–102. https://doi.org/10.1017/S0266467404001701

Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M., & Zuleta, D. (2020). Climate-driven changes in the composition of New World plant communities. *Nature Climate Change*, *10*(10), 965–970. https://doi.org/10.1038/s41558-020-0873-2

Flora, P., Gérard, C., Laura, M., Claude, M., Bokika, N. J.-C., Laurent, R., Victor, N., & Link to external site, this link will open in a new window. (2020). Spatiotemporal Variation in Bonobo (Pan paniscus) Habitat Use in a Forest–Savanna Mosaic. *International Journal of Primatology*, *41*(6), 775–799. http://dx.doi.org.libproxy.boisestate.edu/10.1007/s10764-020-00180-5

Flores, B. M., & Holmgren, M. (2021). White-Sand Savannas Expand at the Core of the Amazon After Forest Wildfires. *Ecosystems*. https://doi.org/10.1007/s10021-021-00607-x

Forrester, T., O'Brien, T., Fegraus, E., Jansen, P. A., Palmer, J., Kays, R., Ahumada, J., Stern, B., & McShea, W. (2016). An Open Standard for Camera Trap Data. *Biodiversity Data Journal*, *4*. https://doi.org/10.3897/BDJ.4.e10197

Galetti, M., Keuroghlian, A., Hanada, L., & Morato, M. I. (2001). Frugivory and Seed Dispersal by the Lowland Tapir (Tapirus terrestris) in Southeast Brazil1. *BIOTROPICA*, *33*(4), 723–726. https://doi.org/10.1646/0006-3606(2001)033[0723:FASDBT]2.0.CO;2

Hallett, M. T., Kinahan, A. A., McGregor, R., Baggallay, T., Babb, T., Barnabus, H., Wilson, A., Li, F. M., Boone, W. W., & Bankovich, B. A. (2019). Impact of Low-Intensity Hunting on Game Species in and Around the Kanuku Mountains Protected Area, Guyana. *Frontiers in Ecology and Evolution*, *7*. https://doi.org/10.3389/fevo.2019.00412

Hashemi-Beni, L., Link to external site, this link will open in a new window, Kurkalova, L. A., Link to external site, this link will open in a new window, Mulrooney, T. J., & Azubike, C. S. (2021). Combining Multiple Geospatial Data for Estimating Aboveground Biomass in North Carolina Forests. *Remote Sensing*, *13*(14), 2731. http://dx.doi.org.libproxy.boisestate.edu/10.3390/rs13142731

Hilson, G., & Laing, T. (2017). Guyana Gold: A Unique Resource Curse? *The Journal of Development Studies*, *53*(2), 229–248. https://doi.org/10.1080/00220388.2016.1160066

Hirota, M., Nobre, C., Oyama, M. D., & Bustamante, M. M. (2010). The climatic sensitivity of the forest, savanna and forest–savanna transition in tropical South America. *New Phytologist*, *187*(3), 707–719. https://doi.org/10.1111/j.1469-8137.2010.03352.x

INEWS. (2019, September 3). Another fire erupts at Waikin Ranch in Region 9. *INews Guyana*. https://www.inewsguyana.com/another-fire-erupts-at-waikin-ranch-in-region-9/

Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A., & Chamberlain, D. (2018). The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. *Journal of Ornithology*, *159*(3), 747–759. https://doi.org/10.1007/s10336-018-1549-9

Jansen-Jacobs, M., & ter Steege, H. (2000). Southwest Guyana: A complex mosaic of savannahs and forests. In *Plant Diversity in Guyana* (pp. 147–157).

Karanth, K. U., & Nichols, J. D. (1998). Estimation of Tiger Densities in India Using Photographic Captures and Recaptures. *Ecology*, *79*(8), 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kark, S. (2017). Effects of Ecotones on Biodiversity. In *Encyclopedia of Biodiversity* (pp. 1–10). https://doi.org/10.1016/B978-012226865-6/00573-0

Kent, M., Gill, W. J., Weaver, R. E., & Armitage, R. P. (1997). Landscape and plant community boundaries in biogeography. *Progress in Physical Geography: Earth and Environment*, *21*(3), 315–353. https://doi.org/10.1177/030913339702100301

Lacher, T. E., & Alho, C. J. R. (2001). Terrestrial Small Mammal Richness and Habitat Associations in an Amazon Forest-Cerrado Contact Zone. *Biotropica*, *33*(1), 171–181.

Lambeck, R. J. (1997). Focal Species: A Multi-Species Umbrella for Nature Conservation. *Conservation Biology*, *11*(4), 849–856. https://doi.org/10.1046/j.1523-1739.1997.96319.x

Laurance, W. F., & Williamson, G. B. (2001). Positive Feedbacks among Forest Fragmentation, Drought, and Climate Change in the Amazon. *Conservation Biology*, *15*(6), 1529–1535. https://doi.org/10.1046/j.1523-1739.2001.01093.x

Maciel, E. A., Martins, V. F., de Paula, M. D., Huth, A., Guilherme, F. A. G., Fischer, R., Giles, A., Barbosa, R. I., Cavassan, O., & Martins, F. R. (2021). Defaunation and changes in climate and fire frequency have synergistic effects on aboveground biomass loss in the brazilian savanna. *Ecological Modelling*, *454*, 109628. https://doi.org/10.1016/j.ecolmodel.2021.109628

Major impact on wildlife feared after huge Rupununi wildfire. (2019, April 29). *Stabroek News*. https://www.stabroeknews.com/2019/04/29/news/guyana/major-impact-on-wildlife-feared-after-huge-rupununi-wildfire/

Marques, E. Q., Hur, M.-J. B., Marimon, B. S., T, M. E. A., Mews, H. A., & Colli, G. R. (2020). Redefining the Cerrado–Amazonia transition: Implications for conservation. *Biodiversity & Conservation*, *29*(5), 1501–1517. http://dx.doi.org.libproxy.boisestate.edu/10.1007/s10531-019-01720-z

Mcgarigal, K., Sermin, Æ., Samuel, T. Æ., & Cushman, A. (2009). Surface metrics: An alternative to patch metrics for the quantification of landscape structure. *Landscape Ecology*, *24*, 433–450.

Mistry, J., Berardi, A., & Simpson, M. (2008). Birds as indicators of wetland status and change in the North Rupununi, Guyana. *Biodiversity and Conservation*, *17*(10), 2383. https://doi.org/10.1007/s10531-008-9388-2

Montambault, J. R., & Massa, O. (Eds.). (2002). A Biodiversity Assessment Of The Eastern Kanuku Mountains Lower Kwitaro River, Guyana. In *Rapid Assessment Program Bulletin of Biological Assessment, 26* (pp. 1–86). Conservation International. https://pdf.usaid.gov/pdf_docs/PNADB868.pdf

Muth, C., Oravecz, Z., & Gabry, J. (2018). User-friendly Bayesian regression modeling: A tutorial with rstanarm and shinystan. *The Quantitative Methods for Psychology*, *14*(2), 99–119. https://doi.org/10.20982/tqmp.14.2.p099

Myers, J. G. (1936). *Savannah and Forest Vegetation of the Interior Guiana Plateau*. https://doi.org/10.2307/2256273

Odum, E. P. (1953). *Fundamentals of Ecology (1953)*. Yale University Press. https://doi.org/10.12987/9780300188479-022

Palminteri, S., Powell, G. V. N., Asner, G. P., & Peres, C. A. (2012). LiDAR measurements of canopy structure predict spatial distribution of a tropical mature forest primate. *Remote Sensing of Environment*, *127*, 98–105. https://doi.org/10.1016/j.rse.2012.08.014

Pérez-Espona, S. (2021). Eciton Army Ants—Umbrella Species for Conservation in Neotropical Forests. *Diversity*, *13*(3), 136. https://doi.org/10.3390/d13030136

Pos, E., Johnson, I., Narine, Z., Johnny, F., Isaacs, A., & Raymond, M. (2016). *Chapter 1 Plants of Southwest Guyana: Rupununi Savannah and Parabara Region* (BAT Survey Report No. 1; Biodiversity Assessment Survey of the South Rupununi Savannah Guyana, pp. 48–66). WWF-Guianas, Guyana Office. Georgetown, Guyana. https://www.researchgate.net/profile/Jackson-Helms-2/publication/315794413_Ants_of_the_South_Rupununi_Savannah_Guyana/links/58e59e0f0f7e9b5622f57073/Ants-of-the-South-Rupununi-Savannah-Guyana.pdf#page=48

Protected Areas Trust (Guyana). (2021). Protected Areas Trust (Guyana). https://protectedareastrust.org.gy/protected-areas/

R Core Team. (2020). *R: A language and environment for statistical computing. R Foundation for Statistical Computing* (Vienna, Austria). R Foundation for Statistical Computing. https://www.R-project.org/

Rajpar, M. N., Ozturk, M., Altay, V., Ullah, S., Ullah, A., Martin, C. O., Gücel, S., & Zakaria, M. (2020). Species composition of dry-temperate forest as an important habitat for wildlife fauna species. *Journal of Environmental Biology*, *41*(2), 328–336. http://dx.doi.org.libproxy.boisestate.edu/10.22438/jeb/41/2(SI)/JEB-08

Ramos Pereira, M., Rocha, R. G., Ferreira, E., & Fonseca, C. (2013). Structure of Small Mammal Assemblages Across Flooded and Unflooded Gallery Forests of the Amazonia-Cerrado Ecotone. *Biotropica*, *45*(4), 489–496. https://doi.org/10.1111/btp.12027

Read, J. M., Fragoso, J. M. V., Silvius, K. M., Luzar, J., Overman, H., Cummings, A., Giery, S. T., & de Oliveira, L. F. (2010). Space, Place, and Hunting Patterns among Indigenous Peoples of the Guyanese Rupununi Region. *Journal of Latin American Geography*, *9*(3), 213–243. JSTOR.

Roopsind, A., Caughlin, T. T., Sambhu, H., Fragoso, J. M. V., & Putz, F. E. (2017). Logging and Indigenous hunting impacts on persistence of large Neotropical animals. *Biotropica*, *49*(4), 565–575. https://doi.org/10.1111/btp.12446

Sales, L. P., Galetti, M., & Pires, M. M. (2020). Climate and land-use change will lead to a faunal "savannization" on tropical rainforests. *Global Change Biology*, *26*(12), 7036–7044. https://doi.org/10.1111/gcb.15374

Santoro, M. (2018). *GlobBiomass—Global datasets of forest biomass* [Data set]. PANGAEA. https://doi.org/10.1594/PANGAEA.894711

Santoro, M., & Cartus, O. (2021). *ESA Biomass Climate Change Initiative (Biomass_cci): Global datasets of forest above-ground biomass for the years 2010, 2017 and 2018, v2* [Application/xml]. Centre for Environmental Data Analysis (CEDA). https://doi.org/10.5285/84403D09CEF3485883158F4DF2989B0C

Schwenk, W. S., & Donovan, T. M. (2011). A Multispecies Framework for Landscape Conservation Planning. *Conservation Biology*, *25*(5), 1010–1021. https://doi.org/10.1111/j.1523-1739.2011.01723.x

Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. *PeerJ*, *2*, e532. https://doi.org/10.7717/peerj.532

Silver, S. (2004). Assessing jaguar abundance using remotely triggered cameras. *Wildlife Conservation Society*, 1–27.

Silvério, D. V., Brando, P. M., Balch, J. K., Putz, F. E., Nepstad, D. C., Oliveira-Santos, C., & Bustamante, M. M. C. (2013). Testing the Amazon savannization hypothesis: Fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1619), 20120427. https://doi.org/10.1098/rstb.2012.0427

Sletto, B. (2011). Conservation planning, boundary-making and border terrains: The desire for forest and order in the Gran Sabana, Venezuela. *Geoforum*, *42*(2), 197–210. https://doi.org/10.1016/j.geoforum.2010.12.006

Smith, I. T., Knetter, S. J., Svancara, L. K., Karl, J. W., Johnson, T. R., & Rachlow, J. L. (2021). Overlap Between Sagebrush Habitat Specialists Differs Among Seasons: Implications for Umbrella Species Conservation. *Rangeland Ecology & Management*, *78*, 142–154. https://doi.org/10.1016/j.rama.2021.06.007

Smith, T. B., Wayne, R. K., Girman, D. J., & Bruford, M. W. (1997). A Role for Ecotones in Generating Rainforest Biodiversity. *Science*, *276*(5320), 1855–1857.

Stevens, N., Lehmann, C. E. R., Murphy, B. P., & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*, *23*(1), 235–244. https://doi.org/10.1111/gcb.13409

ter Steege, H. (2000). *Flora, vegetation, endemism and altitudinal gradients in the Guyana Highland area: A brief overview.*

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G., & Paine, C. E. T. (2008). Tree Recruitment in an Empty Forest. *Ecology*, *89*(6), 1757–1768. https://doi.org/10.1890/07-0479.1

Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., Rabinowitz, A., & Quigley, H. (2016). Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). *Ecological Applications*, *26*(4), 1112–1124. https://doi.org/10.1890/15-0602

Timothy, D., Onisimo, M., Cletah, S., Adelabu, S., & Tsitsi, B. (2016). Remote sensing of aboveground forest biomass: A review. *Tropical Ecology*, *57*(2), 125–132.

Toniol, A. C., Galvão, L. S., Ponzoni, F. J., Sano, E. E., & de Jesus Amore, D. (2017). Potential of hyperspectral metrics and classifiers for mapping Brazilian savannas in the rainy and dry seasons. *Remote Sensing Applications: Society and Environment*, *8*, 20–29. https://doi.org/10.1016/j.rsase.2017.07.004

Vellend, M. (2010). Conceptual Synthesis in Community Ecology. *The Quarterly Review of Biology*, *85*(2), 183–206. https://doi.org/10.1086/652373

Venter, Z. S., Cramer, M. D., & Hawkins, H.-J. (2018). Drivers of woody plant encroachment over Africa. *Nature Communications*, *9*(1), 2272. https://doi.org/10.1038/s41467-018-04616-8

Watkins, G., Oxford, P., & Bish, R. (2010). *Rupununi Rediscovering a Lost World* (A. Williams, Ed.; First Edition). Earth in Focus Editions.

Widiana, A., Yuliawati, A., Hasby, R., & Danil, M. (2020). *The Influence of Edge Effect on Diversity of Amphibian (Ordo Anura)*. https://doi.org/DOI: 10.4108/eai.11-7-2019.2297399

Wiens, J. A., Hayward, G. D., Holthausen, R. S., & Wisdom, M. J. (2008). Using Surrogate Species and Groups for Conservation Planning and Management. *BioScience*, *58*(3), 241–252. https://doi.org/10.1641/B580310

Zemp, D. C., Schleussner, C.-F., Barbosa, H. M. J., Hirota, M., Montade, V., Sampaio, G., Staal, A., Wang-Erlandsson, L., & Rammig, A. (2017). Self-amplified Amazon forest loss due to vegetation-atmosphere feedbacks. *Nature Communications*, *8*(1), 14681. https://doi.org/10.1038/ncomms14681

Zimbres, B., Shimbo, J., Bustamante, M., Levick, S., Miranda, S., Roitman, I., Silvério, D., Gomes, L., Fagg, C., & Alencar, A. (2020). Savanna vegetation structure in the Brazilian Cerrado allows for the accurate estimation of aboveground biomass using terrestrial laser scanning. *Forest Ecology and Management*, *458*, 117798. https://doi.org/10.1016/j.foreco.2019.117798

APPENDIX A

Tables

Table A1 Count of species by camera trap station, and habitat type table. Notice variability of number of species within camera trap sites.

Habitat type	Camera trap station	Count of animal species
Gallery	DAD1	15
Gallery	DAD10	12
Bush Island	DAD11	4
Gallery	DAD12	5
Gallery	DAD13	4
Bush Island	DAD2	13
Gallery	DAD3	13
Bush Island	DAD4	11

Gallery	DAD5	6
Gallery	DAD7	11
Gallery	DAD8	14
Gallery	DAD9	14
Bush Island	RUP10B	3
Bush Island	RUP11	8
Bush Island	RUP12B	10
Lowland	RUP13L	19
Lowland	RUP14	11
Savanna	RUP15	1
Savanna	RUP16S	2
Savanna	RUP17S	1
Savanna	RUP1S	3

Lowland	RUP2L	7
Lowland	RUP3	12
Savanna	RUP4S	8
Savanna	RUP5S	3
Savanna	RUP9S	0
Gallery	SH1	8
Gallery	SH10	13
Savanna	SH12	1
Montane	SH13	6
Montane	SH14	22
Montane	SH15	24
Lowland	SH17	6
Montane	SH18	19

Savanna	SH19	4
Savanna	SH20	7
Bush Island	SH21	10
Montane	SH22	26
Gallery	SH4	12
Gallery	SH5	6
Gallery	SH6	13
Lowland	SH7	8
Savanna	SH8	12
Gallery	SH9	12
Bush Island	SM1	5
Savanna	SM10	8
Gallery	SM2	13

Gallery	SM3	9
Gallery	SM4	13
Bush Island	SM5	17
Bush Island	SM6	13
Gallery	SM7	10
Gallery	YUP10G	6
Savanna	YUP11S	0
Gallery	YUP13G	0
Bush Island	YUP14B	4
Gallery	YUP15B	7
Bush Island	YUP16B	7
Gallery	YUP17G	15
Bush Island	YUP1B	5

Bush Island	YUP2B	17
Bush Island	YUP3B	15
Bush Island	YUP5B	3
Gallery	YUP7G	12
Gallery	YUP8G	10
Gallery	YUP9G	11

Table A2 Animal Species Frequency Table

Number of times each species was detected at a camera trap station.

Species	**Scientific name**	**Count of animal species**
Amazon gladiator tree frog	*Hypsiboas rosenbergi*	1
Amazon lava lizard	*Tropidurus torquatus*	1
Amazonian brown brocket deer	*Mazama nemorivaga*	9
Black curassow	*Crax alector*	32
Brazilian squirrel	*Sciurus aestuans*	3
Brazilian tapir	*Tapirus terrestris*	29
Brown capuchin	*Cebus apella*	9
Capybara	*Hydrochoerus hydrochaeris*	6
Cinereous tinamou	*Crypturellus cinereus*	1
Collared peccary	*Pecari tajacu*	14

Common or gold tegu lizard	*Tupinambis teguixin*	7
Common opossum	*Didelphis marsupialis*	16
Common squirrel monkey	*Saimiri sciureus*	2
Crab eating fox	*Cerdocyon thous*	31
Crab eating raccoon	*Procyon cancrivorus*	11
Crested bobwhite quail	*Colinus cristatus*	4
Crestless curassow	*Mitu tomentosum*	4
Domestic dog	*Canis familiarris*	29
Domestic horse	*Equus caballus*	8
Domestic pig	*Sus scofra*	5
Domestic sheep	*Ovis aries*	2
Domstic cattle	*Bos taurus*	26
Generic mice and rats	*Cricetidae*	18

Giant ameiva	*Ameiva*	4
Giant anteater	*Myrmecophaga tridactyla*	27
Giant armadillo	*Priodontes maximus*	5
Great tinamou	*Tinamus major*	2
Greater grison	*Galictis vittata*	1
Greater long nosed armadillo	*Dasypus kappleri*	1
Grey winged Trumpeter	*Psophia crepitans*	7
Guianan red howler monkey	*Alouatta macconnelli*	2
Iguana	*Iguana*	9
Jaguar	*Panthera onca*	26
Jaguarundi	*Herpailurus yagouaroundi*	4
Little tinamou	*Crypturellus soui*	1
Lowland paca	*Cuniculus paca*	27

Margay	*Leopardus wiedii*	9
Nine banded armadillo	*Dasypus novemcinctus*	21
Ocelot	*Leopardus pardalis*	33
Oncilla	*Leopardus tigrinus*	13
Puma	*Puma concolor*	17
Red acouchi	*Myoprocta acouchy*	3
Red brocket deer	*Mazama americana*	31
Red footed Tortoise	*Chelonoidis carbonarius*	1
Red legged tinamou	*Crypturellus erythropus*	3
Red rumped agouti	*Dasyprocta leporina*	37
South American coatimundi	*Nasua nasua*	21
Southern naked tailed armadillo	*Cabassous unicinctus*	1
Southern tamandua	*Tamandua tetradactyla*	4

Spiny rats	*Echimyidae*	4
Tayra	*Eira barbara*	16
Undulated tinamou	*Crypturellus undulatus*	1
Unidentified tinamou	*Tinamou sp.*	1
White-lipped peccary	*Tayassu pecari*	3
White tailed deer	*Odocoileus virginianus nemoralis*	15
Yellow footed tortoise	*Chelonoidis denticulata*	1

Table A3 Habitat category descriptions

Source: M. Hallett et al. (Pers.comm)

Habitat Category	Abbreviated description	Detailed description
gallery forest (they are both types of gallery forest, I didn't have enough unique samples to separate)	Gallery forest + moriche palm creeks	Gallery forest: Within the cerrado domain, gallery forests accompany the borders of rivers, creeks and streams, forming important corridors for wildlife among patches of remaining vegetation that also protect aquatic ecosystems from substrate input, reducing water temperatures and erosion of riverbanks. Gallery forests are typically much shorter than terra firme, vàrzea, and forest islands, but are very dense, highly closed canopy forests that support the highest above ground biomass per hectare in the cerrado domain. Gallery forests provide critical food and cover for grazing herbivores that inhabit the cerrado savanna, and may serve as corridors for dispersing individuals of forest species.

	Gallery forest + moriche palm creeks	Moriche palm creeks: Mauritia flexuosa, also known as moriche palm, is the most widely distributed species of palm in Amazonia and the dominant tree species in this habitat type. M. flexuosa is characteristic of seasonally flooded swamp-forests such as vrzea, igapo, and gallery located adjacent to rivers and streams but achieves its highest density in permanently flooded swamps. M. flexuosa is frequently a dominant among the palm species found in swampy environments, this observation is recognized in popular and scientific classifications as a distinct formation called a morichal, a buritizal, or an aguajal. While moriche palm creeks are a type of gallery forest that also provide cover and may serve as a corridor through the savanna matrix, we consider them a unique habitat type because moriche palm creeks grow as a low-density monoculture, creating only a very thin buffer with a mostly open canopy that forms along small creeks and swamps that may be dry for much of the year.

montane	Upland mixed tropical forest	Upland mixed tropical forest: Also known as ‘terra firme’ forest, which literally means "firm earth," this habitat classification includes tropical forest that is not inundated by flooded rivers. Terra firme forest is generally noticeably taller and more diverse (>400 species/hectare in some areas) than vàrzea forests. It is found only on dry, well-drained soils at elevations between ~150-200 m and ~1000-1200 m ASL. Terre firme forest does not include cloud forest habitats, which have unique species and soil conditions, and are found only at the very tops of a few of the highest peaks in the Rupununi. Terra firme forest is a mixed forest type and is characterized by a wide variety of tropical hardwood trees, including crabwood (Carapa sp.), greenheart (Chlorocardium rodiei), aromata (Clathrotropis sp.), wadara (Couratar sp.), wallaba (Eperua sp.), kakaralli (Eschweiler asp.), bulletwood (Manilkara bidentate), and purpleheart (Peltogyne venosa).

lowland	Lowland mixed tropical forest	Lowland mixed tropical forest: Also known as ‘flooded forest’ or ‘vàrzea,’ these forest flood seasonally, and as a result, typically contain fewer tree species that are specially adapted to the anoxic site conditions associated with periodic inundation. The duration and height of flooding influences the ecophysiology of trees, creating a zonation of tree communities along the flood-level gradient. Low-vàrzea forests are characterized by a patchwork of microhabitats due to the high geomorphological variations and frequent habitat disturbance by sedimentation and erosion. These forests become established where the annual water column has an average height of >3 m (inundation period > 50 days year). High-vàrzea forests are located at a distance from the main river channels, where the river water energy is reduced when it reaches these more elevated sites. They typically consist of late successional forests that occupy the transitional zone between flooded and non-flooded sites and are

		exposed to inundation of <3 m in height (< 50 days year). For the purpose of this project, we have grouped both low- and high- vàrzea forests into one category that includes all forests that flood seasonally, and hence may impact the movement of medium and large mammals. Unlike swamp forests, varzeà forests have relatively rich soils from the annual replenishment of nutrients from whitewater rivers. Vàrzea forest is a mixed forest type, though ‘reefs’ of mora (Mora excelsa) form near monocultures in the regularly flooded areas nearest to rivers. Species such as kabukalli (Goupia glabra) and ceiba (known as silk cotton in the Rupununi; Ceiba pentandra) are also common in this habitat type, alongside many species of palms.
bush islands	Forest islands	Forest islands: Known as ‘bush islands’ in the Rupununi, forest islands are natural forest fragments that typically form on upon a slightly elevated surfaces within the broader cerrado savanna matrix. In some cases,

		isolated patches of forest may also simply occur in the midst of a savanna grassland on surfaces without any appreciable topographic or substrate difference from that of the surrounding matrix. In such situations, the balance between woody and herbaceous vegetation is largely a factor of fire and/grazing regimes. These islands are utilized by wildlife, livestock, and humans, who all take advantage of their elevation above the seasonal inundation of the surrounding savanna, as well as the shade, cover, and food (i.e., fruits and leaves) they offer in the otherwise open savanna grasslands. Forest islands provide critical food and cover for browsing herbivores that inhabit the cerrado savanna, and may serve as 'steppingstones' for dispersing individuals of forest species.
savanna	Open savanna grasslands	Open savannah grasslands: Open savanna grassland vegetation in the Rupununi consists largely of perennial grasses from the genus Andropogon, Mesosetum, Paspalum and

		Trachypogon, and a shrub layer dominated by the cayembe tree (Curatella americana). Shrub density varies based on soil moisture, nutrients, and history of fire, with hilltops covered by forest fragments, depressions with flooded savannas, and the boundaries of rivers, creeks, and ponds flanked by riparian forest. Open savanna grasslands will be excluded from sampling in this study due to complications presented by the threats of fire (dry season), flood (rainy season), equipment malfunction (from direct sunlight), and false triggers (caused by blowing grasses).

APPENDIX B

Figures

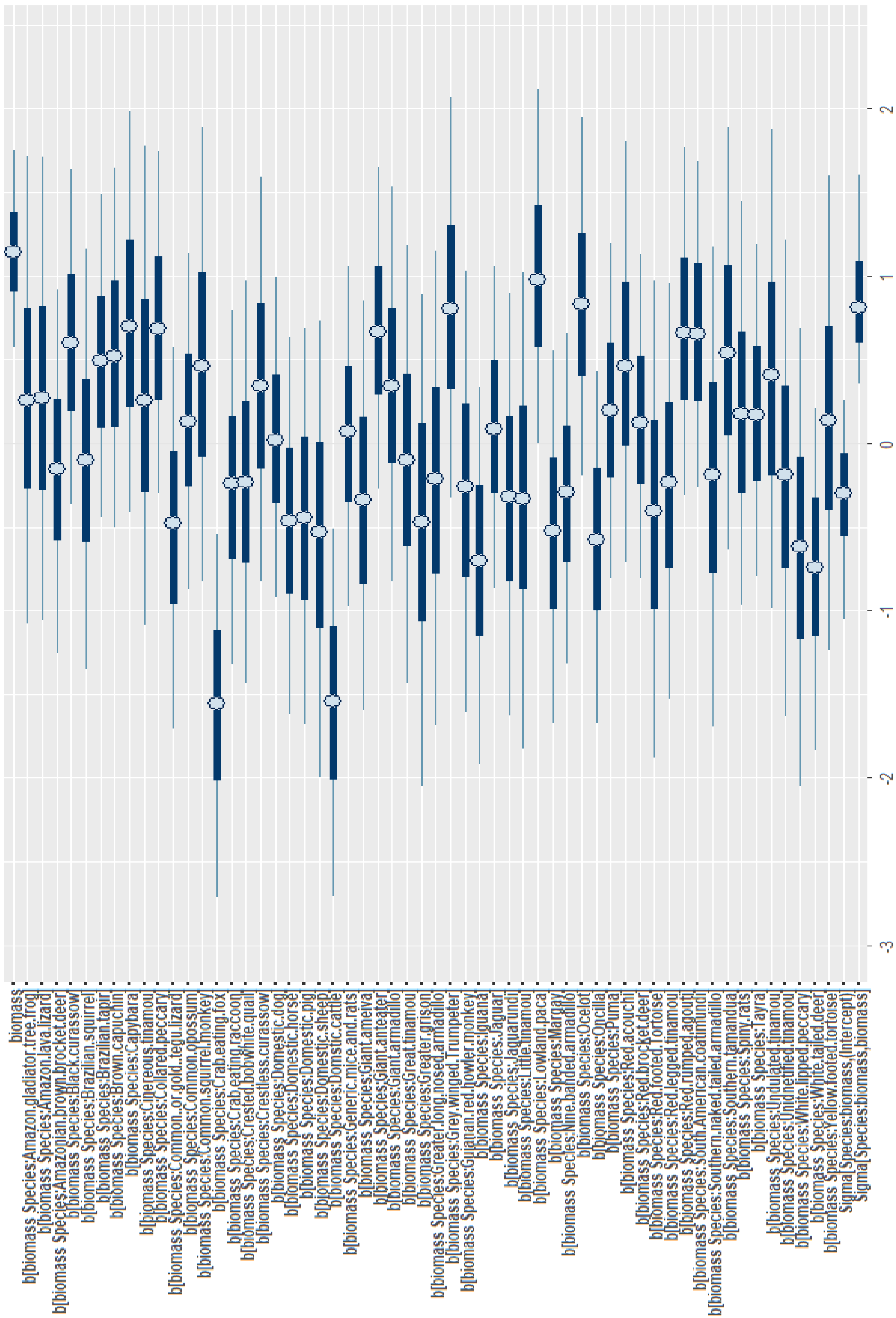


Figure B1 Species-level effects of aboveground biomass for all species in dataset

Effect size represents posterior draws from the random slope parameter of the Generalized Linear Mixed Model (GLMM). Zero represents the average species effect from biomass, so this plot illustrates the deviations from the average species. Species (or estimated effect size) below Zero are indicative of species with a negative presence with biomass (assume preference to savanna habitat), while species above Zero indicate species with a positive presence with biomass (assume preference to forest or trees). The blue dots represent the median for each species, dark blue line is the 50% credible interval (CI), and the thinner blue lines are the 95% CI. If the thin blue lines overlap zero, there is uncertainty in the effect size estimate.