

PRIMARY RESEARCH ARTICLE

Climate and land-use change will lead to a faunal “savannization” on tropical rainforests

Lilian P. Sales¹  | Mauro Galetti^{2,3}  | Mathias M. Pires¹ 

¹Laboratório de Estrutura e Dinâmica da Diversidade (LEDDiv), Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), Campinas, Brazil

²Department of Biology, University of Miami, Coral Gables, FL, USA

³Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

Correspondence

Lilian P. Sales, Laboratório de Estrutura e Dinâmica da Diversidade (LEDDiv), Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), 13083-970 Campinas, São Paulo, Brazil.
Email: lilianpsales@gmail.com

Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 300970/2015-3; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 001; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2014/01986-0; UNICAMP

Abstract

Humans have fragmented, reduced or altered the biodiversity in tropical forests around the world. Climate and land-use change act synergistically, increasing drought and fire frequencies, converting several tropical rainforests into derived savannas, a phenomenon known as “savannization.” Yet, we lack a full understanding of the faunal changes in response to the transformation of plant communities. We argue that the composition of vertebrate assemblages in ecotone regions of forest–savanna transitions from South America will be increasingly replaced by open savanna species, a phenomenon we name “faunal savannization.” We combined projections from ecological niche models, habitat filter masks and dispersal simulations to forecast the distribution of 349 species of forest- and savanna-dwelling mammal species across South America. We found that the distribution of savanna species is likely to increase by 11%–30% and spread over lowland Amazon and Atlantic forests. Conversely, forest-specialists are expected to lose nearly 50% of their suitable ranges and to move toward core forest zones, which may thus receive an influx of more than 60 species on the move. Our findings indicate that South American ecotonal faunas might experience high rates of occupancy turnover, in a process parallel to that already experienced by plants. Climate-driven migrations of fauna in human-dominated landscapes will likely interact with fire-induced changes in plant communities to reshape the biodiversity in tropical rainforests worldwide.

KEYWORDS

Chrysocyon brachyurus, deforestation, fire dynamics, fragmentation, habitat loss, primates, species distribution models

1 | INTRODUCTION

Climate change models forecast an increase in temperature and disruption of rainfall patterns across the globe (IPCC, 2014a). Such changes will redistribute biodiversity as we know it, with consequences for ecosystems worldwide (Pecl et al., 2017). Variation in the composition of communities is one of the first observed shifts (Dornelas et al., 2019), where some species are locally lost or replaced by newcomers (Urban, 2015). A particularly well-documented example is humid forest retreat at the expense of a drier and open-canopy

vegetation in the Amazon (Marimon et al., 2014; Nobre, 2014). The warmer and drier climates observed in the Southeastern Amazon have favored plant lineages that are warm-adapted (Feeley et al., 2020) and dry-affiliated (Esquivel-Muelbert et al., 2019). These changes are expected to promote large-scale compositional shifts, with the gradual replacement of moist forests by seasonal forests and grasslands (Hirota et al., 2010; Lyra et al., 2016). By the end of the 21st century, climate change alone could lead to a reduction of 10%–50% in total humid tropical forest in the eastern Amazon (Lyra et al., 2016).

In the Amazon, precipitation decreases greater than 30% (Salazar & Nobre, 2010), temperature increase above 4°C or deforestation exceeding 40% of the forest area (Nobre et al., 2016) may work as “tipping points” in the conversion of forests into degraded, species-poor, open-canopy vegetation types. Agricultural expansion, selective logging and other land uses also accelerate the rate of forest loss and increase understory fire frequency, favored by fragmentation, which exposes forest edges to escaped ignitions from land management practices (Le Page et al., 2017; Malhi et al., 2008; Zhang et al., 2015). The advance of deforestation, therefore, creates nucleation points that trigger the conversion of the dense moist forest into fire-prone vegetation with lower above-ground biomass (Malhi et al., 2009). Such novel plant communities are structurally similar to savanna physiognomies, yet do not harbor the evolutionary diversity and conservation value of old-growth savannas (Veldman, 2016; Veldman & Putz, 2011). These so-called “derived savannas” (Veldman & Putz, 2011), thus, result of anthropogenic impacts at local (e.g., fire and land-use) and global (climate change) scale, and have led to the hypothesis of future “savannization” of plant communities in tropical rainforests (Nobre et al., 2016; Silvério et al., 2013).

Climate-driven dynamics on forest edges have been mainly assessed with focus on the floristic composition and physiognomic changes. The extent to which faunas undergo a parallel process has rarely been addressed (e.g., Paolucci et al., 2017). However, patterns of occupancy turnover in rainforest remnants indicate the uneven replacement of forest-specialists by open savanna generalist mammals (Beca et al., 2017). Vegetation comprises the habitat for animals, but migrating faunas will likely act as environmental modifiers (Linder et al., 2012), affecting ecosystem structure and functions, such as seed dispersal (Mokany et al., 2014), nutrient cycling (Wolf et al., 2013) and carbon storage (Bello et al., 2015). As a consequence of exposure to non-analog climates in rear edges and colonization of newly suitable environments in leading edges (Thomas, 2010), animals will move and disperse the seeds they ingest, enhancing climate niche tracking by plants (Hampe, 2011), and affecting the structure of their biotic environment (Villar et al., 2019). This biotic component of species response to future environmental change will add a further dynamic layer of uncertainty onto forecasted biome changes (Boulangeat et al., 2012). Here, we tested whether climate-driven redistribution of faunas in South America will follow the same course expected for the vegetation transitions from forests to derived savannas (Figure 1).

To test for a faunal “savannization” of South America rainforests, we projected the potential distribution of forest and savanna-dwelling mammals under climate change and deforestation scenarios (Figures S1–S4). To further investigate the occupancy dynamics of mammal communities, we partitioned composition changes into *turnover* (species replacement) and *nestedness* (species loss/gain). Under this *faunal savannization hypothesis*, we expected to observe range expansion of species associated with savanna and open habitat, but a range contraction of forest-specialist species. We expected to observe high rates of turnover on the limits of rainforest regions, as savanna assemblages replace forest-specialists. Finally, we expected

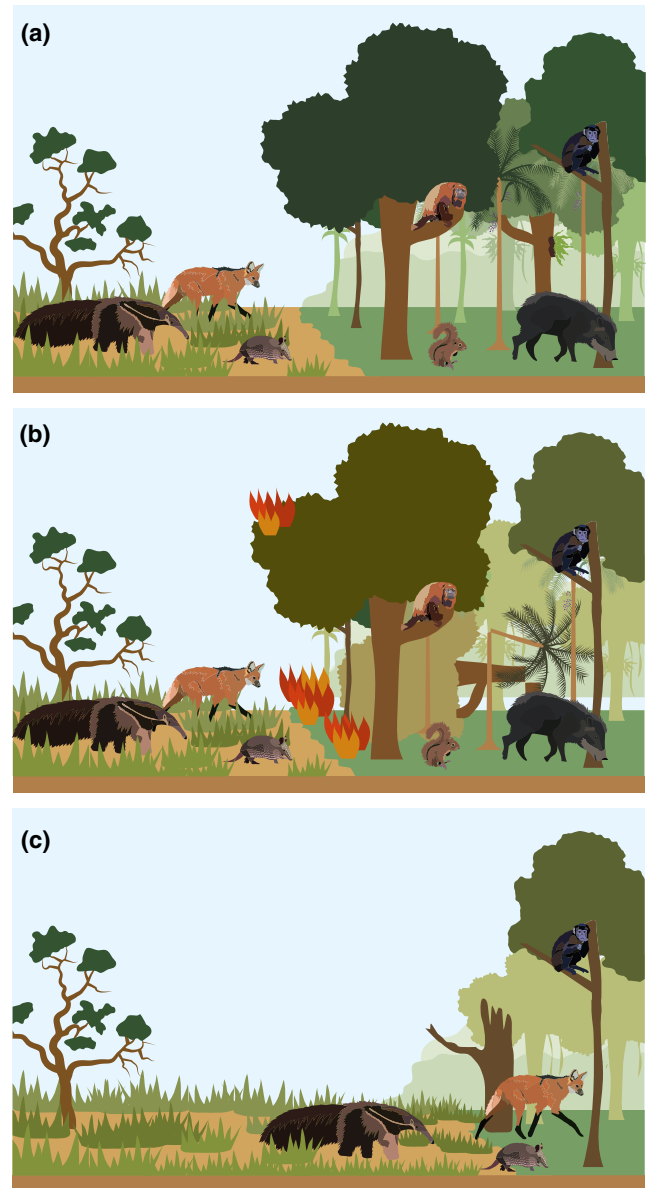


FIGURE 1 Schematic of the “savannization” hypothesis of rainforest faunas. In ecotonal forest–savanna regions (a), anthropogenic stressors acting at local (e.g., fire and deforestation) and global scales (climate change) will lead to warmer, drier and open-canopy habitats (b). These novel environments, unsuitable for forest-specialists, will likely allow the spread of animal species typical from open savannas (c)

savanna assemblages to maintain relatively stable faunal compositions once forest-specialists should not be able to migrate into open areas.

2 | METHODS

2.1 | Species information

South American non-flying terrestrial mammals were chosen as study models because mammals are known to vary in their dependence

on different types of vegetation (Akçakaya et al., 2006). Information from the International Union for Conservation of Nature database (www.iucnredlist.org) was used to characterize the environment within which species occur. Then, we overlaid IUCN maps of extent of occurrence onto a square grid of 10' resolution, to obtain spatial raster files containing cells of suitable climate. Species with less than 30 of such cells (a total of 44 species) were excluded from our analysis, due to the wide variation found in distributional forecasts from small number of occurrence records (Pearson et al., 2007; Peterson et al., 2018), as well as species without information on habitat use and ecology (a total of 77 species). Biogeographic regionalization followed Antonelli et al. (2018) and was used to delimit forested/wet regions (Amazon and Atlantic rainforests) of South America.

2.2 | Environment filters

We assessed the future potential redistribution of forest and savanna-dwelling species from expected patterns on distributional changes, by projecting their realized niches onto environmental forecasts (Peterson et al., 2018), derived from different climate (IPCC, 2007, 2014b) and land-use change scenarios (Li et al., 2017; Figures S1–S4, Data S1). We calibrated and evaluated ensembles of ecological niche models (ENM; Araújo et al., 2019) across the present-day species extent of occurrence, taken from rasterization of IUCN range maps. ENMs had good support from data (Table S1), and a detailed description of the ENMs can be found in Data S1. Climate data referring to the present time (30-year average centered on 1975) were obtained in *Climond* website (www.climond.org), a global repository of bioclimatic information (Kriticos et al., 2012), and downloaded as 10' resolution gridded files.

Climate-calibrated ENMs were then transferred into future environmental projections from years 2030 up to year 2090, as gridded cell-based expectations of climate (Kriticos et al., 2012) across all South America. Future climate forecasts rely on expectations of demographic, economic and technological development of human societies across the globe (IPCC, 2007, 2014a, 2018). Here, we compare the results from two representative concentration scenarios, one that considered “Moderate” levels of emission of greenhouse gases (A1B), and another more “Extreme” scenario (A2). Both forecasts predict temperature increases above the 1.5°C threshold recommended to avoid the deleterious effects of climate change on ecosystems and human well-being (IPCC, 2018).

In addition, we simulated environmental sorting using habitat filter masks, based on the major vegetation types within which species are regularly found (Figures S1–S4), an information obtained at the IUCN website (<https://www.iucnredlist.org/resources/habitat-classification-scheme>). The IUCN habitat type classification scheme is based on expert assessment, as well as biogeography and latitudinal zonation, to assess suitability classes—suitable or marginal—and to indicate whether a habitat type is of major importance for each

species. Based on this classification scheme, we defined that species are habitat-specialists if they occurred in exclusively one major habitat type (Table S1). Species restricted to forest-like habitats (subtropical/tropical, dry/moist, mangrove vegetation above high tide level, swamp or montane forests) were considered *forest-specialists* (FS). Species restricted to savanna-like (dry) habitats were considered *savanna-specialists* (SS). Species who were recorded in savannas, but whose occurrence also encompassed other habitat types (e.g., forests, grasslands, rocky areas, artificial habitats) were considered *savanna-occupants* (SO).

Based on this classification scheme, 285 species were considered *forest-specialists* (FS), 12 species were considered *savanna-specialists* (SS), while 52 species were classified as *savanna-occupants* (SO; Table S1). Any type of habitat where a species had not been recorded was considered unsuitable for that species. Such generalization was useful for providing a community pattern associated with major habitat uses. However, we caution that species-habitat idiosyncrasies and limitations of LULC models will likely make models from some individual species to deviate from general predictions.

2.3 | Dispersal simulations

We modeled the probability of colonization of suitable cells (climate and habitat) as function of species-specific dispersal constraints (Schloss et al., 2012). To do so, we used cellular automata models of dispersal among suitable cells (Engler et al., 2012), where cells with unsuitable environment, as previously defined, were included as barriers to dispersal (Data S1, Methods section). From such dispersal-restricted maps of potential distribution, we derived dispersal scenarios. The first scenario, *unlimited dispersal*, ignores barriers and dispersal constraints, allowing species to colonize all newly suitable environment, which enables us to understand the sole effect of climate over potential distribution patterns. The second scenario, *limited dispersal*, includes unsuitable environment cells as barriers to dispersal, in addition to species dispersal abilities, thus incorporating the accessibility component. The third scenario, *no dispersal*, assumes that species will not be able to move in response to climate change, allowing us to assess how changes in environmental suitability within current range limits may impact species distribution.

2.4 | Community redistribution

Variation on species' potential distribution was calculated as the proportional difference in the number of suitable cells (considering environmental filters and dispersal constraints) and comparing present and future (year 2090) values, as in:

$$\Delta \text{Distr} = \frac{(\text{Future} - \text{Present}) * 100}{\text{Present}}$$

The expected α -diversity (richness) of mammals per habitat-use was calculated as the grid-cell sum of each layer of species potential distribution, as a stack of the presumed presence raster files. To evaluate climate-driven dynamics, we estimated temporal β -diversity, or the variation of species composition in time, using the Sorensen index of similarity. We calculated temporal β -diversity for each grid cell, comparing the change in composition between the present (sum of potential distributions) and future (sum of dispersal-restricted potential distributions attributed to year 2090). Temporal β -diversity may, however, reflect two distinct phenomena, turnover (β_{sim}) and nestedness (β_{sne}), resulting from the antithetic processes of species replacement and species loss, respectively (Baselga, 2010). To evaluate whether changes in β -diversity could be attributed to variation (reduction/expansion) in distribution potential, we compared the maps of expected variation in species richness to the maps of the nestedness (β_{sne}) component of temporal β -diversity. Results depicted in the main document refer to the *Extreme* scenario of climate change (results referring to the *Moderate* scenario are presented as Data S1).

3 | RESULTS

We found that the response to climate and land-use change was contingent on species' preferred habitat type and dispersal scenario (Table S2). In a scenario in which species were able to move freely across suitable land-use types, the *unlimited dispersal* (Figure 2, upper panel), several species would be able to expand their ranges. Under

this unrestricted dispersal projection, 40% of forest-specialists, 75% of savanna-specialists and 69% of savanna-occupants would be able to expand their ranges. As dispersal constraints were strengthened, by assuming that species could only disperse across suitable environment, according to their own movement abilities—the *limited dispersal* scenario—range reduction became more frequent and of greater magnitude, especially for those species who rely heavily on forests (Figure 2, middle panel). We found that most *forest-specialists* (219 species out of 285) would be expected to lose a large proportion of their ranges, having their potential distribution reduced by $84 \pm 31\%$. For species that are able to use savanna habitats and those restricted to savannas, the expected range shifts would be on average positive (Figure 2) and those species expected to undergo range reduction (5 out of the 12 *savanna-specialists* and 18 of the 52 *savanna-occupants*) would show weaker losses compared to forest-specialists (Figure 2). Alternatively, when simulating a scenario where dispersal toward future suitable climates is not allowed—the *no dispersal* scenario—all species are expected to suffer range contractions (Figure 2, lower panel), but again reduction would be greater for *forest-specialists*, which would lose on average more than 90% of their potential distribution.

Species expected to experience the largest total increase in potential suitable area would be savanna dwellers that are highly mobile such as the maned wolf *Chrysocyon brachyurus*, the pampas deer *Ozotoceros bezoarticus* and the giant anteater *Myrmecophaga tridactyla* (Table S2). On the contrary, range contractions were more frequent among forest-specialists whose dispersal ability is contingent on forest cover such as primates, squirrels and arboreal rodents and

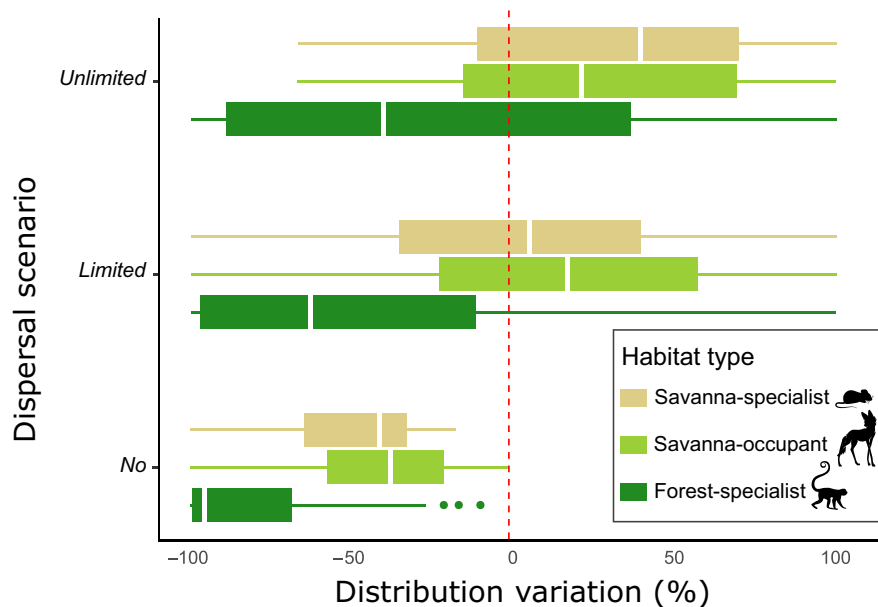


FIGURE 2 Projected variation in the distribution of mammal species, according to habitat type and dispersal scenario. Distribution variation is defined as the % change in suitable potential area from the present to year 2090, where positive and negative values indicate, respectively, range expansion and reduction. Three dispersal scenarios are included: *Unlimited* indicates species can occupy all suitable cells; *Limited* indicates dispersal is restricted by non-analog habitats and species movement abilities; *No* indicates no dispersal beyond current boundaries. Habitat type refers to the species classification as forest-specialist (FS), savanna-occupant (SO) and savanna-specialist (SS). Results refer to the *Extreme* scenario of climate change

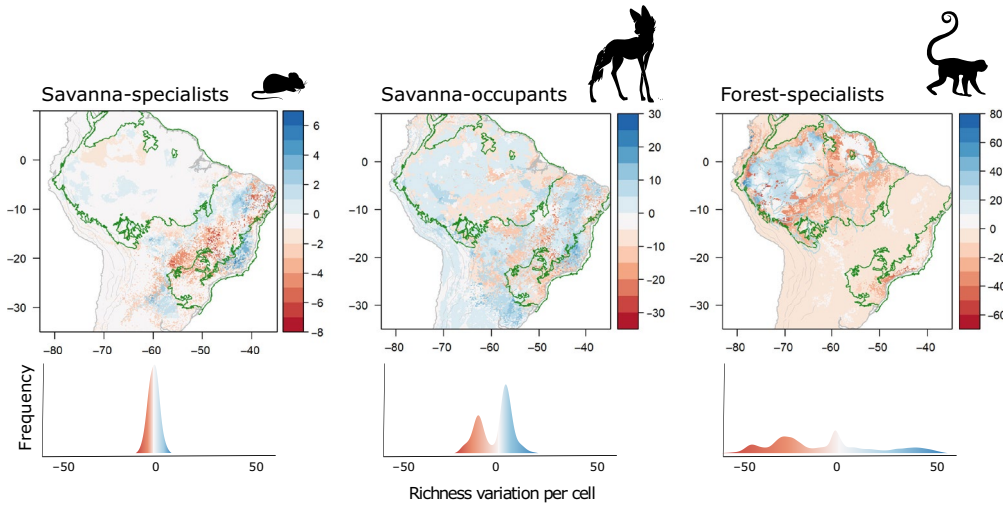


FIGURE 3 Variation in mammal species richness, according to habitat-use type. In upper panels, richness is given as stacked projections of species potential distribution, comparing grid cell estimates in different times (*Future–Present*). Blue color indicates increases in grid cell richness, while red color is for richness reductions. Savanna-specialists (left panel) were predicted to spread over forest–savanna transitions over the Amazon and the Atlantic forest (depicted as empty green polygons). Savanna occupants (middle panel) were predicted to colonize large areas of core forest, while forest-specialists (right panel) were projected to face local extinctions except in the eastern regions of the Andean Amazon. Forecasts of potential distribution refer to an *Extreme* scenario of climate change under *Limited* dispersal

some marsupials. Global extinctions, or the absence of future environmental analogs, were only predicted for forest-specialist species (Table S2).

Transition zones between forest and savanna in the Amazon and the Atlantic forest are likely to gain up to 10 savanna-specialist species (Figure 3; Figures S5 and S6) in all scenarios of climate and land-use change. Reductions in potential distribution were expected for forest-specialists throughout the entire Atlantic forest and the southeastern flank of the Amazon (the main forest–savanna transition of South America; Figure 3; Figures S5 and S6). The Andean Amazon, however, was predicted to gain up to 60 forest-specialists, according to the *limited dispersal* projections. Although the distribution of savanna-specialists was predicted to spread over forest–savanna transitions, some savanna-dominated regions located in central Brazil—the Brazilian *Cerrado*—may experience reductions on local species richness because of range contractions. Such species, however, exhibited range expansion and increases in richness into some areas that are currently forested in the Amazon and the Atlantic forest. Similar to savanna-specialist species, savanna-occupants were expected to suffer range contractions and richness reductions at the core of Brazilian savannas.

Evaluating patterns of compositional changes, we found that the projected temporal beta-diversity was overall high across South America (Figure 4). Partitioning temporal beta-diversity into its components, the epicenter of species replacement (*turnover*) was noticeably located at the lowlands of the Amazon basin and in some scattered regions of the Southern transition between the Atlantic forest and Cerrado savannas. However, the *nestedness* component (signaling species gains or losses) was dominant in the highlands of the Western Andean Amazon. Highlands nestedness patterns were mostly associated with positive richness variation so that compositional changes most likely reflect projected species gains.

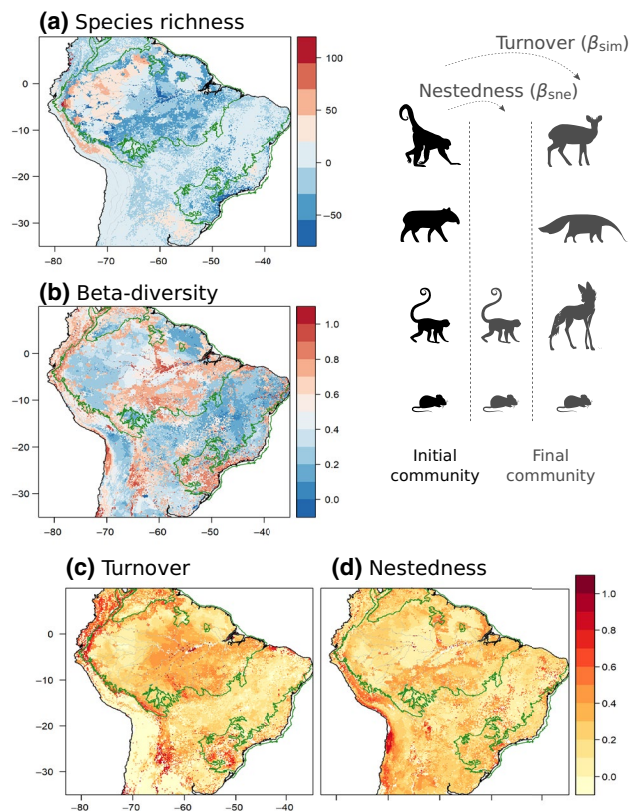


FIGURE 4 Variation in mammal richness (a) and associated temporal beta-diversity (b) in South America. Temporal beta-diversity was disentangled into turnover (c) and nestedness (d) components, while richness variation is $Future_{richness} - Present_{richness}$. Empty green polygons indicate the borders of the Amazon and the Atlantic rainforests. Forecasts of potential distribution refer to an *Extreme* scenario of climate change under *Limited* dispersal

4 | DISCUSSION

Climate and land-use change are leading to warmer, drier and fire-prone environments across ecotonal zones of forests–savanna habitats in South America (Feeley et al., 2020; IPCC, 2019). These conditions will likely favor vegetation types structurally similar to certain types of savanna, creating derived savanna habitats—the “savannization” hypothesis (Franchito et al., 2012; Nobre et al., 2016). Our models forecast that the mammalian fauna will undergo a parallel process, with tropical rainforests faunas increasingly being replaced by species that currently occupy open savannas. We found that savanna-dwelling species are predicted to spread over transition zones, expanding over lowland forest territories. Forest-specialists will most likely experience range contractions and migrations towards core and highland forest zones, which may thus receive a strong influx of migrating species. The high turnover rates we forecast on mammal community composition can already be observed in disturbed assemblages elsewhere (Dornelas et al., 2019). This uneven replacement of forest by savanna species also parallels patterns of disequilibrium in hyperdynamic vegetation communities (Marimon et al., 2014), perhaps suggesting a fundamental mechanism driving transient biotas.

Occupancy of such novel warmer and drier conditions will, however, be conditional to dispersal into human-dominated landscapes. Our analyses show that in a scenario where species cannot migrate in response to changing conditions, all of them are likely to suffer range contractions. If dispersal is allowed, however, savanna-dwelling species are mostly predicted to expand their ranges. Species that preferentially use open areas do not depend on closed-canopy forest. Dispersal across degraded vegetation remnants or even open farmlands could thus allow such species to track their changing environment. However, the same was not true for forest-specialists, which were predicted to experience range contractions in most scenarios of dispersal and climate change. Dispersal across fragmented landscapes will probably not safeguard forest-specialists from exposure to non-analog climates (Ribeiro et al., 2016), because their climate-driven dispersal routes can be disrupted by deforestation (Lawler et al., 2013). Therefore, in addition to reducing and splitting habitat amount, ongoing and forecasted land-use changes might prevent species from moving toward newly suitable environments, as the climate changes (Sales et al., 2019).

The spread of savanna-dwelling species will be mostly directed toward ecotonal zones of Southeastern Amazon and the Northeastern Atlantic forests and outwards the Cerrado savannas. This suggests that core Cerrado savannas may no longer provide suitable environments for savanna-specialist species in the future, which explains our forecast of savanna-specialists range contraction. This region, in addition to extensive habitat loss and degradation from land-use conversion into farmlands (Barretto et al., 2013), is also likely to experience reduction in water and heat flux from humid forests (da Rocha et al., 2009). Those changes lead to vegetation–climate feedbacks predicted to convert vast areas of tropical savannas into grasslands (Hoffmann & Jackson, 2000). Such degraded grassland-like savannas will probably become unsuitable for several

vertebrate species (D’Odorico et al., 2019). Meanwhile, our projections indicate that newly savanna-like climate conditions may become available at the periphery of current forest borders allowing colonization by savanna-dwelling species.

Predicted movement of forest-specialist species will probably follow an opposite trend: range contraction inwards core forest areas. As forest–savanna transition zones become degraded, inhabiting forest-specialists will face unsuitable climate and vegetation conditions, likely to exceed thermal tolerances and not provide required resources (Ribeiro et al., 2016). These peripheral populations face higher risks of local extinction (Channell & Lomolino, 2000), thus leading to range contractions (Thomas, 2010). Such a shadow of local extinctions of forest-specialists may lead to an overall reduction on species richness in ecotonal zones. In a warmer South America, large extensions of humid tropical forests are expected to persist only in core areas of the Amazon basin (Zelazowski et al., 2011). This is considered an epicenter of tropical biodiversity (Rangel et al., 2018), and a climate refugia for paleoecological (Gavin et al., 2014) and future environmental change (Sales et al., 2017, 2019).

Our results show that forest-specialist species will mostly find humid forest conditions in such climate “haven” of the Amazon basin center (Keppel et al., 2012), thus facing range contractions at proximate boundary regions (Channell & Lomolino, 2000). Similar increase in richness due to migration of species from adjacent habitats has already been observed at local scale in forest remnants (Beca et al., 2017). How a potential increase in species richness and composition change may affect biotic interactions in these regions is, however, an open question. The biodiversity accrual from the influx of migrants, for example, can increase competition and form transient species-rich communities, whose biodiversity surplus may later translate into extinction debts (Jackson & Sax, 2010).

Shift in community composition is one of the earliest “symptoms of the Anthropocene,” or the geologic age dominated by humans (Malhi, 2017), where high turnover rates are usually more frequent than species extinctions or declines in abundance (Dornelas et al., 2019). We found an overall support for a “faunal savannization” hypothesis with an expected increase in richness of savanna mammals across South America rainforests. The projected movement of savanna mammals toward regions currently occupied by tropical forests is related to the expected spread of drier, warm-adapted vegetation, typical of derived savannas, at the expense of a retraction of humid tropical forests (Brando et al., 2014; Franchito et al., 2012; Nobre et al., 2016). Forecasts of higher resilience of savanna biomes facing climate change (Anjos & de Toledo, 2018) and local observations of derived savannas across South America (Nobre, 2014) do not still account for the faunistic component of such a process. Yet, the replacement of forest by savanna mammals was already observed in rainforest fragments of the Atlantic Forest (Beca et al., 2017), as well as the expansion of the distribution of species typical of savannas into the Amazon and Atlantic rainforests (Bereta et al., 2017; Silva-Diogo et al., 2020).

Vegetation indeed comprises the habitat for animals, but the migrating fauna may also pose a counterforce, acting as environmental

modifiers (Linder et al., 2012). Grazing by herbivores, for example, is known to mediate fire dynamics, reducing the amount of combustible matter, whereas the consumption of seedlings by browsers may affect regeneration and prevent woody plant encroachment (Hempson et al., 2015; Venter et al., 2018). Such animal-mediated changes will likely reshape ecosystem processes and services, such as seed dispersal (Mokany et al., 2014), nutrient cycling (Wolf et al., 2013) and carbon storage (Bello et al., 2015).

Feedbacks of vulnerability to climate change mediated by the loss of animal-plant interactions may, therefore, accelerate the spread of derived savannas, although this is yet to be tested. Our findings indicate that ecotonal faunas may be hyperdynamic and expected to experience high occupancy turnover rates, in a process parallel to the formation of derived savannas (Marimon et al., 2014; Veldman & Putz, 2011). Climate-driven migrations in human-dominated landscapes associated with fire-induced changes in vegetation communities will determine the future of faunal communities in tropical rainforests in the Anthropocene.

ACKNOWLEDGEMENTS

L.P.S. is funded by the PNPd (*Programa Nacional de Pós-Doutorado*, in Portuguese) at the Campinas State University (UNICAMP). This study was financed in part by the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001*. M.G. receives a fellowship from CNPq (300970/2015-3) and FAPESP (Biota Program—2014/01986-0). We acknowledge three anonymous reviewers who helped improve the quality of the paper.

DATA AVAILABILITY STATEMENT

The climate data used in this work can be downloaded at <https://www.climond.org>. Polygons of extent of occurrence were downloaded at <https://www.iucnredlist.org>. Land-use land-cover models can be found in <http://geosimulation.cn/GlobalLUCCProduct.html>. High-resolution raster files and the species-specific maps may be obtained upon email request to the corresponding author.

ORCID

Lilian P. Sales  <https://orcid.org/0000-0003-1159-6412>

Mauro Galetti  <https://orcid.org/0000-0002-8187-8696>

Mathias M. Pires  <https://orcid.org/0000-0003-2500-4748>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sales LP, Galetti M, Pires MM. Climate and land-use change will lead to a faunal “savannization” on tropical rainforests. *Glob Change Biol*. 2020;00:1–9. <https://doi.org/10.1111/gcb.15374>