Original investigation

Primate and ungulate responses to teak agroforestry in a southern Amazonian landscape

Angele Tatiane Martins Oliveira [a,1], Christine Steiner São Bernardo [a],
Fabiano Rodrigues de Melo [b], Manoel dos Santos-Filho [a], Carlos Augusto Peres [c],
Gustavo Rodrigues Canale [a,d,*]

[a] Centro de Pesquisas em Limnologia, Biodiversidade e Etnobiologia do Pantanal, CELBE, Laboratório de Mamíferos, Universidade do Estado de Mato Grosso, Cáceres, Mato Grosso, Brazil
[b] Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Avenida Purdue, s/nᵒ, Campus Universitário, Edif. Reinaldo de Jesus Araújo, 36.570-900, Viçosa, Minas Gerais, Brazil. Associate Professor II, Institute of Biosciences, Federal University of Goiás, Regional Jataí, 75801615, Jataí, GO, Brazil
[c] Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, United Kingdom
[d] Grupo de Ecologia Animal, GECA, Instituto de Ciências Naturais, Humanas e Sociais, NEBAM, Federal University of Mato Grosso, Sinop, Mato Grosso, Brazil

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ABSTRACT

Agroforestry systems are widely extolled as a biodiversity-friendly alternative to food and wood production. However, few studies on large-vertebrates in the tropics consistently support this assumption. In the Amazonian 'arch of deforestation', commodity cropland and pastures for beef production have relentlessly replaced native forests. Agroforestry should therefore be both economically profitable and a more wildlife-friendly land-use alternative. Here we assess the local abundance and habitat use by forest primates and ungulates in a landscape mosaic containing large areas of primary forest and teak (*Tectona grandis*) agroforestry. We focused on animals of these groups because they have similar day ranges and home ranges, and are at the same trophic level. We surveyed 12 transects in both of these environments, totalling 485 km walked. We recorded four ungulate (*Tayassu pecari, Pecari tajacu, Mazama americana,* and *Tapirus terrestris*) and seven primate species (*Ateles chamek, Lagothrix cana, Sapajus apella, Saimiri ustus, Chiropotes albinasus, Plecturocebus* cf. *moloch* and *Mico* cf. *emiliae*). We indicate the importance of a species-level approach to evaluate the contribution of agroforests to population persistence. Large-bodied atelids, which are ripe-fruit-pulp specialists, were never recorded in teak agroforest. Sakis were more common in primary forest, while the smallest faunivore-frugivores had similar sighting rates in both environments. Ungulates exhibited subtler differences in their use of space than primates, but their sighting rates and track counts indicated temporal niche partition. White-lipped peccaries and red brocket deer were the only ungulates more frequently recorded in primary forest areas. Teak agroforestry still harbours some large and midsized frugivores, which may contribute with some biotic ecosystem services if their patches are connected to primary tropical forests. However, teak agroforestry should not be used to justify population subsidies for all Amazonian forest vertebrate species, since at least some threatened species clearly avoid forest stands dominated by this fast-growing exotic tree.

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Introduction

Agroforestry has been widely considered as a "green" alternative to reconcile economic gains with biodiversity retention across the tropics (Bhagwat et al., 2008). However, evidence suggests that managing agroforests in the interest of tropical forest wildlife inevitably reduces crop or timber yields (Phalan et al., 2011). Thus, the role of tropical agroforestry in the trade-off between biodiversity retention and economic benefits to farmers and silviculturalists remains controversial. A human-modified landscape

mosaic surrounded by old-growth and secondary forests may provide foraging sites for tropical forest species, as well as corridors and stepping-stones, which facilitate animal movements between habitat patches. However, intensively-managed farmlands are typically less wildlife-friendly than secondary forests and well-managed agroforests (Edwards et al., 2014).

Facing rapid conversion of primary forests into silvi-agriculture land-uses, researchers and conservation practitioners argue that the balance between agricultural production and biodiversity conservation may be reached either by maintaining biodiversity within a spatially-heterogeneous and well-managed agricultural landscape (i.e. land-sharing), or maximizing yields within a confined area while setting aside biodiversity reserves elsewhere (i.e. land-sparing) (Phalan et al., 2011). The debate on the pros and cons of land-sparing vs. land-sharing persists (Kremen, 2015), but it has been suggested that both strategies could be complementary at regional to global scales because optimal choices are very context specific (von Wehrden et al., 2014).

There is an increasing number of ecological studies on the use of agroforests by Neotropical forest fauna, most of which are concentrated on agroforestry of shade coffee and shade cacao associated with native trees (Cassano et al., 2012; Estrada et al., 2012). Although timber from teak (*Tectona grandis* Linn. f) comprises one of the most sought-after wood products in international markets, only a few studies have addressed the use of teak stands by large mammals, but these are restricted to monoculture plantations in the Afrotropics (Bonnington et al., 2007; Jenkins et al., 2003), and there are no studies on the use of teak agroforestry by large tropical forest vertebrates.

Teak is the top-ranking fast-growing tree species showing the fastest expansion rate in plantation area worldwide. While the ˜23 million hectare (Mha) of teak-dominated Asian natural forests are declining due to commercial timber extraction, the total area of cultivated teak trees worldwide has increased in the last decade, with recent estimates of 4.3 Mha of additional teak plantations (Kollert and Cherubini, 2012). South America still accounts for only ˜6% of global scale area of teak plantations, but arguably has the greatest potential for expansion of teak yields. This is led by Brazil (plantation area ≈ 67,000 ha), which also recorded the highest expansion rate of teak plantations according to the most recent survey, amounting to a 20% increase from 2000 to 2010 (Kollert and Cherubini, 2012). Teak plantations in Brazil will likely continue to grow due to recent lenient changes in Brazilian forest policy (Forest Code Law no. 12,651), which legally endorses the restoration of minimal required forest set-asides within private landholdings with commercially valuable exotic trees. This has been resoundingly supported by state legislators, for whom landowner constituents have a strong political voice, but remains highly controversial in the Brazilian forest policy debate (Soares-Filho et al., 2014).

High tropical deforestation rates, including the rapid conversion of natural forests into commodity production farmland (Gibbs et al., 2010), places stronger urgency on studies of anthropogenic habitat use by large tropical forest vertebrates. This calls for a better understanding of the demographic role of human-modified landscapes for native fauna, and particularly the degree to which species can persist in different types of man-made habitats. Here we compare the prevalence of habitat use by Amazonian forest primates and ungulates within both teak plantations mixed with native trees and continuous areas of adjacent primary forest to assess the degree to which these species tolerate this pattern of agroforestry land-sharing. We focused on primates and ungulates because they have similar diets and have large home ranges and day ranges, which increase the chances of local populations to use both forest and agroforest.

Material and methods

Study area

We conducted this study in the southern Brazilian Amazon, at the Fazenda São Nicolau (10,000 ha) (09°51′17.8″ S and 58°14′53.7″ W) located in the municipal county of Cotriguaçu, Mato Grosso (Fig. 1). The farm contains 1700 ha of teak agroforest surrounded by largely undisturbed continuous primary forest. Between 1981 and 1998, the original forest was gradually replaced by pasture, which was then replaced with teak agroforestry. The current patch size and plant species composition of the teak agroforest area have been stable since 2004 (Arruda et al., 2004).

The large agroforestry patch is dominated by 10 native tree species, which are interspersed with teak trees and represent 80% of total stand in terms of stem density (Supplementary Fig. A1). Seedlings of native species were grown from seeds collected in the surrounding forest, namely: *Ficus maxima*, *Astronium* sp., *Chorysia speciosa*, *Handroantus* sp., *Simaruba amara*, *Spondias mombin*, *Schizolobium amazonicum*, *Cordia* sp., *Jacaranda copaia*, and *Torresea acreana* (Rodrigues et al., 2011). Thinning of native trees and trail cleaning is carried out once a year. The understorey remains mostly intact with few trails used by researchers and farm staff. Narrow corridors of riparian forests (< 20 m in width along each stream margin) are spared by landholders, linking agroforest patches to the surrounding primary forest (Fig. 1). The agroforest canopy height is between 15–20 m, the mean diameter at breast height (DBH cut-off $\leq$ 5 cm) is 15.92 ± 8.61 cm, tree density is 48 trees·ha^{-1}, tree basal area is 12.3 m^2·ha^{-1} (N = 115 trees) and canopy openness = 42%. These measurements include native and teak trees in the sampling plots (MOC Neyra, unpublished data).

The continuous closed-canopy environment (i.e. only 9% of canopy openness) consists of undisturbed upland (*terra firme*) forest (i.e., that is never seasonally flooded) with tree heights of 30–40 m, reaching up to 50 m, the mean diameter at breast height (DBH $\leq$ 5 cm) of forest trees is 13.90 ± 11.17 cm, tree density is 84 trees·ha^{-1}, and tree basal area is 21.12 m^2·ha^{-1} (N = 280 trees) (MOC Neyra, unpublished data). The understorey density of continuous primary forest is similar to that of neighbouring agroforestry areas, the climate is warm and humid, with an average annual temperature of 24 °C, 85% relative humidity and annual precipitation of 2300 mm (Rodrigues et al., 2011).

Faunal surveys

We cut twelve 1-m wide transects, six of which in each habitat. These transects were at least 1 km apart to maximize independence, and 4–5 km in length in primary forest and 3–3.8 km in length in teak agroforest (Fig. 1). The length of transects were shorter in teak agroforest due to the configuration of this habitat, as it was not possible to set longer transects and keep them 1 km apart simultaneously. Therefore, we have also conducted analyses using truncated data at 3.7 km for all twelve transects, worth to note that we did not observe significant differences between analyses using all data or truncated data (analyses of truncated data not shown). Moreover, transects were not perfectly straight because we have avoided steep elevations and terrain depressions which hampered visual detection of large and midsized mammals. In the agroforest, we have also avoided intensively managed parts of the teak agroforest to reduce confounding effects due to human presence during data collection.

We walked each transect 10 times to record primates and ungulates across both habitat types, including sighting rates and track counts, as a measure of habitat use. We also provide results, in the supplementary materials, on three habitat generalist midsized mammals (*Dasypus novemcintus*, *Dasyprocta azarae* and *Cerdocyon*
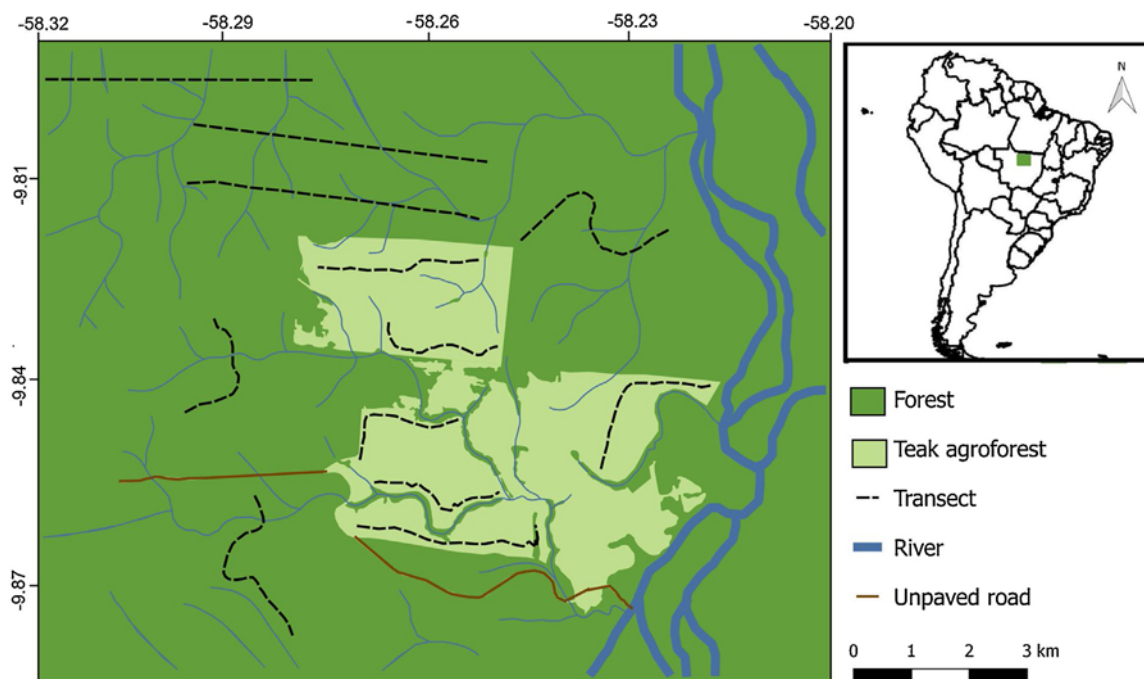
Fig. 1. Geographic location of the study area in the southern Amazonian municipal county of Cotriguaçu, Mato Grosso, Brazil. Green square in the inset map (right) is represented in the left panel showing areas of primary forest (dark green) and teak agroforestry (light green). Survey transects in both of these habitat types are indicated by black dashed lines (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

thous), which were recorded in at least three distinct transects (Supplementary Fig. A2). Total survey effort amounted to 485 km, of which 279 km and 206 km were walked in continuous forest and teak agroforest, respectively. Surveys were conducted during the mornings (06:00 h to 10:00 h) and afternoons (14:00 h to 18:00 h), avoiding the hottest hours of the day when animals tend to be less active. Transects were walked at an average pace of 1.25 km/h with stops of about 1 min every 100 m to listen to animal calls and movements (Peres and Cunha, 2011). Sightings of social species (e.g., primates, peccaries) were considered as a single detection event. In such cases, we measured the perpendicular distance to the first individual of each species sighted in a group, and estimated the group spread.

Sighting rates of ungulates may be underestimated due to their secretive habits and/or crepuscular or nocturnal activity time (Espartosa et al., 2011; Mayle et al., 2000). Therefore, as a complement to direct sightings, we used track counts to estimate the frequency of habitat use by ungulates. The use of track counts to estimate vertebrate abundance is fairly common in studies of large-bodied mammals in North America, Europe, and Africa, but relatively infrequent in Neotropical studies (Fragoso et al., 2016). Ungulate tracks were only counted when they crossed transects to avoid detection bias due to differences in litter accumulation and soil compaction between primary forest and teak agroforest. Tracks were assigned to a single detection event for (1) solitary species (i.e., red brocket deer and lowland tapir) and (2) social species (i.e., both peccary species), meaning that a multiple trackway of a herd of peccaries was defined as a single track count. We marked track locations with coloured rubber bands to avoid double-counting the same trackway during subsequent survey walks. Data were collected by an experienced field assistant working with ATMO, who had been previously trained in transect sampling techniques. The surveys were conducted from February to July 2014, covering both the wet (late September to early April) and dry (late April to early September) seasons evenly. Both habitat types were surveyed alternately along subsequent days within each month to avoid confounding effects between habitat types and seasonality. Thus, the

transects were surveyed in the two habitats every other day. In addition, all transects were surveyed five times in the mornings and five times in the afternoons. We re-surveyed each transect after a minimum interval of two days.

Data analysis

We calculated sighting rates (sightings/10 km) by dividing the total number of detection records by the total length (km) of survey effort in each habitat type, and multiplying this by 10. The same was done for track counts (tracks/10 km). Sighting rates and track counts for each species were used to quantify the frequency of habitat use by the species. We used sighting rates, rather than estimates of population density, for comparisons due to the low number of sightings. We did not calculate sighting rates for species sighted only twice in the study area (e.g. Titi monkeys, *Plecturocebus* cf. *moloch*). A measure of aggregate biomass was calculated by multiplying the body mass of each species by the number of individuals recorded during surveys in each habitat type. The result was then log-transformed ($\log_{10}$ x) and divided by the total distance walked in either primary forest or teak agroforest. A log-ratio of encounter rates was calculated by dividing the species (i) encounter rate in the agroforest (a) by its encounter rate in primary forest (f). A small value (0.01) was added to both encounter rates to ensure calculations of equations for which the divisor was zero (1).

$$\text{Log-transformed ER ratio} = \log_{10}((\text{ER}_{ia}+0.01)/(\text{ER}_{if}+0.01)) \quad (1)$$

To minimize detectability effects due to differences in vegetation structure, we truncated survey data, excluding detections with perpendicular distances greater than 50 m, a conservative distance considering other large-vertebrate studies in Amazonian forests with varying degrees of forest disturbance (Bicknell and Peres, 2010; Parry et al., 2009). In doing so, however, only one observation (of a group of capuchin monkeys) was excluded beyond this truncation cut-off.

Comparisons of sighting rates or track counts for each species between habitat types were performed using the Wilcoxon Sum

Table 1
Sightings and track detection rates (per 10 km walked) of ungulates and primates recorded in primary forest and teak agroforest in a southern Brazilian Amazon landscape. Status indicates the IUCN conservation status of each species: EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern, DD = data deficient.

ORDER/Family/Species	Silhouettes	Common name	Primary forest					Teak agroforestry			
			Status	Sight	Rate	Track	Count	Sight	Rate	Track	Count
ARTIODACTYLA **Tayassuidea**											
Tayassu pecari		White-lipped peccary	VU	40	1.4	14	0.5	12	0.6	10	0.5
Pecari tajacu		Collared peccary	LC	10	0.3	7	0.2	14	0.7	36	1.7
Cervidae											
Mazama americana		Red brocket deer	LC	15	0.5	39	1.4	2	0.1	30	1.4
PERISSODACTYLA **Tapiridae**											
Tapirus terrestris		Lowland tapir	VU	4	0.1	21	0. 7	3	0.1	33	1.6
PRIMATA **Atelidae**											
Ateles chamek		Black-faced black spider monkey	EN	22	0.8			0	–		
Lagothrix cana		Woolly monkey	EN	51	1.8			0	–		
Cebidae											
Sapajus apella		Brown capuchin monkey	LC	30	1.1			24	1.2		
Saimiri ustus		Golden-backed squirrel monkey	NT	1	0.03			12	0.6		
Pitheciidae											
Chiropotes albinasus		White-nosed saki	EN	22	0.8			2	0.1		
Callithrichidae											
Mico cf. *emiliae*		Snethlage's marmoset	DD	5	0.2			4	0.2		

Rank Test using the *stats* package within R 3.1.3. In addition, we performed a Wilcoxon Sum Rank Test with a Bonferroni correction to compare sighting rates or track counts of ungulates in each habitat.

Results

Seven primate and four ungulate species were recorded by either sightings or tracks across the study area (Table 1). The endangered woolly monkey (*Lagothrix cana*, n = 51 sightings) was the most frequently recorded primate in primary forest and the brown capuchin monkey (*Sapajus apella*), classified as least concern, was the most frequently sighted primate in teak agroforest (n = 24 sightings). With respect to ungulates, the most sighted species in primary forest was the vulnerable white-lipped peccary (*Tayassu pecari*, n = 40 sightings), whereas the collared peccary (*Pecari tajacu*, n = 14 sightings), classified as least concern, were the most sighted species in teak agroforest, but closely followed by white-lipped peccaries (n = 12 sightings) (Table 1). Considering ungulate tracks, the red brocked deer (*Mazama americana*, n = 39 tracks), least concern species, was the most recorded species in primary forest, whereas collared peccaries (*Pecari tajacu*, n = 36 tracks) were the most frequent in teak agroforest, closely followed by the vulnerable lowland tapirs (*Tapirus terrestris,* n = 33 tracks) and red brocked deer (*Mazama americana*, n = 30 tracks) (Table 1).

Of all large mammals investigated here, three primates diverged the most in their habitat-specific encounter rates in primary forest and agroforest, namely the woolly monkey, the endangered black-faced black spider monkey and the endangered white-nosed saki. Along with white-lipped peccaries and red brocket deer, they were far more abundant in primary forest compared to agroforest (Fig. 2A). On the other hand, the capuchin monkeys, the near threatened squirrel monkeys and the collared peccaries were more common in teak agroforest. On the basis of track detection rates, however, lowland tapir and collared peccary were more abundant in teak agroforest than in adjacent primary forest (Fig. 2B). Teak agroforest sustained 37% lower population biomass of primates and ungulates compared to primary forest, particularly in light of large-bodied primates such as spider monkey, which apparently did not use agroforest but were common in primary forest (Fig. 2C-D). Although white-lipped peccaries exhibited a high biomass in both environments, their biomass in agroforest was 27% lower than in primary forest (Fig. 2C-D).

The two large-bodied ateline primates – black-faced black spider monkey and the woolly monkey – were exclusively sighted in primary forest, whereas the white-nosed saki was more common in primary forest than in teak agroforest (W = 34, p = 0.01) (Fig. 3). The woolly monkeys were the most sighted primates in primary forest (Fig. 3), but those sighting rates were only significantly higher than those of squirrel monkeys (W = 36, p = 0.03) and Snethlage's marmosets (W = 36, p = 0.04). Capuchin monkeys had the highest sighting rate in teak agroforest (Fig. 3), but this was not significantly different from sighting rates of squirrel monkeys and marmosets in the same habitat (p > 0.05). It is important to consider
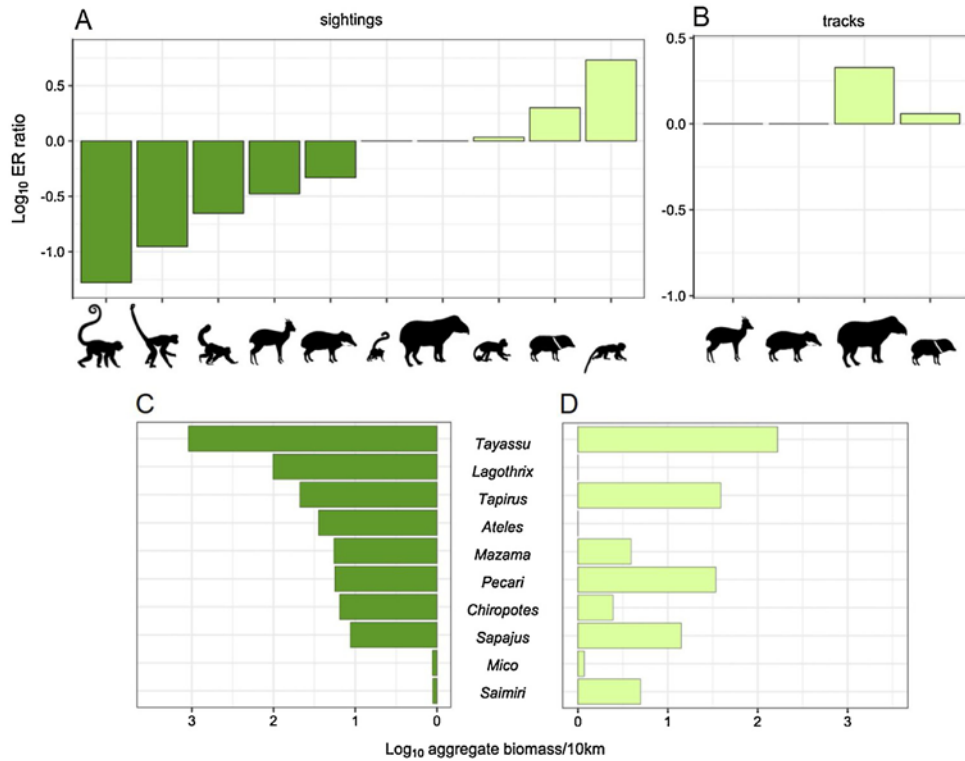
Fig. 2. Contrasts on log-transformed sighting rates (A) and track counts (B) of primates and ungulates in primary forest (dark green) and teak agroforest (light green). Species are ordered left to right from the highest to the lowest relative abundance in primary forest. Contrasts on log-transformed aggregate biomass of primates and ungulates in (C) primary forest and (D) teak agroforest. Species are ordered top to bottom from the highest to the lowest relative aggregate body mass in primary forest. Silhouettes are referenced in Table 1 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
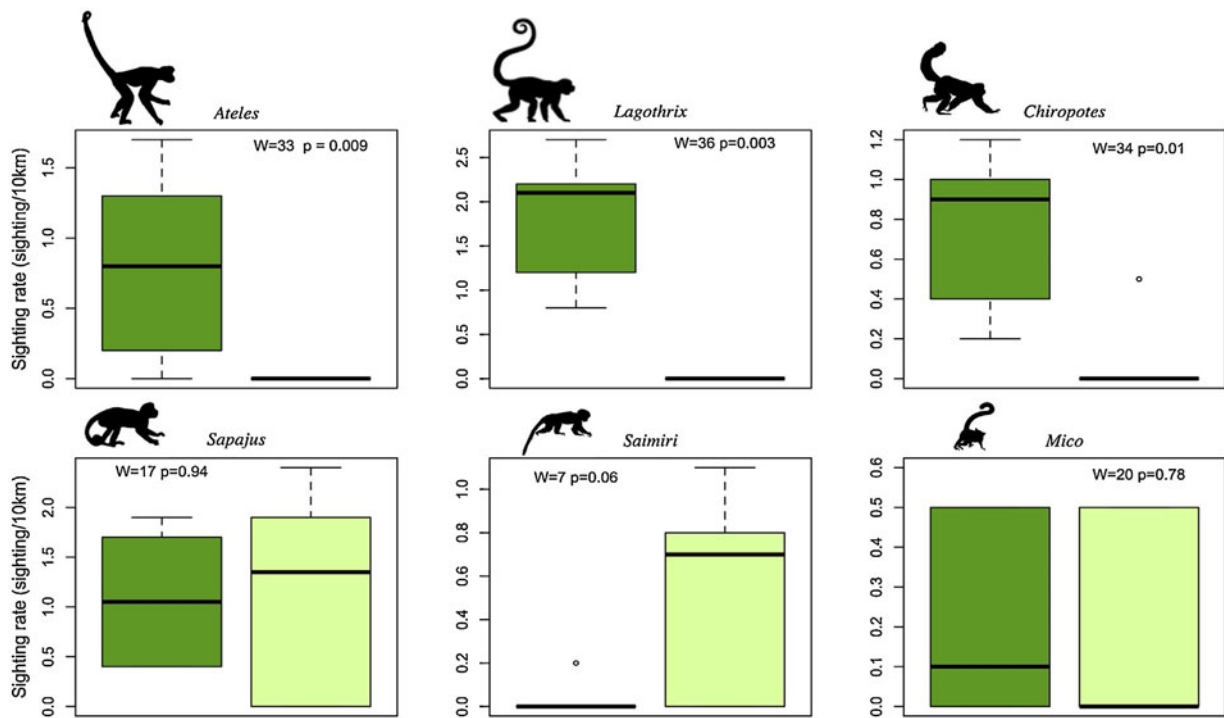
Fig. 3. A comparison of sighting rates of primates in two habitat types, primary forest (dark green) and teak agroforest (light green) in southern Amazonia, Mato Grosso, Brazil. Boxplot central bars and whiskers indicate means and maximum/minimum values, respectively. Circles indicate outliers and boxes indicate interquartile range containing 50% of values. W corresponds to test statistic values (Wilcoxon signed-rank test) followed by the probability value (p). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
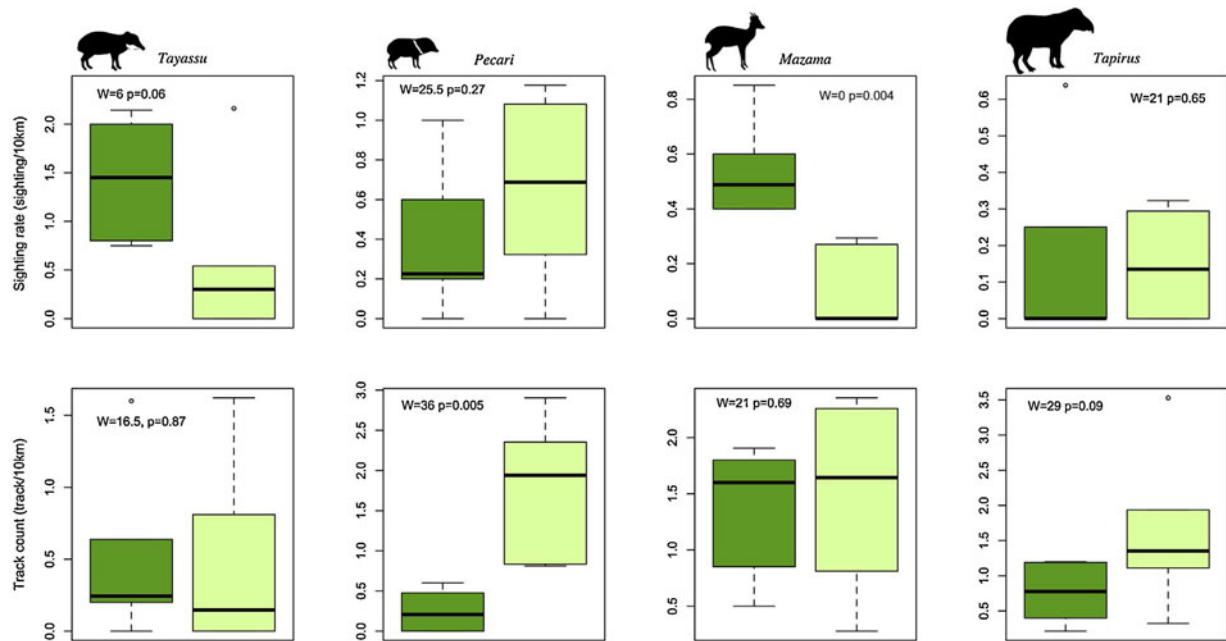
Fig. 4. A comparison of sighting rates and track counts of ungulates in two habitat types, in primary forest (dark green) and teak agroforest (light green) in southern Amazonia, Mato Grosso, Brazil. Boxplot central bars and whiskers indicate means and maximum/minimum values, respectively. Circles indicate outliers and boxes indicate interquartile range containing 50% of values. W corresponds to test statistic values (Wilcoxon signed-rank test) followed by the probability value (p) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

that species differ in their behaviour (e.g. frequency of long calls, agonistic displays and intra-group aggression), differences in group size and body mass – factors that likely influence species, which are likely to influence species detectability. Thus, comparison of sighting rates among primate species using the same habitat type must be discussed with caution, bearing in mind that differences in detectability are relevant.

White-lipped peccaries and red brocket deers were primarily sighted in the primary forest, rather than in the teak agroforest (respectively, $W = 6$, $p = 0.06$; $W = 0$, $p = 0.004$); while the lowland tapirs and collared peccaries had similar sighting rates in both habitats (Fig. 4). However, only the collared peccaries had higher track counts in teak agroforest ($W = 36$, $p = 0.005$) (Fig. 4). The large-herd-living white-lipped peccary was the most frequent sighted ungulate in primary forest ($W = 36 – 34$, $p < 0.01$), whereas the red brocket deer had the highest track counts in this habitat (Fig. 4), significantly higher than white-lipped and collared peccaries (respectively, $W = 4$, $p = 0.03$; $W = 1$, $p = 0.008$). All ungulates presented similar sighting rates in teak agroforest (Fig. 4). However, white-lipped peccaries had the lowest track counts recorded for any ungulate in teak agroforest, which were significantly lower than those for collared peccaries ($W = 3$ $p = 0.02$).

Discussion

Preserving forest biodiversity without substantially curbing economic growth is a major challenge for tropical forest countries (Chaudhary et al., 2016). The Brazilian Amazon is the world's largest tropical forest area controlled by a single country and is a central part of the national geopolitical strategies to expand economic growth. This region has been dramatically modified for commodity production due to its climatic conditions and large expanses of arable land (Silva and Lima, 2018). Most forest remnants in this region are within private landholdings, which are legally required to set-aside a forest area of 50%–80% of each landholding. Only smallholders are exempted from complying with these regulations (Soares-filho et al., 2014). However, according to the current

Brazilian Forestry Bill (Law No 12.651/2012), landowners can compensate for part of their forest set-asides using agroforestry systems containing up to 50% of exotic species, such as *Tectona grandis*. It is therefore recommended, whenever possible, to investigate responses to agroforestry land-uses at species, rather than aggregate community level (e.g. measures of α- and β-diversity), to clearly elucidate the effects of human-modified landscapes on the persistence of the local fauna and ultimately the ecosystem services they provide.

Primates and ungulates diverged in their use of primary forest and teak agroforest in our study landscape. Our results indicate that populations of strict forest-dwelling primates (spider monkeys, woolly monkeys, and white-nosed sakis) and ungulates (white-lipped peccaries and red brocket deer) can only thrive in a landscape of forest and mixed teak plantations if they are supported by surrounding areas of primary forest.

In revisiting the land-sparing vs. land-sharing debate (Phalan et al., 2011), the option of land-sparing is decidedly the best, if not the only alternative if the conservation priority is to retain viable populations of large frugivorous primates. Large canopy-dwelling primates (i.e., spider monkeys and woolly monkeys) were not observed using teak agroforest, and groups of white-nosed sakis were only rarely sighted in agroforestry patches. Atelid primates rely heavily on ripe fleshy fruits and white-nosed saki monkeys specialize on immature seeds of large-seeded trees and woody lianas, exhibiting one of the highest degrees of frugivory in their diet among Neotropical primates (Hawes and Peres, 2013). This supports the high level of dependence of these primates on relatively undisturbed species-rich primary forest environments, rather than teak stands which retained only 10 species of native fruit trees.

On the other hand, land sharing may be a suitable alternative for the smallest faunivore/frugivore primates, as they used both forest habitats at similar frequencies. However, the spatial configuration of the teak agroforestry at Fazenda São Nicolau allows primates and other forest mammals to move through primary forest corridors to reach core areas of the agroforest patch, and yet return to primary forest within the same day. The degree to which forest

mammals using the teak agroforest are subsidized by primary forest to supplement their ecological requirements cannot be resolved by this study. Smaller-bodied monkeys, namely squirrel monkeys, capuchin monkeys and marmosets, typically have a more generalist diet, feeding on smaller fruits as well as invertebrates and small vertebrates (Hawes and Peres, 2013). These dietary differences may be associated with their ranging ecology and habitat use: large primates use high-quality core forest areas, while the small-bodied species often occupy edge-dominated and/or disturbed environments (including secondary forests and agroforests) (Hawes and Peres, 2013).

Low yield teak agroforest under low intensity management may also be a suitable alternative to support ungulate populations if they are directly connected to primary forest, especially for collared peccary and lowland tapir, which were sighted in teak agroforest and primary forest at similar rates. Moreover, track counts of collared peccaries were even more frequent along agroforest transects than those in primary forest. Long-term persistence of ungulates under a land-sharing strategy, however, is not given if human-modified land uses are isolated from neighbouring areas of primary forest. We further note that, white-lipped peccaries and red-brocket deer were apparently more forest-dependent than lowland tapir and collared peccaries. Although largely solitary, red brocket deer exhibited more track counts in primary forest than both peccary species. Amazonian red brocket deer is more nocturnal than either peccaries (Tobler et al., 2009), thus their nocturnal and solitary habits decrease the odds of visual detections during diurnal surveys, which explains the relatively low sighting rates compared to their track counts in primary forest, which were the highest among all ungulates. Tapirs and red brocket deer were difficult to detect visually during diurnal censuses but are in fact relatively abundant in teak agroforest. For instance, they had similar track counts compared to those of collared peccaries, which were frequently sighted in agroforestry areas. In fact, most of these ungulates are commonly reported to move through open habitats (e.g., grasslands and degraded forests) and must be fairly capable of using and moving through teak agroforestry while foraging on foliage and fruits of native plant species in that environment (Tobler et al., 2009).

These outcomes at the species-level are important because in general, agroforestry systems are thought to provide a wildlife-friendly environment to native tropical forest fauna due to the retention of relatively intact canopy connectivity and vegetation structural complexity, all of which may contribute to food provision (Bhagwat et al., 2008; Estrada et al., 2012). Although teak agroforests can contribute to larger canopy tree cover, the sclerocarpic fruits of *Tectona grandis* are unattractive to Amazonian vertebrate frugivores and their flowers produce only small amounts of nectar (Healey and Gara, 2003). Teak monoculture plantations are far from high-quality habitats for large vertebrates, even under low-intensity management regimes (Harikrishnan et al., 2012). Nevertheless, some herbivores feed on young leaves of teak trees and, consequently, may attract large predators to these plantations (Bonnington et al., 2007). The high density of native fruit trees within the teak plantations at Fazenda São Nicolau is inescapably a critical feature of this agroforestry system, colouring any conclusion we can draw from this landscape. Moreover, the permeable landscape mosaic of teak agroforest surrounded by primary forest was highly benign to some primates and most ungulates and other terrestrial mammals in our study area. However, the presence of large areas of primary forests was critical for strict old-growth forest-specialists such as white-nosed sakis and white-lipped peccaries; black-faced spider-monkeys and woolly monkeys apparently avoided teak agroforestry altogether. That said, the protection of large forest set-aside areas within a land-sparing strategy is more appropriate to these forest-dwellers than the use of teak agroforestry in any land-sharing approach.

The evidence for land-sharing presented here is in fact conservative in terms of the wider ecological value of Amazonian teak agroforestry at Cotriguaçú, Mato Grosso, as this fast-growing exotic tree species accounted for only 20% of the overall tree density in the stands surveyed here (Rodrigues et al., 2011). Most tropical teak plantations strive for much higher profits and a far greater dominance of teak trees, typically thinning out all remaining native trees. We therefore expect that teak stands would have been much more hostile to both terrestrial and arboreal forest mammals, had their tree densities between teak and native species been optimized at, for example, a stand-scale ratio of 50:50. However, the inherent tradeoffs between teak tree density and the biodiversity value of teak agroforestry remains poorly understood.

We could advocate in favour of a land-sharing strategy to protect vertebrate populations that use the 'shared' environment (i.e. agroforest) more frequently or at least at a similar rate than they use primary forest. This is relevant considering that in a land-sharing strategy the less intensive management of the 'shared' environment may reduce yield, thereby justifying the expansion of agricultural land-use over forests. In practice, a combination of large forest set-asides and an environmentally-friendly land use demanding less-intensive management is the best scenario compared to any highly-mechanised farmland production, such as conventional soy plantations, if the same extent of forest set-asides is maintained in private landholdings complying with the current Brazilian Forest Bill. According to the Brazilian Forest Bill, forest set-asides in the political region of 'Legal Amazonia', which includes the State of Mato Grosso, must be at least 80% of the total private landholding area. However, a state decree established that forest set-asides might be reduced to 50% of landholding area if local deforestation was previous to 26th May 2000 (Decree 1,031, 2nd June 2017). On the basis of this study, however, we do not recommend a land-sharing strategy as a forest protection alternative to truly sparing either 50% or 80% of any given private landholding area.

Conclusions

Our approach is based on species and population level (e.g. abundance measure) rather than community level (e.g. diversity measures), identifying which primate and ungulate species are either most sensitive or most resilient to a relatively benign teak agroforestry enterprise embedded in large areas of primary forest. A species-level approach may be preferable to examine land sharing vs. land sparing strategies, because each management option will depend on the idiosyncrasies of species responses to the type and magnitude of forest disturbance (Fischer et al., 2014). In addition, the use of species-level data by stakeholders is an important step towards achieving sustainable consumption patterns, informing regional markets about the sustainability pathways of teak yields as consumers become more conservation-savvy, and taking into account the biodiversity impacts that are "hidden" in commercial wood products when forest lands are acquired for 'green' compensatory purposes (Chaudhary et al., 2016).

In the "arch of deforestation" of southern Amazonia, half of the primates and ungulates occurring in this agroforestry mosaic are listed as threatened (i.e. VU, EN) according to the latest IUCN Red List (2018). While populations of habitat-generalist primates and ungulates are partly supported by teak agroforests in association with native fruit trees, evidence presented here shows that the most threatened primates were largely restricted to adjacent primary forests. Considering that endangered species avoid teak agroforests, even under a hands-off, low-yield plantation regime that is still dominated by native fruit trees, land sparing is the only alternative if the priority is to maximize conservation of the most extinction-prone species. However, some large and midsized frugivores (e.g., lowland tapir, collared peccary and capuchin monkey)

were highly resilient to teak agroforestry and land sharing may be considered as a suitable management alternative if teak agroforests under low intensity management can remain connected to large areas of relatively undisturbed primary tropical forest.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.mambio.2019.03.015.

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