



Original investigation

Use of early and late successional forest patches by the endangered Lowland tapir *Tapirus terrestris* (Perissodactyla: Tapiridae)

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ABSTRACT

Large herbivores play crucial ecological roles, affecting the structure and function of terrestrial ecosystems. Their effect, however, depend on how they select plants and vegetation patches for foraging. At the landscape scale, succession is one of the processes that should generate vegetation patches with different nutritional quality, affecting selection by herbivores. Earlier successional stages should be preferred as they are dominated by plants with nutritious and palatable leaves. Here, we investigate if the Lowland tapir prefers early compared to late successional forest patches, aiming at contributing to the understanding of the ecological role of the largest terrestrial South American herbivore, and to conservation strategies for this endangered species. We sampled 12 vegetation patches varying in successional stages across a 20,000-ha continuously-forested landscape in the Brazilian Atlantic Forest, recording tapirs through standardized camera trap and track surveys, and quantifying vegetation structure and treefall gaps. Whereas the number of individuals using each patch was not influenced by successional stage, intensity of use was higher in patches in earlier successional stages, in particular patches with higher density of smaller trees and higher cover of treefall gaps. Although inferences on the effects of tapir on plant community depends on future, smaller-scale studies, our results suggest herbivory by tapirs affects forest regeneration, potentially contributing to the maintenance of plant diversity. Results also point out to the potential of mosaics encompassing old-growth and secondary forests for the conservation of the Lowland tapir.

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Introduction

Large herbivores play crucial ecological roles, affecting the structure and function of terrestrial ecosystems. Through herbivory, they influence plant germination and growth, composition and diversity of plant communities, and ecosystem function, such as nutrient cycling, carbon storage and primary production (Danell et al., 2006). However, the effects of large herbivores depend on how they select plants or parts of plants for feeding, and areas or patches for foraging. According to the optimal foraging theory, foraging strategies result from individuals maximizing the net rate of energy intake, depending on the availability and quality of food and environmental heterogeneity. Thus, food resource selection is associated with the balance between energy gain and energy expenditure with the search, capture and ingestion of food (Stephens and Krebs, 1986).

Large herbivores are faced with a wide variety of plants species and plants parts that differ in their nutritional and defense properties (Coley and Barone, 1996), taking foraging decisions on a range of spatial (from bites to landscapes) and temporal (from seconds to years) scales (Senft et al., 1987). They select plants, feeding stations or micro patches within plant communities, plant communities or large vegetation patches within landscapes, and, in the case of nomadic or migratory species, landscapes within regions. At the landscape scale, one of the processes that can generate vegetation patches with different nutritional qualities for herbivores is vegetation succession, which leads to changes in vegetation composition associated with varying plant strategies (McCook, 1994).

Compared to late successional communities, plant communities in earlier successional stages are dominated by species that present higher growth rates and dispersal ability, but shorter life cycles, lower heights, lower tolerance to grow under the shade of other plants (McCook, 1994), and invest less in defense against herbivory (Herms and Mattson, 1992). Generally, early successional plants produce short-lived leaves with higher specific leaf area, higher nutrient concentrations and higher photosynthetic rates (Reich et al., 1992; Poorter and Bongers, 2006). These thin and

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tender leaves, with higher water content and lower lignin concentration, are preferred by herbivores in tropical forests (Poorter et al., 2004). Therefore, earlier successional stages should represent vegetation patches with higher palatability for herbivores (Coley and Barone, 1996), and this has been well established for insects. For instance, in early successional stages, 93% of the insect community consists of herbivores and this proportion decreases as succession progresses (Schulze et al., 2005). Furthermore, herbivory rates by insects are higher for light-demanding plants compared to shade-tolerant plants (Ruiz-Guerra et al., 2010), declining with species successional position (Poorter et al., 2004).

Although the impacts of large mammalian herbivores on vegetation regeneration is widely acknowledged (Danell et al., 2006), few studies have focused on the effects of successional stages on patch selection by these species. In boreal and temperate forest, these large herbivores do indeed select early successional stages for foraging (Pastor and Naiman, 1992), including treefall gaps (Kuijper et al., 2009). In tropical forests, however, studies on plant and patch selection by large mammalian herbivores are limited. Nonetheless, the selection of early successional stages for foraging may explain the commonly observed pattern of higher abundance of ungulates in secondary compared to primary tropical forests (Parry et al., 2007).

Here, we investigate if the Lowland tapir (*Tapirus terrestris*) prefers early compared to late successional forest patches, aiming at contributing to the understanding of the ecological role of the largest terrestrial South American herbivore, and to conservation strategies for this endangered species. By sampling 12 vegetation patches across a 20,000-ha continuously-forested landscape in the Brazilian Atlantic Forest, we tested the hypothesis that tapirs use more intensively vegetation patches in earlier succession stages and/or with more treefall gaps, as expected by the optimal foraging theory.

Material and methods

Study species

The Lowland tapir (*Tapirus terrestris*) is the largest terrestrial mammalian herbivore in South America. They are solitary browsing ungulates that feed on a wide variety of species and plant parts (Hibert et al., 2011; Tobler, 2002). Although there are many studies on the diet of the Lowland tapir, the vast majority is based on the identification of seeds in feces and stomach contents (e.g. Bodmer, 1990). However, most of the ingested food is composed of fibers and leaves (Hibert et al., 2011; Tobler, 2002) of tree species (Simpson et al., 2013). Thus, the Lowland tapir should play a key ecological role in structuring plant communities via herbivory given their body size (Padilla and Dowler, 1994), relatively large home ranges (Cabrera et al., 2016), high percentage of activity time (~90%) spent on foraging (Medici, 2010), and the large amount of consumed food (Clauss et al., 2009).

The number of studies on the use and selection of vegetation patches by tapirs, however, is considerably lower than those dedicated to their diet. Some studies have addressed habitat characteristics, such as slope, water availability, and vegetation types (e.g. Salas, 1996; Tobler, 2002). Some of them indicate that *T. bairdii* and *T. terrestris* frequently use secondary forests and treefall gaps (Foerster and Vaughan, 2002; Naranjo, 1995; Salas, 1996). In contrast, Medici (2010) noted that *T. terrestris* avoids secondary areas, preferring riparian and tall mature forests in the Atlantic Forest, and other studies also reported that primary forest was more frequently used by *T. pinchaque* (Lizcano and Cavelier, 2000). Nevertheless, none of these studies was specifically designed to compare the use of forest patches in different successional stages by tapirs.

Study area

The study was conducted in an area of about 20,000 ha within the largest tract of continuous Atlantic Forest in Brazil (Fig. 1), located in the plateau of Serra do Mar, a coastal mountain range in the State of São Paulo covered by dense ombrophilous forest, at about 900 m of altitude. The area is situated within one of the most humid regions in Brazil. Despite the seasonal variation in temperature and rainfall – January is the month of highest temperature and precipitation (average 22 °C and 246 mm) and July the coldest and driest month (average of 15.1 °C and 46 mm) – there is no hydric deficit (Peel et al., 2007), and the forest is evergreen.

The 20,000-ha area encompasses part of a protected area (Serra do Mar State Park) and neighboring forested areas in private land, and it is covered mainly by old-growth forest that has not been clear-cut in the past, but may have suffered selective logging of the Juçara palm *Euterpe edulis*. Interspersed within the old-growth forest, there are patches of secondary forest that regenerated after clear-cutting or intense logging in the past.

The study area is home to a significant population of *T. terrestris*, and tapirs are often seen in the study area. However, the species is considered extinct in 14% of its original range, including extensive areas in Argentina, Brazil, Colombia and Venezuela. In the Atlantic Forest, the species is currently absent in many remnants outside protected areas (Canale et al., 2012).

Sampling design

Within the 20,000-ha study area, we established 12 sampling sites (Fig. 1), six located in forest patches in earlier successional stages (i.e. patches of secondary forest that regenerated after clear-cutting or intense logging in the past) and six in patches of later succession stages (old-growth forests that were not clear-cut or intensively logged) (see Appendix S1 in Supplementary material). Forest patches in different successional stages were first identified from satellite images (Google Earth™ Digital Globe/2010 Geoeye) and aerial photographs, and, subsequently, visited to check the successional stage in the field. We chose the largest available patches (minimum size 12-ha) with no sign of hunting activity found in the field, which were structurally connected to continuously-forested areas (with no paved roads, eucalyptus plantations or human settings isolating them) and at least 1000 m apart from each other (Fig. 1). All patches were accessible on foot, being at most 1000 m from dirty roads.

In each sampling site we established two 320-m long perpendicular transects, marked every 20 m from the central point (33 sampling points in total), defining 32 20-m long sampling sectors (Fig. 1).

Use of forest patches by *Tapirus terrestris*

At each of the 12 sampling sites, we carried out six sampling sessions between March and August 2011. In the first sampling session, each site was sampled for seven nights (excepting one sampled for 10 nights), and in the remaining five sessions, for four nights (excepting one sampled for eight nights in the third session). The interval between sampling sessions within the same site ranged from 16 to 27 nights.

In each sampling session, each site was visited twice. On the first visit, two camera traps were installed in front of each other in the central point, and transects were inspected to erase tracks of *T. terrestris*. At the end of each session, the sites were revisited to uninstall the camera traps and map the new tracks found within 1.5 m from both sides of the transects.

For each site, we quantified (1) capture history along the six sampling sessions (presence-absence of tapir in each session as

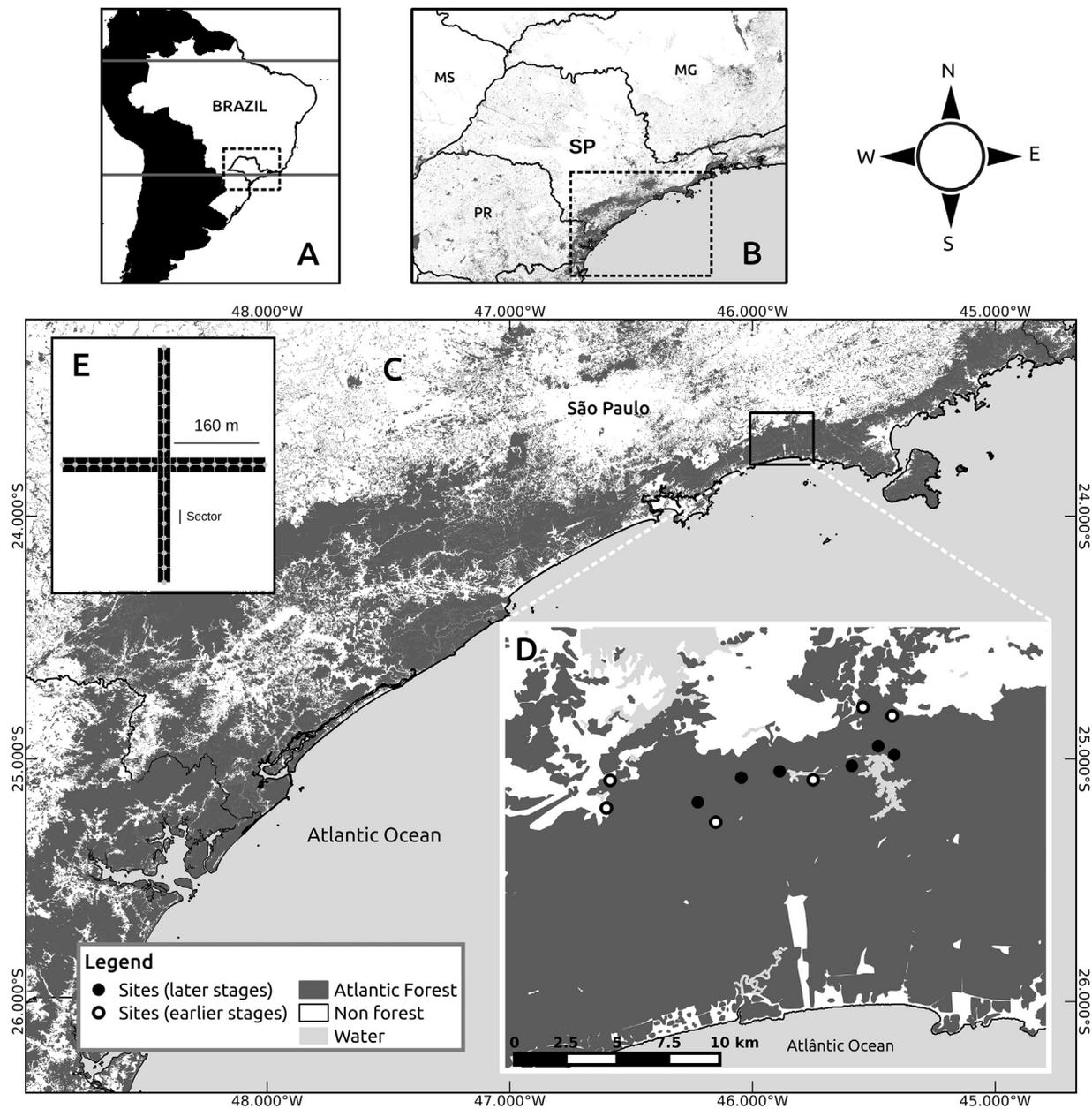


Fig. 1. Map of the study area showing (A) the location of the State of São Paulo in Brazil, and the Equator and the tropic of Capricorn, for reference, (B) the distribution of Atlantic Forest remnants concentrated along the coast, (C) the location of the study area within the largest tract of continuous Atlantic Forest in Brazil, (D) the distribution of the 12 sampling sites in earlier and later successional stages, and (E) a schematic representation of the two 320-m long transects used to collect data in each sampling site.

recorded by either cameras or new tracks) and (2) the number of transect sectors in which we recorded new tracks of *T. terrestris* (see Data analysis below).

Quantification of successional stage and treefall gaps

Successional stage does not depend only on time since abandonment, but also on factors such as distance from propagule sources and land use intensity before abandonment (Guariguata and Ostertag, 2001). As such, the quantification of key vegetation characteristics associated with forest succession is a better approach to determine the successional stage of forest patches than the age of the patches alone (Pinotti et al., 2012). To characterize the successional stage of each patch, we measured 13 vegetation structure variables that define the successional stages in the Atlantic Forest (Brasil, 1994) and in tropical forests in general (Clark, 1996)

at the 33 points along the transects of each site. At each point, we measured canopy height (the average of three measures taken by three observers using a range finder), and we estimated in four categories (from 0 to 3 – absent, low, medium, and high) the density of the understory, of herbaceous ground cover, of palm trees (family Arecaceae), of tree ferns (genus *Dicksonia*), of heliconias (family Heliconiaceae) and of trees in four classes of DBH (<5 cm, 6–20 cm, 21–50 cm, and >50 cm). We also estimated leaf litter decomposition, and size and abundance of epiphytes in four categories (from 0 to 3 – absent, little decomposed/small/rare, decomposed/medium-sized/common, and strongly decomposed/large/very abundant). In addition to these 13 vegetation structure variables, we registered the presence of visible treefall gaps from each of the 33 points of each site.

From these data, we calculated for each site the mean canopy height and the median value of the 12 remaining vegetation struc-

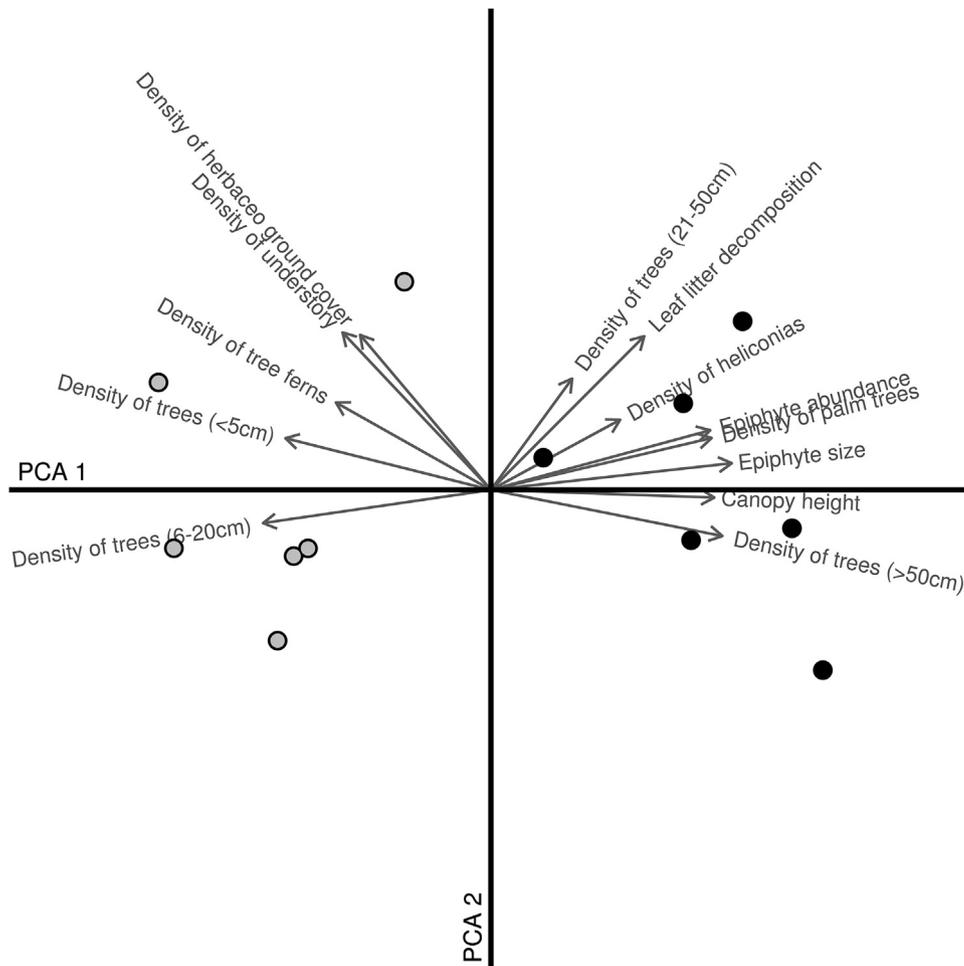


Fig. 2. Principal component analysis of the 13 vegetation structure variables associated with forest succession across the 12 sampling sites. Successional stages of the sampling sites: early stages (light circles) and late stages (dark circles). Site scores on the first axis (PCA1) were used as a continuous variable representing the main changes in vegetation structure during succession. For the density of trees, the range in DBH is presented in parentheses.

ture variables among the 33 points. The 13 vegetation structure variables were then used in principal component analysis (PCA) in a correlation matrix, and the scores of sites on the first axis of this analysis were used as a continuous, synthetic variable representing differences in successional stages among the 12 sampled patches (Fig. 2). We also calculated the number of points where treefall gaps were visible, as a standardized and relative estimate of the area of the patch covered by treefall gaps.

Data analysis

We performed two different analyses to evaluate the influence of successional stage and treefall gaps on patch use by tapirs. First, the capture history (presence-absence of camera or track records of tapirs) in each site along the six sampling sessions was used in abundance models (modified from occupancy models) to estimate the number of tapirs using each forest patch. Second, the number of transect sectors with new tracks in each sampling session and site was used to estimate the intensity of use of each patch by tapirs and was analyzed using mixed-effects models. By computing the number of transect sectors with new tracks, we aimed to minimize the spatial dependence between sequential tracks, as tracks were counted only if in distinct sectors (although some dependency may still exist between tracks in different sectors). However, because all sampled patches contained the same number of perpendicular transects of the same size, the number of 20-m long sectors with

new tracks of tapirs at the end of the sampling session represents a standardized and relative measure of the area of the patch used by tapirs across the 12 sampling patches.

In both analyses, the candidate models were constructed to evaluate the effects on patch use by tapirs of (1) the successional stage of forest patches (quantified by the each of 13 vegetation structure variables, and synthesized into the PCA1 in Fig. 2), and (2) treefall gaps (quantified as the number of transect points with visible treefall gaps). As such, the candidate models included only a variable related to successional stage, only the variable related to treefall gaps, or both a variable related to successional stage and the variable related to treefall gaps, besides a model with no variable (as a reference). We considered not only PCA1 but also each of the 13 vegetation structure variables measured to quantify successional stage in the candidate models to be able to evaluate which aspect of the vegetation change during succession is important to determine patch use by tapirs. However, as they are (and should be) highly correlated (Fig. 2) and are synthesized in PCA1, we did not include models with more than one of these variables.

First analysis

Abundance models, modified from occupancy models (MacKenzie et al., 2002), were developed to allow the estimation of abundance from presence-absence data (capture history along sampling sessions) without having to uniquely identify the individuals (Royle and Nichols, 2003). The model estimates two

parameters: λ (abundance, i.e. the number of individuals per site) and r (detection probability per individual of the species). Given the small size of the sampling sites relative to the home range of *T. terrestris*, the abundance parameter (λ) should be interpreted as an estimate of the number of individuals that use the sampling site (Chandler et al., 2011), i.e. the number of individuals whose home ranges encompass the sampling site, irrespectively of the individuals being or not the same between sites.

We considered the following set of 32 candidate models following the general reasoning explained above: one model with both parameters (r and λ) constant (as a reference); 14 models with each of the 14 successional stage variables (each of the 13 vegetation structure variables plus the synthetic PCA1) as covariates of abundance (λ) and detection probability (r) constant; one model with the treefall gap variable (the number of points with visible treefall gaps) as a covariate of abundance (λ) and detection probability (r) constant; 14 additive models with the treefall gap variable together with each of the 14 successional stage variables as covariates of abundance (λ) and detection probability (r) constant; a model with sampling effort (number of sampling nights in each sampling session at each site) as a covariate of detection probability (r) and abundance (λ) constant; a model with sampling session as a covariate of detection probability (r) and abundance (λ) constant. These last two models were included to take into account the effects of the variable sampling effort and the different sampling sessions on the results.

Second analysis

To evaluate the intensity of use of forest patches by tapirs, we used the number of transect sectors with new tracks of tapirs at each site and sampling session as the dependent variable in generalized mixed-effects models (GLMM), which allow to incorporate spatial and temporal dependence as random effects (Bolker et al., 2009). We modeled the dependent variable as a Poisson variable, using log as the link function and site and sampling session as random factors. However, because variance in the dependent variable was greater than the mean, we accounted for overdispersion by adding an observation-level random effect (a new grouping variable with a separate level for every observation in the data set), as a way to add more variance to the distribution (Harrison, 2014). The resulting lognormal-Poisson distribution is similar to a negative binomial distribution. As sampling effort varied among sites, in all models we inserted the effort (sampling nights in each site and session) as an offset variable (regression coefficient equal to 1), so that the dependent variable was divided by this term (Crawley, 2007). The set of 30 candidate models followed the same general reasoning used for the abundance models, and comprised: a model with no fixed factors (as a reference); 14 models containing as the fixed factor each of the 14 successional stage variables (each of the 13 vegetation structure variables plus the synthetic PCA1); one model containing as the fixed factor the treefall gap variable (the number of points with visible treefall gaps); and 14 additive models containing as fixed factors the treefall gap variable together with each of the 14 successional stage variables.

In both analyses, models were compared using Akaike Information Criterion for small samples (AICc) (Burnham and Anderson, 2004). The plausibility of each alternative model in relation to the first-ranked model was estimated by differences in AICc values (ΔAICc), with $\Delta\text{AICc} \leq 2$ indicating equally plausible models. All analyses were performed in R environment (R Development Core Team, 2016), using the packages “vegan” and “MASS” for the principal components analysis (PCA), the “Unmarked” package for abundance models and the “lme4” package for mixed-effects models.

Results

Variation in vegetation structure and successional stage among forest patches

The first axis of the principal component analysis explained 55% of the variation in vegetation structure among the 12 sampling sites. This axis represented a gradient from patches in earlier successional stages (left side of the chart) to patches in later successional stages (right side of the chart) (Fig. 2). Patches in earlier stages presented higher density of small trees (DBH <5 cm and DBH 6–20 cm), of the understory, of herbaceous ground cover, and of tree ferns. In contrast, patches in later stages presented higher canopy height, higher density of large trees (DBH 21–50 cm and DBH >50 cm), of palms, and of heliconias, higher epiphyte size and abundance, and greater decomposition of the leaf litter (Fig. 2).

Use of forest patches by *Tapirus terrestris*

On every occasion (sampling session per site) when *T. terrestris* was recorded by camera traps it was also registered through its tracks. All 12 sampling sites were occupied by *T. terrestris* during the sampling period, i.e. all sites presented records of tapirs in at least one of the six sampling sessions. In contrast, the number of sessions with records ranged widely among sites, from 1 to 6 sessions in sites classified a priori as earlier successional stages (mean = 4.33 and SD = 1.96), and from 2 to 5 sessions in sites classified a priori as later successional stages (mean = 3.66 and SD = 1.21). The number of transect sectors with new tracks in each sampling session ranged from 0 to 10 sectors in sites classified a priori as earlier successional stages (mean = 2.58 and SD = 2.86) and from 0 to 9 in sites classified a priori as later successional stages (mean = 1.80 and SD = 2.06).

Two abundance models were selected, the one with both parameters (λ and r) constant being the first ranked (Table 1). The second selected model contained – as a covariate of abundance – the density of heliconias, indicating that the number of tapirs that used patches increased as the density of these plants, that are characteristics of later successional stages, decreased. As estimated from the first-ranked constant model, the number of individuals that used each forest patch during the study was 5.3 (SE = 3.8) and detection probability was 0.20 (SE = 0.14).

In contrast, six generalized mixed-effects additive models were selected (Table 2). All of them contained the treefall gap variable (number of points with visible treefall gaps, positive effect) plus one of the following successional stage variables: the density of small trees (DBH 6–20 cm, positive effect), the density of large trees (DBH >50 cm, negative effect), canopy height (negative effect), the successional stage as synthesized by PCA1 (negative effect), litter decomposition (negative effect) or the size of epiphytes (negative effect). This set of selected models thus indicates that *T. terrestris* used more intensively patches with a higher cover of treefall gaps and those in earlier successional stages, where smaller trees were common, larger trees were uncommon, the canopy was lower, leaf litter was less decomposed and epiphytes were smaller.

Discussion

Our findings suggest that the Lowland tapir select forest patches in earlier successional stages, including those with higher cover of treefall gaps. Since the Lowland tapir spend approximately 90% (Medici, 2010) of their activity time foraging, we assume that this preference is mainly associated with foraging. The selection of forest patches in early successional stages is in agreement with optimal foraging theory (Stephens and Krebs, 1986), as these vegetation patches present higher availability of palatable plants (Cates

Table 1
Ranking of abundance models for the Lowland tapir across 12 forest patches varying in the successional stage. Highlighted in gray are selected models ($\Delta\text{AICc} < 2$). λ : abundance; r : detection probability; K : number of parameters; Log-likelihood: Maximum likelihood estimation; AICc: Akaike Information Criterion for small samples; ΔAICc : difference in AICc between the model considered and the first-ranked model; AICc weight: weight of evidence; Coef.: coefficients; SE: standard error; CI: 95% confidence interval; Low: low limit; Upper: upper limit. The table shows the models with weight of evidence ≥ 0.03 .

Models	K	Log-likelihood	AICc	Δ AICc	AICc weight	First variable				Second variable			
						Coef.	SE	95 % CI		Coef.	SE	95 % CI	
								Low	Upper			Low	Upper
λ (.), r (.)	2	-44.491	94.315	0	0.174								
λ (Heliconias), r (.)	3	-42.746	94.493	0.177	0.159	-0.395	0.202	-0.791	0.000				
λ (Canopy height), r (.)	3	-43.909	96.818	2.502	0.050	-0.050	0.046	-0.140	0.041				
λ (Understory), r (.)	3	-43.910	96.819	2.504	0.050	0.376	0.346	-0.303	1.055				
λ (DBH > 50 cm), r (.)	3	-43.985	96.971	2.655	0.046	-0.307	0.318	-0.930	0.315				
λ (Herbaceous cover), r (.)	3	-43.986	96.973	2.657	0.046	-0.260	0.259	-0.768	0.248				
λ (Tree ferns), r (.)	3	-44.074	97.148	2.833	0.042	-0.229	0.252	-0.722	0.264				
λ (Heliconias + Gaps), r (.)	4	-41.753	97.221	2.906	0.041	-0.528	0.233	-0.985	-0.071	0.052	0.038	-0.021	0.126
λ (Canopy height + Gaps), r (.)	4	-41.863	97.441	3.126	0.036	-0.156	0.071	-0.295	-0.016	0.100	0.047	0.009	0.192
λ (DBH 21-50 cm), r (.)	3	-44.242	97.484	3.169	0.036	0.481	0.632	-0.758	1.719				
λ (Epiphytes size), r (.)	3	-44.334	97.668	3.352	0.033	-0.128	0.231	-0.581	0.325				
λ (Litter decomposition), r (.)	3	-44.375	97.750	3.435	0.031	0.172	0.360	-0.877	0.534				
λ (Gaps), r (.)	3	-44.407	97.813	3.498	0.030	0.015	0.036	-0.055	0.084				

and Orians, 1975; Poorter et al., 2004), which are accessible to large terrestrial mammals because trees are smaller and shorter (Simpson et al., 2013). Similarly, plants growing under treefall gaps in tropical forests have high primary production rates and invest less in defenses against herbivores (Coley and Barone, 1996). Thus, *T. terrestris* seems to maximize energy intake and minimize search costs by selecting forest patches where plants are more nutritious

and palatable, and primary productivity is higher and concentrated close to the ground (Poorter et al., 2004; Simpson et al., 2013).

Despite the scarcity of studies on tapirs, the selection of either vegetation patches in early successional stages (including treefall gaps) or more palatable pioneer plants seems to be a recurrent pattern for other large mammalian browsers (Kuijper et al., 2009; Pastor and Naiman, 1992). For instance, in boreal forests where the few tree species differ sharply in distribution across the landscape

Table 2
Ranking of generalized mixed-effects models (GLMM) for the intensity of use by the Lowland tapir of 12 forest patches varying in the successional stage. Highlighted in gray are selected models ($\Delta\text{AICc} < 2$). K : number of parameters; Log-likelihood: maximum likelihood estimation; AICc: Akaike Information Criterion for small samples; ΔAICc : difference in AICc between the model considered and the first-ranked model; AICc weight: weight of evidence; Coef.: coefficients; SE: standard error; CI: 95% confidence interval; Low: low limit; Upper: upper limit. The table shows the models with weight of evidence ≥ 0.03 .

Models	K	Log-likelihood	AICc	Δ AICc	AICc weight	First variable				Second variable			
						Coef.	SE	95 % CI		Coef.	SE	95 % CI	
								Low	Upper			Low	Upper
DBH (6-20 cm) + Gaps	6	-138.369	290.030	0	0.140	0.905	0.332	0.254	1.556	0.132	0.044	0.045	0.219
DBH (> 50 cm) + Gaps	6	-138.725	290.743	0.713	0.098	-0.867	0.354	-1.561	-0.174	0.098	0.038	0.023	0.174
Canopy height + Gaps	6	-138.828	290.949	0.919	0.089	-0.165	0.071	-0.304	-0.027	0.144	0.054	0.038	0.249
Synthesis variable + Gaps	6	-138.925	291.142	1.112	0.080	-0.237	0.101	-0.434	-0.040	0.119	0.045	0.030	0.207
Litter decomposition + Gaps	6	-139.096	291.485	1.455	0.068	-0.864	0.377	-1.603	-0.126	0.112	0.044	0.026	0.197
Epiphytes size + Gaps	6	-139.115	291.522	1.492	0.067	-0.577	0.259	-1.084	-0.069	0.095	0.040	0.017	0.173
Constant (null model)	4	-141.809	292.214	2.185	0.047								
Heliconias + Gaps	6	-139.584	292.461	2.431	0.042	-0.468	0.244	-0.946	0.009	0.072	0.037	-0.001	0.145

and in C:N ratio (Vancleve et al., 1983), moose (*Alces alces*) forage preferably in patches in early successional stages (Pastor and Naiman, 1992) of poplars (*Populus* spp.) and birches (*Betula* spp.) – highly palatable pioneer species (Bryant and Kuropat, 1980). Similarly, large herbivores in European temperate forests forage more frequently and spend more time inside forest gaps than in mature forest (Kuijper et al., 2009).

More specifically, our results suggest that the successional stage of forest patches influences not necessarily the number of tapirs using vegetation patches, but the intensity of use of these patches by individuals, as indicated by the number of transect sectors with tracks. Given the body mass of *T. terrestris*, its relatively large home range size and vagility (Medici, 2010; Cabrera et al., 2016), an effect on the number of individuals would indeed have been expected only at larger spatial scales, in landscapes dominated by forest patches in earlier successional stages compared to landscapes dominated by patches in later successional stages, for instance.

The variables included in the GLMM selected models also indicate that tapirs used more intensively patches characterized mainly by a higher cover of treefall gaps and by higher densities of smaller and shorter trees, and consequently lower densities of larger and taller trees. These results are in accordance with previous knowledge on the biology and diet of tapirs. First, although previous studies on tapirs did not directly compare use of patches in different successional stages, there is some evidence that *T. terrestris* indeed prefers treefall gaps for foraging, as browsing signs are more frequent and severe in plants under treefall gaps than close-canopy areas (Hibert et al., 2011; Salas, 1996). Second, it is generally recognized that ungulate browsers, such as tapirs, are and have always been associated with forest environments (Agustí and Antón, 2002), where their diet consists predominantly of leaves and new shoots of several trees species and shrubs (Gill, 2006) supplemented by small thin twigs (Shipley et al., 1999). Hibert and colleagues (2011) identified that 1/3 of plants consumed by *T. terrestris* are tree species, 1/3 are bushes, and only 1/4 are herbaceous. Similarly, Simpson et al. (2013) studied browsing signs of the Malayan tapir (*Tapirus indicus*) in a 30-ha natural tropical forest enclosure and identified that about 70% of the browsed plant individuals are tree saplings and 23% are shrubs, and tapirs usually browse on leaves, shoots, twigs and branches. Correspondingly, we found no evidence of tapirs preferring herbaceous vegetation, commonly dominated by grasses in the study area. Only grazers such as horses (*Equus caballus*), elk (*Cervus elaphus*) and cattle (*Bos primigenius*) present hipodont teeth (with tall crowns and continuous growth), capable of grinding abrasive grasses (MacFadden, 2000).

It is important to highlight that, although we show here that tapirs select patches in earlier successional stages to forage, this does not mean that old-growth forest is not necessary for the persistence of the species. Old-growth forests offer several key resources to tapirs, especially fruits, which are important components of their diet (Bodmer, 1990; Camargo-Sanabria and Mendoza, 2016), but also treefall gaps, water bodies and mineral licks (Tobler et al., 2009). Hence, in contrast to continuously forested successional mosaics, composed by both old-growth forest and secondary forest patches (as studied here), tapir populations may not persist in landscapes dominated only by secondary forests or in those composed by isolated secondary forest patches (Norris et al., 2008).

Implications

Our results indicate that *T. terrestris* uses more intensively and forages more frequently in patches of forest in earlier successional stages (areas with higher density of smaller and shorter trees) and in patches with a high cover of treefall gaps that tend to be more common in later successional stages. This suggests that mosaics encompassing both old-growth and secondary forests are suitable

habitats for tapirs. As the rates of degradation and conversion of rainforests are increasing worldwide, and secondary forests are expanding due to land abandonment (Wright, 2010), the inclusion of neighboring secondary forests in protected areas of old-growth forest (Chazdon et al., 2009) is an alternative to the conservation of *T. terrestris*.

Our results indicate that herbivory by the largest terrestrial herbivore of the Neotropics is more intense in patches in earlier successional stages, including treefall gaps, suggesting that tapirs may influence forest regeneration. Large mammalian herbivores can accelerate, hold or delay the succession process depending on, among other factors, the intensity of herbivory (Hester et al., 2006), the ratio of palatable and non-palatable plant species (Olf et al., 1999) and the ability of plant species to prevent (escape or defense) or tolerate herbivory (Rosenthal and Kotanen, 1994). Tapirs consume a wide variety of plant species, the majority of which are infrequently eaten, and even for species that are frequently eaten, not all individuals are browsed and rarely all available foliage is consumed (Simpson et al., 2013). Together with the fact that tapirs are solitary animals, this suggests that the intensity of herbivory should be low and tapir foraging may favor forest regeneration and the maintenance of plant diversity. It is important that future studies test this hypothesis, by investigating the selection by tapirs of plant species and plant parts within patches of secondary vegetation, and the responses of plants to tapir herbivory.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2017.08.001>.

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