Effects of seasonality and habitat on the browsing and frugivory preferences of *Tapirus terrestris* in north-western Amazonia

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Abstract: Herbivore foraging is influenced by spatial and seasonal changes in the production of leaves and fruits. To understand how herbivores respond to these changes, it is necessary to identify their habitat preferences and how they use the vegetation available. In the Neotropical region, one of the largest terrestrial herbivores is the lowland tapir (*Tapirus terrestris*), a species important for its dual role as browser and seed disperser. The objective of this study was to determine the species and plant components (leaves, fruits) utilized by *T. terrestris* in different time periods and habitats, in relation to changes in food availability in the north-western Amazon. Tapir diet was established through identification of browsing signs and faecal analysis, from data collected in the field during the months of March, April, August and September of 2015. Plant species availability for browsing was sampled in ten 2 × 50-m transects and fruit productivity was estimated in linear transects (∼9 km). We found that *T. terrestris* mostly consumed vegetative parts, i.e. fibre (70–90%), and to a lesser extent fruits (10–30%). Food consumption was selective and concentrated in habitats with higher availability of preferred plants. When fruit intake increased, selectivity in browsing became more intense and limited to preferred species. This information, coupled with our findings about seasonal differences in browsing vs. frugivory patterns, provides valuable knowledge for understanding how environmental heterogeneity may influence the foraging ecology of the lowland tapir.

Key Words: diet selection, food availability, large herbivore, lowland tapir, tropical humid forest

INTRODUCTION

The lowland tapir (*Tapirus terrestris*, Linnaeus, 1758), one of the largest terrestrial herbivores in South America, is a browser and frugivore that plays an important role in long-distance seed dispersal (Bello *et al.* 2015, Fragoso *et al.* 2003), and high browsing rates of certain plant species (Salas & Fuller 1996). *Tapirus terrestris* occurs from Colombia to northern Argentina and is found in heterogeneous landscapes composed of habitats of different composition, structure and phenological patterns (Chalukian *et al.* 2013, Medici 2010, Tobler *et al.* 2009). Both differences in habitat composition and seasonal variation are known to affect animals, which respond by dietary switching and changes in habitat use (Fleming *et al.* 1987, Ricklefs 1977, van Schaik *et al.* 1993).

One theory regarding the expected use of heterogeneous food sources, is the optimal foraging theory (OFT) which proposes that animals should maximize their energy intake in foraging activities (Pianka 2008). OFT predicts that animals have different selection criteria in diet and habitat use (Fortin *et al.* 2003), such that they choose quality resources that are best able to satisfy their requirements for survival and reproduction (Manly *et al.* 2002). In a diet selection scenario, it is expected that different food types are eaten independent of their abundance in the habitat, except for preferred food types (whose consumption depends on their availability) (Pyke *et al.* 1977). On the other hand, in a habitat-selection scenario, it is expected that animals will allocate more time in areas with a greater abundance of preferred food (Pyke *et al.* 1977).

Empirical studies have also emphasised the importance of food abundance and resource distribution in structuring feeding decisions (Stevenson 2004a) and habitat use of animal species (Fragoso 1997, Salas 1996). Downer (2001) reported that the Andean forest is a critical habitat for the mountain tapir (*Tapirus pinchaque*) because it contains a range of its preferred food items, including nitrogen-fixing plants. Furthermore, Salas

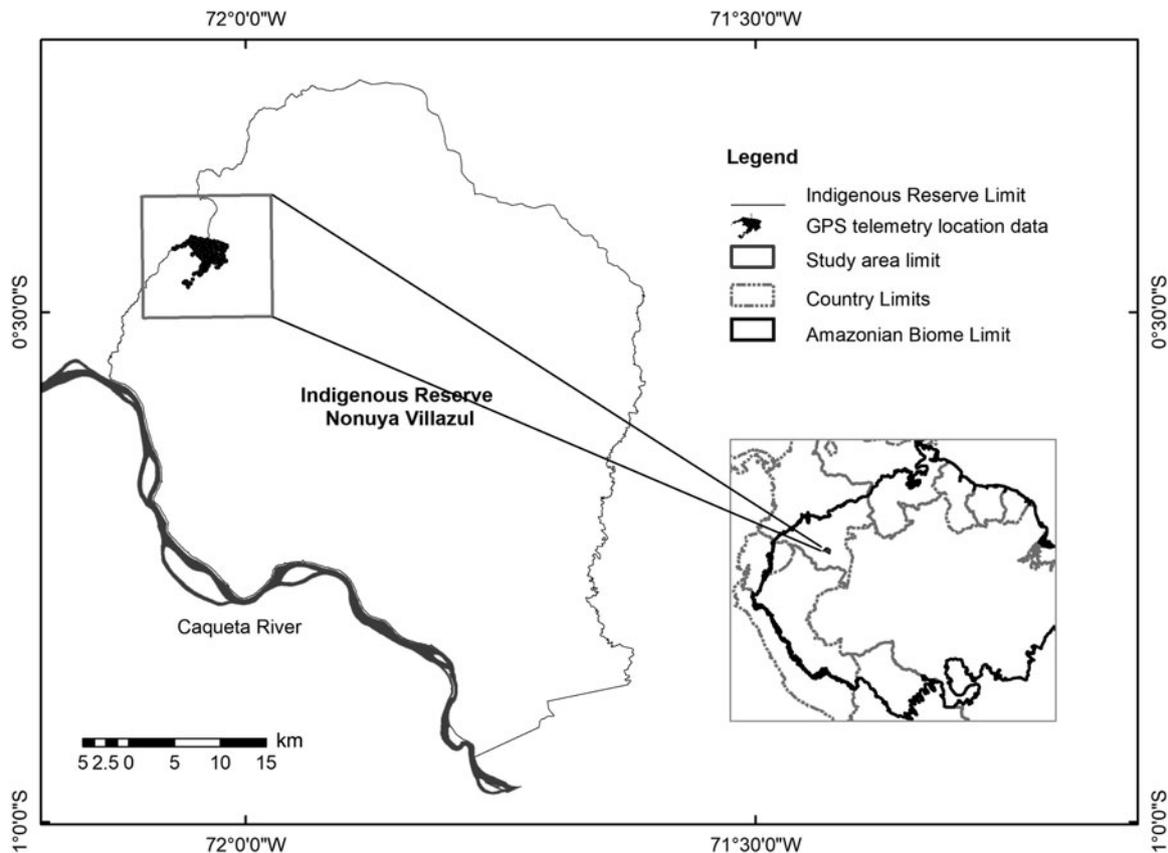* Corresponding author. Email: julianavelezgomez@gmail.com

Figure 1. Location of the Indigenous Reserve Nonuya Villazul (Department of Amazonas, Colombia). Black points represent GPS telemetry data of the lowland tapir in the study area.

(1996) found that *T. terrestris* consumes just a portion of available species and selects secondary-forest patches for browsing, probably due to the high density of understorey plants. However, many aspects of tapir interactions with vegetation, such as plant species selection and responses to seasonal variation in the presence of leaves and fruits, are not fully understood because of regional differences in the tapir's diet (Hibert *et al.* 2011, 2013). Given the spatial and seasonal heterogeneity of tropical forests, understanding how keystone species such as the lowland tapir use available resources (leaves vs. fruits), may help to identify how they respond to environmental change and impact forest dynamics (Hibert *et al.* 2011).

The objective of this study was to determine the species and plant components (leaves vs. fruits) utilized by *T. terrestris* in different time periods and habitats, in relation to changes in food availability in a heterogeneous area of the north-western Amazon, that contains high intra-regional variation in floristic composition (Duivenvoorden 1996, Londoño & Álvarez 1997). The hypotheses are: (1) the lowland tapir uses plant species independent of their abundance due to selectivity in its diet, probably related to differences in nutritional content of food items (Salas & Fuller 1996), (2) *T. terrestris* displays dietary shifts and

variation in plant consumption due to changes in food availability during different time periods, and (3) habitats with higher intensity of use by the lowland tapir contain higher abundance of plants selected in its diet.

METHODS

Study area

The study area lies in the Caquetá River Middle Basin (72°2′32′′W, 0°27′14′′S) (Figure 1), at an altitude varying from 150 to 300 m asl. It is located in the Indigenous Reserve Nonuya de Villazul, Department of Amazonas (Colombia). The climate is tropical with an average annual rainfall of 3060 mm and an average temperature of 25.7°C (Duivenvoorden & Lips 1995). The driest months are from December to February and the wettest from April to June, with a slight reduction in rainfall in the month of August (Duivenvoorden & Lips 1993). The area belongs to the tropical rain-forest system of Holdridge life zones (Holdridge *et al.* 1971). It comprises different geomorphological units, including floodplains of the Amazonian rivers and Tertiary sedimentary

plains (Duivenvoorden & Lips 1995), which differ in their respective landscape and floristic composition (Duivenvoorden 1996, Duivenvoorden & Lips 1993).

Plant species availability

In the months of March and August of 2015, ten transects (2 × 50 m, 0.1 ha) (Gentry 1982, Villarreal *et al.* 2004) were randomly established in habitat types used by *T. terrestris* during its feeding activity (17h00–9h00), according to a satellite telemetry study performed in the area (González *et al.* in press). Areas with higher intensity of use by the lowland tapir corresponded to *Mauritia flexuosa* swamps (extensive palm formations, where this species is dominant in the canopy) and the ecotone that it forms with the seasonal floodplain forest (hereafter floodplain) (González *et al.* in press). Areas with lower intensity of use by *T. terrestris* corresponded to terra firme forest (hereafter terra firme) (González *et al.* in press), of the Tertiary sedimentary plain, which presents a flat to undulating topography and is characterized by a high species richness (Duivenvoorden & Lips 1993, Parrado 2005).

In order to document the plants available for browsing, five transects were located in areas of higher intensity of use (*M. flexuosa* swamp and floodplain) and five in the area of lower intensity of use (terra firme). Each transect was longitudinally traced with a central rope, from where we measured 1 m to each side (Villarreal *et al.* 2004). The transects were distributed at random and placed at least 20 m apart (Villarreal *et al.* 2004). According to the optimal range for tapir browsing (Foerster & Vaughan 2002, Salas & Fuller 1996, Terwilliger 1978), any plant with a height of 30–150 cm (including branches within that range) and with a stem diameter greater than 0.7 cm (measured at 30 cm from the ground), was recorded, collected and identified (Table 1). The number of plants and basal areas were recorded in order to calculate the abundance, frequency and dominance of each species (Villarreal *et al.* 2004).

Fruit productivity

To estimate fruit productivity in the tapir's home range, three linear transects of ∼3 km each (with a total length of 8.7 km), were randomly established in trails (Stevenson 2017), located in areas of both high and low intensity of use by the lowland tapir. Two transects were distributed in terra firme due to the high proportion of this habitat in the home range (∼75%) and one transect was established covering the *M. flexuosa* swamp and the floodplain ecotone. The transects were sampled in March, April, August and September of 2015. During this time,

the procedure for the estimation of fruit productivity proposed by Stevenson (2004b) was followed, which involved recording and identifying all of the fruiting trees that projected their crown over the transects (Table 1).

A visual estimate of crop size was made by counting the number of fruits per tree (Chapman *et al.* 1992) and subsequently calibrated with fruit trap estimates (Stevenson 2004b). To do so, five plant species with capsular fruits or follicles (*Hevea* cf. *guianensis* Aubl., *Mollia lepidota* Spruce ex Benth., *Virola sebifera* Aubl., *Virola* JVG049, *Virola* JVG062) were selected and their fruit crop was calculated according to visual and fruit-trap estimates. Species with capsular fruits or follicles were used because fruit valves not ingested by frugivores can be counted to estimate crop size (Stevenson pers. comm.). Two individuals were sampled per species and five 1-m^2 fruit traps were established below each tree (Stevenson pers. comm.). The log-log linear relationship between the two estimates allowed for the correction of the visual estimates, determined as:

$$Ln\ (number\ of\ fruits) = -0.804 + 0.930$$
$$\times Ln\ (visual\ estimate)$$

Using the above formula, an R^2 of 0.79 was obtained. The correction was applied neither to palms nor cauliflorous plants (a total of 15 species) because they have fruits that are not covered by leaves and in many cases are clustered, so the original visual estimates are likely less biased (Stevenson 2004b).

The productivity of each fruiting tree was calculated by multiplying the average mass of 1–10 dried fruits, by the corrected estimate of the crop size. Fruit productivity of a given species was calculated by adding the productivity of the sampled individuals of that species and dividing by the sampling area (Stevenson 2004b). Because the probability of fruit detection is higher for large trees, their effective sampling area is larger than the one of small trees (Stevenson 2004b). In this way, we calculated the sampling area as the product between the total transect length (8.7 km) and the effective transect width for a given species (Stevenson 2004b). The sampling area for the recorded fruiting species ranged from 1–20 ha.

Browse sampling

During the sampling of the ten transects, which were established to document the availability of browsing plants in the months of March and August, plants that showed recent browsing signs such as freshly broken stems, cut leaves and remaining petioles (Hibert *et al.* 2011) were recorded and collected (Table 1). Only browsing signs with fresh tapir footprints underneath

Table 1. Methods used for the sampling of species availability, browsing signs, faeces and fruit productivity, in the Indigenous Reserve Nonuya Villazul (Department of Amazonas, Colombia), during March, April, August and September of 2015.

Components of the study	Sampling units	Number of units	Total sampled area (ha)	Sampling method
Plant species availability	Linear transects	10	0.1	Count of plants with a height of 30–150 cm, stem diameter > 0.7 cm
Browsing signs sampling	Linear transects	10	0.1	Count of browsed plants with a height of 30–150 cm, stem diameter > 0.7 cm
Fruit productivity	Linear transects	3	1-20	Fruit productivity estimation of fruiting trees projecting their crown over the transects
Faecal sampling	Faeces units	19	20	Faeces collection and macroscopic identification of fruit residuals

were recorded to minimize the error of recording signs of other ungulates (Downer 2001, Hibert *et al.* 2011, Lizcano & Cavelier 2004). The plant material was identified using keys, literature (Galeano & Bernal 2010, Gentry 1993, Steyermark *et al.* 1995) and consulting botanical experts.

Faecal sampling

Although leaves and twigs are expected to be the primary components of the tapir's diet (Hibert *et al.* 2011), we also evaluated fruit consumption by the lowland tapir, through the collection of dung samples during field expeditions in March (n = 6) and in August (n = 13) (Table 1). We walked the trail system established for fruit productivity estimation (8.7 km) eight times mo^{-1} in search of faeces. Most of the faeces were found in *Mauritia flexuosa* swamps (n = 15) and the rest were obtained in streams (n = 2) and in terra firme (n = 2). Only faeces that were relatively fresh (deposited a few days before), judged by their odour and colour, were collected (Tobler *et al.* 2010). Dung samples were deposited and washed in filter bags with a mesh size of 0.1 mm. They were dried in sunlight for a period of ∼2 wk and then they were placed in a plant drying oven at 70°C for 3 d (Tobler *et al.* 2010). They were sifted using a metal sieve with a 1-mm^2 grid size. For particles larger than 1 mm^2, the fibrous material and the fruit residuals (seeds, pieces of pericarp and scales) were separated and independently weighed to determine the percentage of each component in dung samples (Bodmer 1990). For particles smaller than 1 mm^2, this procedure was performed on a subsample of 3–10 g. The mass of the fibrous and fruit material was then extrapolated to the entire sample of small particles (Bodmer 1990). Fruit residuals were macroscopically identified by comparing them with a reference collection detailing the fruits available in the study area, with herbarium specimens and photographs (Salas & Fuller 1996). The relative mass (g) and relative frequency of each plant species was thereby obtained.

Data analysis

To evaluate which plant species are selected by the lowland tapir in the study area, meaning that they are consumed in greater proportion than their availability in the habitat, the Jacobs' selection index (D) was calculated for each species with: $D = \frac{r-p}{r+p-2rp}$ (Jacobs 1974). r represents the relative abundance of species in the tapir's diet and p the relative abundance of species available in the environment (Jacobs 1974). Values < 0 indicate negative selection (avoidance) and values > 0 indicate positive selection (preference). For the fruit component, the selection index could not be estimated for all species because of the low correspondence between fruiting species available in the habitat and those identified in the faeces. This type of index that uses availability in its denominator can present biased results as food items can frequently be present in the faeces but not in the sampled area (Tanentzap *et al.* 2009). Therefore, the selection index was calculated exclusively for species found both in the transects and in the faeces. To calculate the selection index for fruiting species, the relative frequency of each species in dung samples was used instead of the relative abundance. For browsed species that were found in the two sampling periods, the selection index was obtained by taking the average value from the two periods.

The relationship between food availability and plants' use by the lowland tapir was evaluated by means of a linear regression model (Salas & Fuller 1996). Analyses were conducted for each sampling period, using the data from the habitats where browsing signs were found (*Maurtia flexuosa* swamp and floodplain). The availability of each plant species was obtained with the Importance Value Index (IVI) expressing values of abundance, frequency and dominance (Phillips 1959, Villarreal *et al.* 2004) and the use of browsing species was estimated by referring to a combined index of use (CIb), which was calculated by adding the relative abundance and relative frequency of each browsed species (Downer 2001, Phillips 1959). Model residuals were obtained to identify the plant species that were the most or least consumed in relation

to their availability. A combined index of use of fruits (CIf) was also calculated by adding the relative frequency and the relative dominance of each plant species whose fruits were eaten by the lowland tapir. The relative frequency of a species with fruits consumed, was represented as the frequency of the species (number of faecal samples where the species was registered, divided by the total number of samples), divided by the sum of all species frequency. The relative dominance of a species with fruits consumed, was represented as the sum of the dry mass (g) of seeds or fruit residues of a species found in faecal samples, divided by the sum of all species dominances. The relationship between the CIf and fruit productivity of each plant species was evaluated by a regression analysis to determine whether fruit consumption depends on fruit availability. An average value of fruit productivity was calculated from the estimates obtained in March and April (hereafter, March) and those obtained in August and September (hereafter August), to establish two sampling periods that could later be compared. The mean values obtained were logarithmically transformed to better interpret patterns in the data.

To evaluate dietary shifts and understand how browsing and fruit consumption by the lowland tapir varies over time, an analysis of variance (ANOVA) was used to ascertain the differences in the dung´s fibre and fruit percentages during the two sampling periods (March and August). This was done after checking the normality distribution of the data set.

To analyse variation in plant consumption by *T. terrestris* in different time periods and determine which factors influence the presence of tapir browsing for a particular plant, a generalized linear mixed model (GLZ) was developed. This analysis was based on a saturated binomial model comprising the following fixed variables: family and sampling period (March and August), for each individual plant found along transects. Transect identity was delineated as a random variable to remove spatial autocorrelation. In the model, the three most abundant plant families were included (Rubiaceae, Melastomataceae and Fabaceae), while a fourth category included plants of the Arecaceae and Clusiaceae (A/C) families, and a fifth category comprised the rest of the families that are less abundant in the area (other). This grouping was necessary to acquire the three minimum data points required by the model when evaluating the variables of transect, family and sampling period in conjunction. The model with the lowest AIC value was selected. Because the model showed a significant interaction between the variables of family and sampling period, a Tukey–HSD test was performed to determine differences between various combinations of the levels of the two variables.

Finally, to assess the differences in the abundance of plant species available for the tapir in the different habitats

used (*M. flexuosa* swamp – floodplain and terra firme) (González *et al.* in press), a contrast of homogeneity from a chi-squared test was performed using data of plant individuals found along transects.

RESULTS

Use and selection of plant species in the lowland tapir's diet

From 1966 plant individuals recorded in the different habitat types present in the area, we found a total of 147 browsing signs. Browsing signs were only found in the two habitats highly visited by the tapir in the study area, according to telemetry data: i.e. *M. flexuosa* swamp and floodplain. A total of 50 out of 307 species recorded in these habitats were browsed, distributed among 35 genera and 25 families (Appendix 1). The Fabaceae, Melastomataceae and Rubiaceae had the largest number of positively selected species (Appendix 2). The three most abundant species in the tapir's diet, *Psychotria egensis*, *Psychotria campyloneura* and *Tococa macrosperma*, are relatively abundant in the habitat. However, these were consumed in greater proportion than expected by their availability, which was indicated by their positive selection index (D) (Appendix 2). Other abundant species in the habitat, such as *Graffenrieda* cf. *limbata*, were moderately consumed, and others completely avoided, for example, Rubiaceae sp. 11, *Ischnosiphon arouma* and *Oenocarpus bataua*.

Fruits from 24 species were consumed by *T. terrestris*, of which 18 could be identified to the family level, 17 to genus and three to species (Appendix 1). The most used taxa were *M. flexuosa* and *Pouteria* sp., which presented positive selection index values (D) (Appendix 2). Only three species were consumed in a lower proportion than that expected by availability (*Micropholis* sp., *Parinari* sp. and *Palicourea* sp.). A total of 81 fruiting species were not detected in the faecal analysis and 18 species consumed by the tapir were not recorded as fruiting in the study area.

A positive and significant association was found between browsing species availability (IVI) and the combined index of use of browsed species (CIb) in March ($R^2 = 0.22$, P < 0.001, N = 134) and August ($R^2 = 0.06$, P < 0.001, N = 240) (Figure 2a). These results were strongly influenced by the presence of some preferred species (*Psychotria campyloneura*, *Psychotria egensis*, *Psychotria limitanea*, *Tococa macrosperma* and *Zygia* cf. *inaequalis*) which presented intermediate abundances and positive residuals due to a high consumption by the lowland tapir (Figure 2b).

The consumption of fruits by *T. terrestris* showed a positive association with fruit production in March ($R^2 = 0.84$, P < 0.05, N = 11) and August ($R^2 = 0.69$,
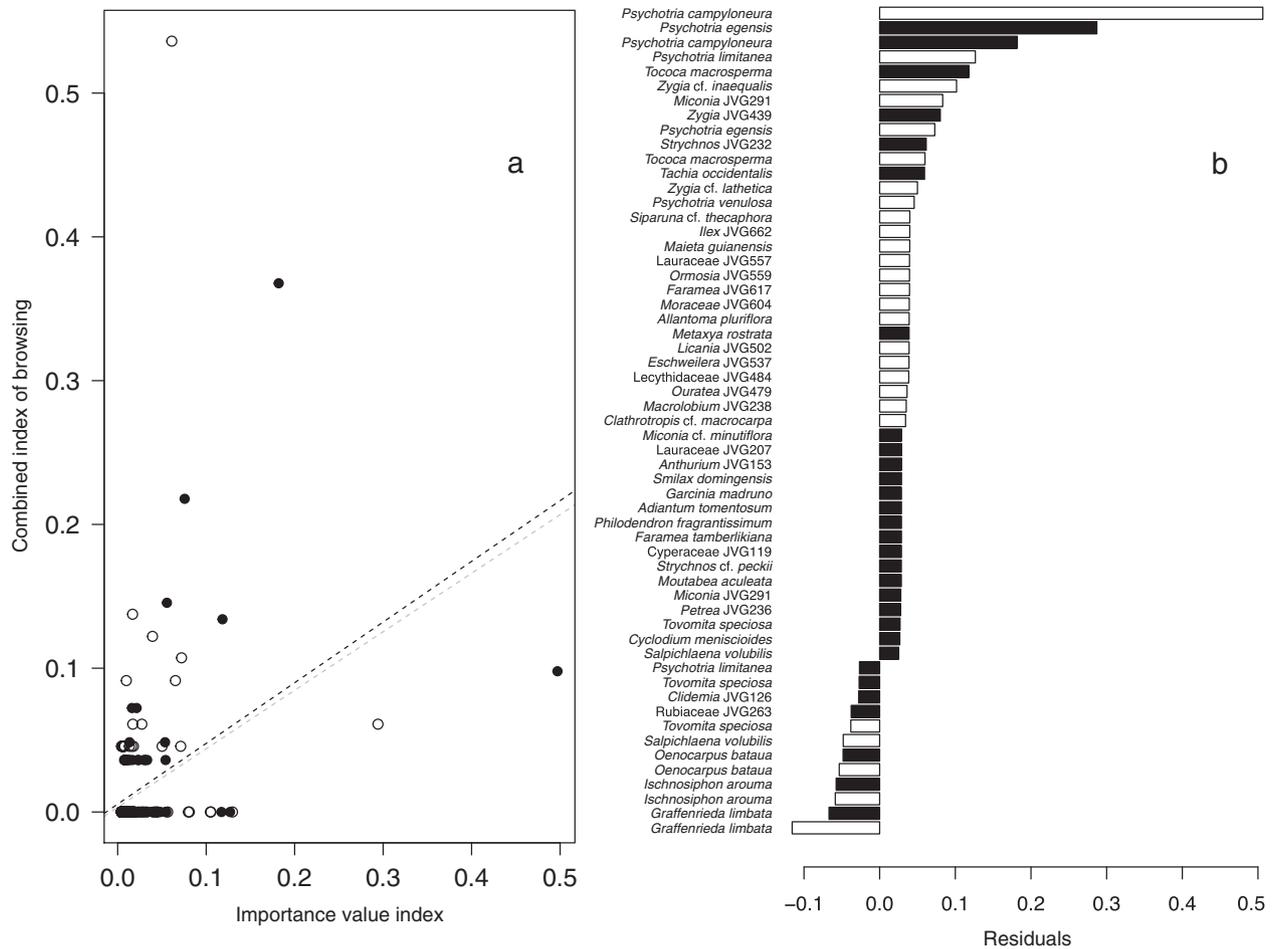
Figure 2. Analysis of *Tapirus terrestris* browsing in relation to food availability, in the Indigenous Reserve Nonuya Villazul (Department of Amazonas, Colombia), during March and August 2015. Relationship between the Combined Index of species browsed (CIb = Relative Abundance + Relative Frequency), with the Importance Value Index of species available in the habitat (IVI = Relative Abundance + Relative Frequency + Relative Dominance) in March (black) and August (white), 2015 (a). Residuals (< −0.025 and > 0.025) of the relationship between CIb and IVI are shown for each plant species (b).

$P < 0.05$, $N = 19$). However, this was due mainly to the high consumption of fruits from *Mauritia flexuosa* (Figure 3), which is very abundant in the area.

Seasonal variation in the tapir's diet

The diet of *T. terrestris* was mainly composed of vegetative (fibre) parts (70–90%) and to a lesser extent fruit (10–30%). Yet the percentage of fibre and fruit found in the faeces was significantly different in the two sampling periods (ANOVA, $F_{1,16} = 11.6$, $P < 0.001$), meaning fibre intake by the tapir was higher in March than in August, while the converse was true for fruit intake.

No differences were found in the browsing probability across families in March ($P > 0.05$) (Figure 4), but in August the browsing probability of the Rubiaceae was significantly higher than that of the other families

(except Fabaceae) ($P < 0.001$) (Figure 4). Comparing the browsing probability of each family in the two sampling periods, there were no significant differences for any family except for the category other, which reflected a higher browsing proportion in March than in August ($P < 0.001$) (Figure 4).

Food availability in the vegetation types used by tapir

From the two sampling periods (March and August), 438 plant species available for browsing by *T. terrestris* were identified, these being distributed in 103 genera and 61 families. The relative abundance of plant families was significantly different in the various habitat types ($\chi^2 = 820$, df = 112, $P < 0.001$). In the terra firme forest, the relative abundance of Arecaceae, Marantaceae, Myristicaceae and Marattiaceae was notably higher. In the *Mauritia flexuosa* swamp,
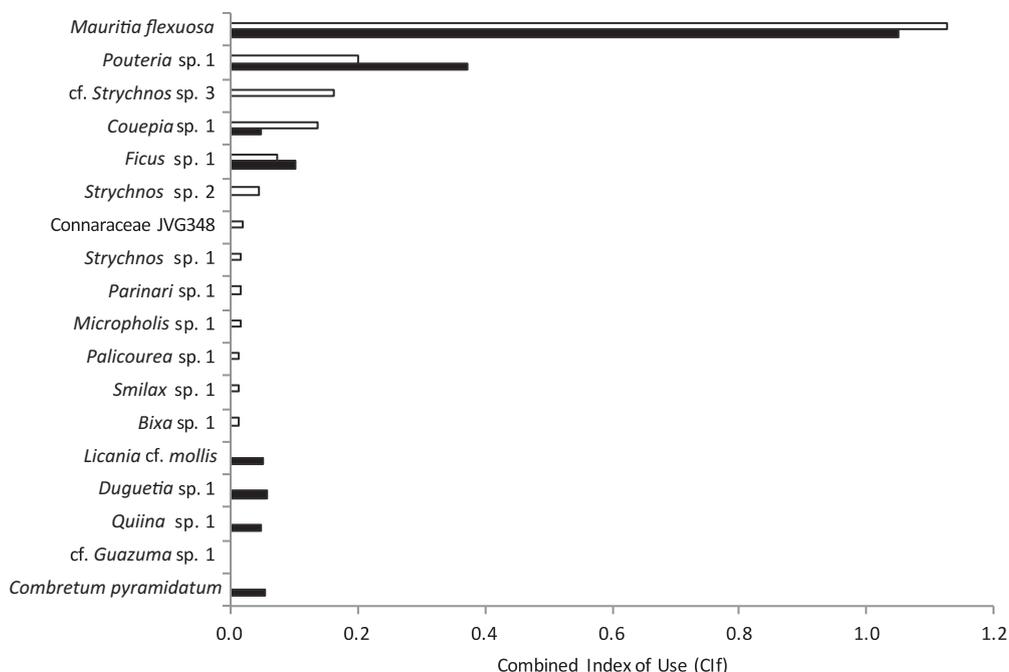
Figure 3. Combined index of fruit consumption found in the macroscopic analysis of *Tapirus terrestris* faeces retrieved from the Caquetá River Middle Basin. Black bars represent species consumed in March and white bars denote species consumed in August 2015.
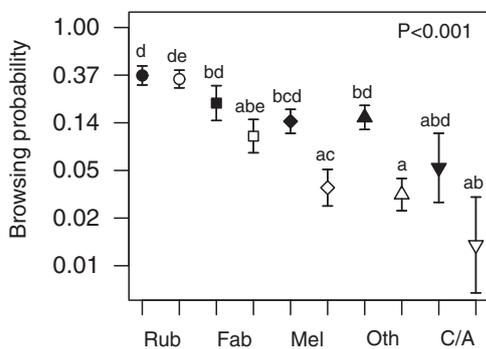

Figure 4. Browsing probability of different plant families found in the habitat of *Mauritia flexuosa* swamp and the floodplain forest ecotone in the month of March (black symbols) and August (white symbols), 2015. Different letters indicate significant differences in browsing probability between plant categories, according to the Tukey–HSD test. Acronyms for plant categories are Rub (Rubiaceae), Fab (Fabaceae), Mel (Melastomataceae), Oth (all other families) and C/A (Clusiaceae and Arecaceae).

Euphorbiaceae, Gentianaceae, Melastomataceae and Myrtaceae were significantly more abundant, while in the floodplain forest ecotone, Fabaceae, Malvaceae, Ochnaceae, Rubiaceae and Vochysiaceae were found in greater proportions.

Concerning fruit production, a total of 206 individual plants were fruiting during the sampling periods. Ninety species were identified, distributed among 57 genera and 33 families. Forty-two species were fruiting in March, 46 in April, 21 in August and 26 in September. Significant

differences in the relative abundance of fruiting species corresponded with different types of habitat ($\chi^2 = 322$, df = 174, P < 0.001). In the *M. flexuosa* swamp, the abundance of the species *Clusia* cf. *amazonica* Planch. & Triana, *Macrolobium* cf. *bifolium* (Aubl.) Pers. and *Mauritia flexuosa* L.f. was significantly higher. In the terra firme forest, the palms *Lepidocaryum tenue* Mart. and *Wettinia augusta* Poepp. & Endl. had a detectably larger abundance.

DISCUSSION

The results suggest that resource abundance and distribution are major forces driving tapir feeding and habitat use. The foraging of *T. terrestris* is influenced by the interaction between plant species availability in different habitats and seasonality, with the fruiting period of *M. flexuosa* largely affecting the diet of the tapir (Bodmer 1990).

The number of browsed species listed in this study (n = 50) is the highest ever reported for Colombia (Arias 2008, Solano *et al.* 1996), although lower than records in other countries such as French Guiana (Hibert *et al.* 2011). We also found a higher richness of plants with fruits consumed by the tapir than other studies in Peru (Bodmer 1990, Montenegro 2004), but lower than findings in Brazil (Barcelos *et al.* 2013).

In support of our first hypothesis, the results show a selective use of plant species by the lowland tapir, which is consistent with expectations from foraging theory (Pyke

et al. 1977) and with reports of selective browsing by the tapir in Venezuela (Salas & Fuller 1996). The positive association between CIb and IVI had low R^2 coefficients in both time periods (especially for August), and indicates that factors different from availability (e.g. secondary components) may influence plant use by the tapir (Salas & Fuller 1996). We found that the plants selected in this study (e.g. *Psychotria egensis* and *P. campyloneura*) differ from the species selected in other regions (*Amphirrhox longifolia*, *Mabea* cf. *piriri* and *Heteropsis flexuosa* in Salas & Fuller 1996), and we suggest that an evaluation of the nutritional composition in plants selected in different areas will help to identify key components that drive tapir browsing.

Regarding the frugivory diet of the tapir, the positive association between fruit productivity and fruit consumption indicate that *T. terrestris* may eat the species whose fruits are most abundant. However, we recognize that this relationship is primarily affected by the selective use of *M. flexuosa* (Bodmer 1990, Fragoso & Huffman 2000), which has a high fruit productivity in Amazonian forests (Castaño *et al.* 2007). In addition, this relationship may also be affected by the limited number of faeces found (n = 19), and a larger sample size will be useful to better evaluate the correlation between CIf and fruit productivity.

Although our sampled area is far from representing the home-range area occupied by the lowland tapir, we highlight the contribution of this study to the knowledge about its food preferences and the seasonal dietary shifts, especially concerning the consumption of fruits vs. browsing. We identified that the diet of *T. terrestris* reflects periodic changes that are associated with seasonal variation in fruit productivity and browsing availability, which is consistent with our second hypothesis. In the two study periods, tapir fruit consumption was influenced by fruit productivity of *M. flexuosa*, similar to the reports by Bodmer (1990) in the Peruvian Amazon. Fragoso & Huffman (2000) found that the fruit ripening pattern of *M. flexuosa* was reflected in its occurrence in *T. terrestris* faeces year-round, with the lower occurrence corresponding to the months of lowest availability of *M. flexuosa* fruits. In addition to the importance of *M. flexuosa* in fruit consumption, the availability of these fruits is also a factor that influence tapir browsing. For example, browsing selection appeared more pronounced in August, when fruit consumption increased because of the availability of *M. flexuosa*. Also in August, browsing was reduced and restricted to preferred species, particularly of the Rubiaceae, and the consumption of other plant families was significantly lower, than that recorded in March.

We found that tapir foraging activities are concentrated in the *M. flexuosa* swamp and floodplain, which may be explained by the significantly higher proportion of the most selected families for browsing (Rubiaceae, Fabaceae and Melastomataceae), in addition to the high fruit productivity of *M. flexuosa* (Bodmer 1990). These habitat types had the higher intensity of use by the tapir, even in periods when *M. flexuosa* fruits were not available (González *et al.* in press) and the tapir's diet was mainly fibre. These findings are in line with our third hypothesis, which proposes that habitats with higher intensity of use by animals, may contain higher abundance of plants selected in the diet, based on optimal foraging assumptions (Pianka 2008). Although these results should be cautiously interpreted due to the limited sampling period and number of transects in our study, it must be stressed that no browsing signs were found in areas of the terra firme forest with GPS-based locations of the lowland tapir (González *et al.* in press). This selective browsing in the *M. flexuosa* swamp and floodplain, where both vegetation types have open canopies, is similar to previous findings that claim that the lowland tapir usually avoid species under closed canopies and select secondary forests or gaps for foraging (Salas 1996). This foraging preference in open canopies may also be shared with *Tapirus bairdii*, which focuses its feeding in the earliest successional stage habitats of floodplains and logged forests (Fragoso 1991). It has been suggested that this is due to the presence of pioneer species in forest gaps that invest more energy in growth than in mechanical and chemical defences, compared with primary-forest species that contribute more energy to defences against herbivores (Foerster & Vaughan 2002, Salas 1996, Tobler *et al.* 2006). In this way, by having an open canopy that favours a pioneer plant community established in the understorey, the *M. flexuosa* swamp and floodplain could play an essential role in the tapir's browsing. This particular habitat use, where browsing prevails in the *M. flexuosa* swamp and floodplain, suggest that *T. terrestris* has a strong impact on the dynamics of plant recruitment in these types of vegetation and further studies are needed to better understand this effect.

These results highlight the importance of understanding plant species selection in order to identify relevant details of habitat use and home range distribution in Neotropical landscapes. The changes between browsing and fruit consumption, especially during different seasons, is a key finding for understanding how large herbivores respond to environmental heterogeneity and phenological changes of food availability (Chapman *et al.* 2005). The understanding of the interaction between the lowland tapir and its preferred plant species (e.g. *Psychotria campyloneura*, *Psychotria egensis*) is crucial to explain habitat-use patterns. Resource selection identification can be used to characterize habitat quality, estimate parameters through models of diet prediction (Manly *et al.* 2002) and identify factors that determine animal use of space.

ACKNOWLEDGEMENTS

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Appendix 1. Plants species consumed by *Tapirus terrestris* in the Indigenous Reserve Nonuya Villazul (Department of Amazonas, Colombia). Browsed plants (B) were identified by browsing sign sampling and fruits (F) were determined by faecal analysis, from data collected during March, April, August and September of 2015.

Taxon	B/F
Annonaceae	
Duguetia sp. 1	F
Aquifoliaceae	
Ilex JVG662	B
Araceae	
Anthurium JVG153	B
Philodendron fragrantissimum (Hook.) G.Don	B
Arecaceae	
Mauritia flexuosa L.f.	F
Bixaceae	
Bixa sp. 1	F
Blechnaceae	
Salpichlaena volubilis (Kaulf.) J. Sm.	B
Chrysobalanaceae	
Couepia sp. 1	F
Licania cf. *mollis* Benth.	F
Licania JVG502	B
Parinari sp. 1	F
Clusiaceae	
Garcinia madruno (Kunth) Hammel	B
Tovomita speciosa Ducke	B
Combretaceae	
Combretum pyramidatum Desv. ex Ham.	F
Connaraceae	
Connaraceae JVG348	F
Cyatheaceae	
Cyathea JVG168	B
Cyperaceae	
Cyperaceae JVG119	B
Dryopteridaceae	
Cyclodium meniscioides (Willd.) C. Presl	B
Fabaceae	
Brownea JVG151	B
Clathrotropis cf. *macrocarpa* Ducke	B
Macrolobium JVG675	B
Ormosia JVG559	B
Zygia cf. *inaequalis* (Willd.) Pittier	B
Zygia JVG439	B
Zygia cf. *lathetica* Barneby & J.W. Grimes	B
Gentianaceae	
Tachia occidentalis Maguire & Weaver	B
Lauraceae	
Lauraceae JVG557	B
Lauraceae JVG207	B
Lecythidaceae	
Allantoma pluriflora S.A.Mori, Ya Y.Huang & Prance	B
Eschweilera JVG537	B
Lecythidaceae JVG484	B

Appendix 1. Continued

Taxon	B/F
Loganiaceae	
Strychnos sp. 1	F
Strychnos sp. 2	F
cf. *Strychnos* sp. 3	F
Strychnos JVG232	B
Strychnos cf. *peckii* B.L.Rob.	B
Malvaceae	
cf. *Guazuma* sp. 1	F
Melastomataceae	
Graffenrieda limbata Triana	B
Leandra aristigera (Naudin) Cogn.	B
Maieta guianensis Aubl.	B
Miconia cf. *minutiflora* (Bonpl.) DC.	B
Clidemia JVG126	B
Miconia JVG173	B
Miconia JVG291	B
Tococa macrosperma Mart.	B
Metaxyaceae	
Metaxya rostrata (Kunth) C. Presl	B
Moraceae	
Ficus sp. 1	F
Moraceae JVG604	B
Myristicaceae	
Virola JVG802	B
Ochnaceae	
Ouratea JVG479	B
Quiina sp. 1	F
Polygalaceae	
Moutabea aculeata (Ruiz and Pav.) Poepp. & Endl.	B
Pteridaceae	
Adiantum tomentosum Klotzsch	B
Rubiaceae	
Duroia cf. *paruensis* Steyerm.	B
Faramea tamberlikiana subsp. *sessifolia* (P.H.Allen) C.M.Taylor	B
Faramea JVG617	B
Palicourea sp. 1	F
Psychotria campyloneura Müll.Arg.	B
Psychotria egensis Müll.Arg.	B
Psychotria limitanea Standl.	B
Psychotria venulosa Müll.Arg.	B
Sapotaceae	
Micropholis sp. 1	F
Pouteria sp. 1	F
Siparunaceae	
Siparuna cf. *thecaphora* (Poepp. & Endl.) A.DC.	B
Smilacaceae	
Smilax domingensis Willd.	B
Smilax sp. 1	F
Strelitziaceae	
Phenakospermum guyannense (A.Rich.) Endl. ex Miq.	B
Verbenaceae	
Petrea JVG236	B

Appendix 2. Jacobs' selection index (D) for species positively selected by *Tapirus terrestris* in the Indigenous Reserve Nonuya Villazul (Department of Amazonas, Colombia). Browsed plants (B) were identified by browsing sign sampling and fruits (F) were determined by faecal analysis, from data collected during March, April, August and September of 2015.

Taxon	D	B/F
Aquifoliaceae		
Ilex JVG662	0.86	B
Araceae		
Anthurium JVG153	0.73	B
Philodendron fragrantissimum (Hook.) G.Don	0.73	B
Arecaceae		
Mauritia flexuosa L.f.	1.00	F
Blechnaceae		
Salpichlaena volubilis (Kaulf.) J. Sm.	0.73	B
Chrysobalanaceae		
Licania cf. *mollis* Benth.	0.35	F
Licania JVG502	0.74	B
Clusiaceae		
Garcinia madruno (Kunth) Hammel	0.73	B
Connaraceae		
Connaraceae JVG348	0.18	F
Cyatheaceae		
Cyathea JVG168	0.35	B
Dryopteridaceae		
Cyclodium meniscioides (Willd.) C. Presl	0.52	B
Fabaceae		
Ormosia JVG559	0.86	B
Zygia cf. *inaequalis* (Willd.) Pittier	0.58	B
Zygia cf. *lathetica* Barneby & J.W. Grimes	0.74	B
Lauraceae		
Lauraceae JVG557	0.86	B
Lauraceae JVG207	0.73	B
Lecythidaceae		
Allantoma pluriflora S.A.Mori, Ya Y.Huang & Prance	0.86	B
Eschweilera JVG537	0.86	B
Lecythidaceae JVG484	0.74	B
Melastomataceae		
Maieta guianensis Aubl.	0.86	B
Miconia JVG173	0.35	B
Miconia JVG291	0.69	B
Tococa macrosperma Mart.	0.21	B
Moraceae		
Moraceae JVG604	0.86	B
Ochnaceae		
Ouratea JVG479	0.54	B
Rubiaceae		
Faramea tamberlikiana subsp. *sessifolia* (P.H.Allen) C.M.Taylor	0.73	B
Faramea JVG617	0.86	B
Psychotria campyloneura Müll.Arg.	0.68	B
Psychotria egensis Müll.Arg.	0.39	B
Psychotria venulosa Müll.Arg.	0.42	B
Sapotaceae		
Pouteria	0.98	F
Siparunaceae		
Siparuna cf. *thecaphora* (Poepp. & Endl.) A.DC.	0.86	B
Smilacaceae		
Smilax domingensis Willd.	0.73	B