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Review

Plant diversity in the diet of Costa Rican primates in contrasting habitats: a meta-analysis

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Abstract: In human-modified tropical landscapes, the survival of arboreal vertebrates, particularly primates, depends on their plant dietary diversity. Here, we assessed diversity in the vegetative diets of Costa Rican non-human primates (i.e. *Alouatta palliata palliata*, *Ateles geoffroyi*, *Cebus imitator*, and *Saimiri oerstedii*) inhabiting a range of habitat types. Specifically, we assessed: (i) richness and dietary plant diversity, (ii) the β-diversity of dietary plant species and the relative importance of species turnover and nestedness in contributing to these patterns, and (iii) the main ecological drivers of the observed patterns in dietary plant assemblages. Data on diet were available for 33 *Alouatta*, 15 *Cebus*, 8 *Ateles*, and 5 *Saimiri* groups, from 37 published and unpublished studies. Considering all studies, dietary plant species richness was highest in *Alouatta* (454 spp.), followed by *Ateles* (329 spp.), *Cebus* (237 spp.), and *Saimiri* (183 spp.). However, rarefaction curves indicated that the α-diversity of plant species in diet was higher in *Ateles* than in the other three primate species. The γ-diversity of plants was 868 species (range=1664-2041 species). The three top food species were *Spondias mombin*, *Bursera simaruba*, and *Samanea saman*. Species turnover was the mechanism responsible for most of the dissimilarity in the plant assemblages in diet ($\beta_{sim} = 0.76$). Finally, primate species, habitat type and, to a lesser degree, sampling effort were the best predictors of the dietary plant assemblages. Our findings suggest that primate diets are diverse, even in severely-disturbed habitats.

Keywords: dietary plant diversity; behavioral flexibility; forest fragmentation; Neotropical primates; species richness

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1. Introduction

Diet diversity and behavioral flexibility are key factors on the survival probability of most animals (including humans) worldwide, because food resource availability frequently fluctuates spatial-temporally [1–3]. Resource fluctuations are particularly prominent in human-modified landscapes worldwide because non-sustainable, anthropogenic activities (e.g. forest deforestation, hunting, urbanization, etc.) often transform large, diverse and heterogeneous forests into low-diversity and homogeneous poor-quality habitats [4,5]. Habitat degradation can promote diverse behavioral adjustments in animals, including, diet diversification, diet supplementation with exotic and/or cultivated food species, alterations in the foraging patterns and food preferences, temporal changes in time budget, inventions of new traditions (including the consumption of new food items), and others [6–9].

Among vertebrates, non-human primates (NHP) are one of the most eclectic or flexible groups with respect to diet [2,10–12], a crucial behavior for their medium and long-term survival in human-modified and/or strongly seasonal habitats (2,12-14). While some NHP species are highly specialized (e.g. seed-predator pitheciine monkeys: [15]), many have diverse and flexible diets (e.g. atelid monkeys: [12,16,17]). This flexibility can favors the survival of these animals because they often depend on food resources provided by forest tree species [14,18]; resources that are constantly declining due strong human pressures such as extensive agricultural practices, urbanization, and other disturbances [19,20]. Therefore, the persistence of NHP in disturbed habitats and their relative tolerance to spatio-temporal shifts in food is strongly influenced by their ability to diversify their diets, including the opportunistic exploitation of plant foods available in the forest edges and/or anthropogenic matrices (e.g. *Alouatta* spp.: [9,13], *Cebus* spp. [21,22]).

Plant diet diversity can be decomposed into nested levels of organization to elucidate the mechanisms regulating the inclusion of plant species in animal diets: (i) α-diversity, or the diversity of species in a given site, (ii) β-diversity, or the variation of species composition among sites or species dissimilarity, and (iii) γ-diversity or the total diversity of species in a landscape or geographic area [23,24]. The β-diversity can also be considered via two ecological mechanisms to explain the dissimilarity between plant species assemblages in primate diets: turnover and nestedness [25]. Turnover measures the replacement of plant species in one site by distinct species in the other site, while nestedness refers to the loss (or gain) of species in only one of the sites and, as consequence, the poorest site contains only a subset of the species composition of the richest one [25,26]. Both α and β-diversity patterns of plants (or animals) are influenced by environmental variability and a number of dynamic ecological processes such as inter-specific competition, species-specific fecundity, and dispersal abilities [24,26].

The diversity of plants used as food sources by neotropical primates depends, among other factors, on aspects of their natural history, such as trophic guild, the social organization, the group size, and the local plant diversity and plant species-specific abundance. For instance, highly frugivorous primates living in large groups such as spider monkeys (*Ateles* spp.) invest more time traveling and foraging on a more diverse array of plants compared with more folivorous primates, living in small group size groups, such as *Alouatta* spp. [27–30]. It has been hypothesized that, in contrast with mature leaves, the distribution of fleshy fruits (and immature leaves) are sparse in space and time, forcing animals to diversify their diets [17,27,30] and, in the particular case of *Ateles* spp., the fusion-fission social group dynamics can increase the probability of finding new food resources, because they can forage in multiple subgroups in different regions, over a large area throughout the forest [28,31,32].

In Mesoamerica, Costa Rica supports the largest diversity of primates after Panama, with a total of four species and ca. six subspecies: mantled howler monkeys (*Alouatta palliata palliata*), spider monkeys (*Ateles geoffroyi frontatus*, *A. g. geoffroyi*, *A. g. ornatus*), squirrel monkeys (*S. oerstedii citrinellus*, *S. o. oerstedii*), and capuchin monkeys (*Cebus imitator*). *Alouatta* is the most widely distributed primate in the country, inhabits a large variety of natural and human-modified habitats [33,34], the groups can range from <6 to ca. 45 individuals. As with most species in the genus *Alouatta*, its diet is often classified as folivorous-frugivorous [12,13,27]. In contrast, *A. geoffroyi* is mainly restricted to continuous/large well-preserved forests, inhabit in fusion-fission communities >25 individuals, and its diet is strongly frugivorous [17,31,33]. *C. imitator* is distributed in a variety of continuous and fragmented habitats throughout the country; their groups vary from 8 to 35 individuals and its diet is classified as insectivorous-frugivorous [28,33,35]. Finally, *S. oerstedii* is an endemic species restricted to the central and southern Pacific coast of Costa Rica (and part of the Chiriqui province, Panama), their groups can range from 20 to >90 individuals and, as *C. imitator*, its diet is described as insectivorous-frugivorous [33,34,36].

Due to ongoing destruction of their natural habitats and the growing contact between these animals and humans, particularly in highly touristic and/or urbanized areas throughout the country, e.g. [37], the former three species are considered at risk of extinction locally according to the Costa Rican environmental authorities [38], endangered or vulnerable across their former distribution [39]. However, to date, our knowledge on the diversity and flexibility of diet in Costa Rican non-human primates (hereafter CR-NHP) inhabiting contrasting habitats remains incipient. There is a number of published and unpublished data on the feeding behavior of these animals, but no studies to date have attempted to summarize the available information on the topic. This issue impedes any generalization about the resource use by these locally threatened animals and their feeding ecology and constrains the design and implementation of appropriate management strategies of them and their habitats. For instance, detailed data on the diet diversity of CR-NHP may be crucial to improve the habitat connectivity, via reforestation with preferred plant food species, between highly disturbed adjacent forest remnants inhabited by different primate groups (e.g. *A. palliata*: [40,41]).

In this study, we investigated, for the first time, the diversity of plant species in the diet of the four CR-NHP in different habitats. For this, we reviewed countrywide published and unpublished information on feeding ecology of these animals. Our main objective was to describe and compare the diversity of plant species included in their diet under different habitats (i.e. diet flexibility), in addition, we explore several potential ecological drivers to explain the pattern found in this review. Specifically, we assessed: (i) the α-diversity of plants in diet and and the most important plant food species for each primate species, (ii) the dissimilarity of food plant assemblage between CR-NHP (i.e. β-diversity) and the relative importance of plant species turnover and nestedness to explain these patterns, and (iii) the role of different habitats traits and CR-NHP specie as predictors of the observed plant assemblages in the diet. Finally, we discuss the implications of the observed diet patterns on the conservation and management of the four CR-NHP and their habitats. We predict that the α-diversity of plants species in the diet of the most frugivorous primates will be higher (e.g. *A. geoffroyi)* than in the diet of less frugivorous and/or omnivorous primates (e.g. *A. palliata, C. imitator*, and *S. oerstedii).* We also expect that species turnover, rather than nestdness, will be the main ecological mechanism influencing the β-diversity patterns in plant diet of CR-NHP. This is because throughout the country they inhabit life zones with contrasting diversity of plant composition (e.g. Tropical Dry Forest and Tropical Rain Forest [42,43]) and disturbance levels.

2. Materials and Methods

2.1. Study Region

The habitat of the CR-NHP comprises a non-determined percentage of the ca. 3.8 Mha of forest area present in the country up to 2022 [44]. However, the studies reviewed for this meta-analisis were performed in a discrete number of private and public forested areas distributed throughout the seven provinces of Costa Rica (Figure 1). Historically, most multi-year and long-term primate studies in Costa Rica have been focused, in three regions: northern Costa Rica (e.g. sector Santa Rosa of the Área de Conservación Guanacaste, Hacienda La Pacífica, and Palo Verde National Park, Guanacaste), the central Pacific coast (e.g. Manuel Antonio National Park, Puntarenas), and southern Pacific coast (e.g. Península de Osa, Puntarenas; Figure 1). Overall, these areas cover four main Holdridge's Life Zones HLZ [43,45]: Tropical Dry Forest (TDF), Tropical Rainforest (TRF), Tropical Lowland Rainforest (TLRF), and Tropical Wet Forest (TWF). Throughout the study region, primates inhabit a large range of private forest fragments extensions (ranging from

<10 ha to 250 ha) under different successional stages and areas of continuous forest located within national parks (Figure 1).

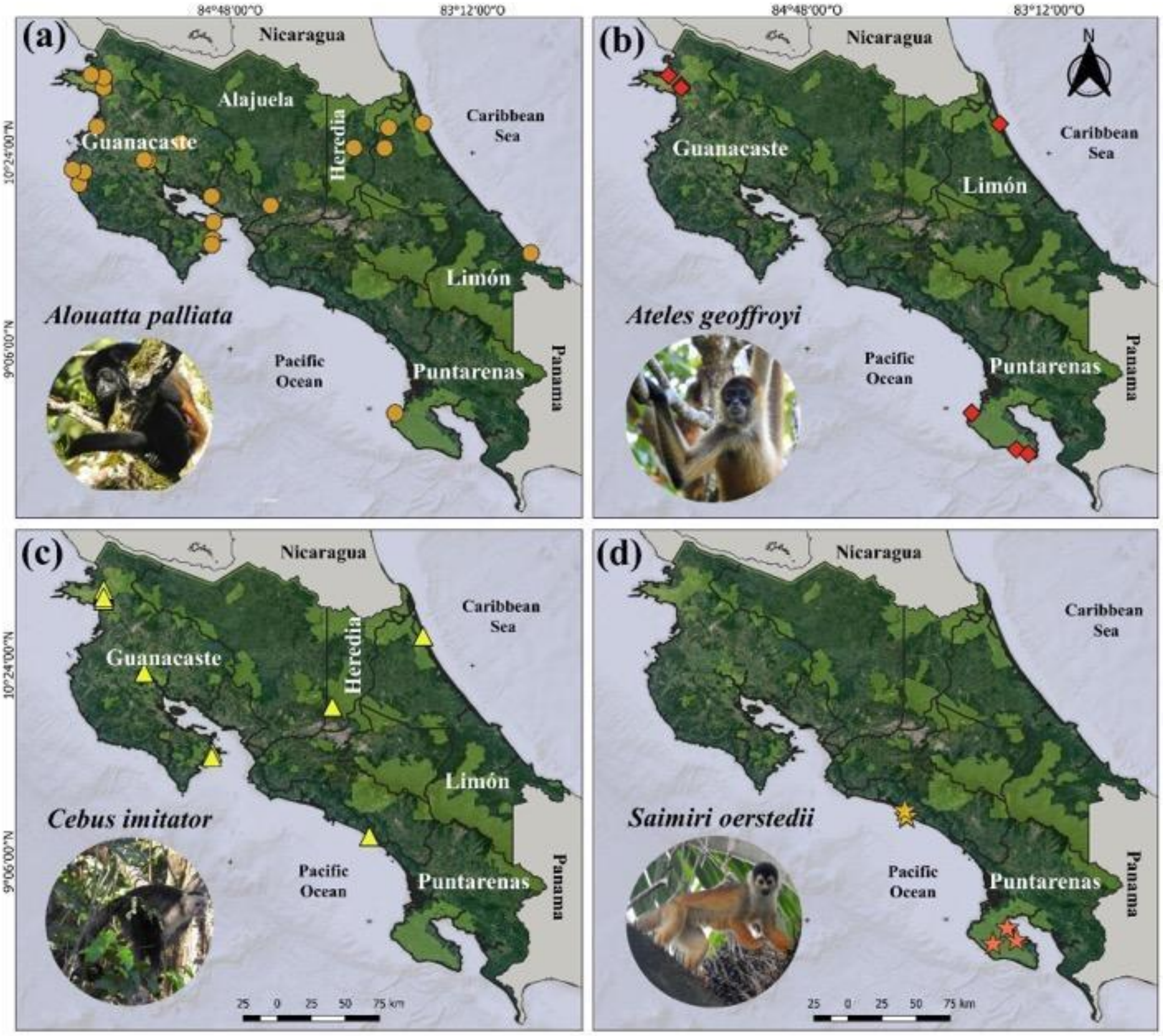


Figure 1. Distribution of the study sites for each primate species according to the information provided by the authors of the studies included in the review. The exact location of forest fragments for *Alouatta palliata palliata* (a), *Ateles geoffroyi* (b), *Cebus imitator* (c) and *Saimiri oerstedii* (d) are indicated with different symbols and colors. Pale green polygons represent the protected areas of Costa Rica. Photos by Ó.M. Chaves. The first figure layer is a free Google Earth® satellite image.

The TDFs of Guanacaste represent a large extension coastal lowlands with a markedly climatic seasonality [45,46] and, typically, they are constituted by a complex mosaic of pastures, agricultural lands, forest remnants of different sizes and successional stages (often inhabited by one or more groups of howler monkeys), and scattered human settlements [46]. The dry season starts in late November and extends into late April, while the rainy season extends from early May to November. Most of the canopy trees are deciduous and in the dry season, many species are defoliated. The annual average precipitation is ca. 1975 mm (range= 900-2400) and the average annual temperature is ca. 26 ºC. Conversely, in the other three HLZ, the seasonally is low or moderate, annual average precipitation can ranges from >3300 mm to >5500 mm according to the region, and the average annual temperature is ca. 28 ºC. Finally, most fragmented forest areas inhabited by CR-NHP and some highly-visited national parks (e.g. Manuel Antonio and Corcovado National Parks) are upon strong human pressures such as accelerated urbanization, extensive agriculture, cattle ranching, and uncontrolled tourist developments and visitation rates, which can affect negatively the health and survival of these animals [41,47]

2.2. Literature Review and Data Collection

During a 9-mo period (from January to September 2022) we searched for all published and unpublished information using two general online databases: Google Scholar (https://scholar.google.com), and Web of Science (https://mjl.clarivate.com). Furthermore, to access dissertations from Costarican universities, we used the Kerwa repository from the Universidad de Costa Rica (https://www.kerwa.ucr.ac.cr/) and Biodoc repository from the Universidad Nacional (https://repositorio.una.ac.cr/). Overall, we restricted literature search to the period of 1975-2022 because references before 1975 are very scarce and rarely available online. We used specific keywords such as 'Costa Rican primate diet', 'diet of Costa Rican primates', 'feeding behavior of Costa Rican primates', and several combinations of keywords including common and scientific names of primates such as 'diet + *Saimiri oerstedii* + squirrel monkeys + Costa Rica'. We also used the same keywords in Spanish to improve the probabilities to find dissertations and/or papers from local researchers.

Due the relative scarcity of literature on the topic, we included diverse information sources such as: (i) papers published in peer-reviewed scientific journals, (ii) book chapters from non-predatory editorials, (iii) academic dissertations (including undergraduate and graduate theses), and (iv) technical reports. We also included unpublished data provided by coauthors of this meta-analysis. We only considered field studies on wild, free-ranging monkey groups using standardized observational methods (e.g. instantaneous scans, focal animal, and *ad libitum* observations:[48]) and with a sampling effort ≥ 6 study months to be included in the meta-analysis. Datasets that did not fulfill these discrimination criteria were not considered in the statistical analysis, but were included in the online meta-analysis dataset (see Appendix 1 and 2 in [49]).

Overall, we found 57 published and unpublished datasets on the diet of one or more CR-NHP (see Appendix 3 in [49]), most of these were scientific papers (59%), followed by dissertations (M.Sc. theses (13%), Ph.D. theses (7%) and unpublished data (7%), degree theses and technical reports (5.6% each), and a book chapter (1.9%). Commonly, these studies were focused in one or two different primate groups (range= 1-8 groups), in total, data on diet was available for 33 *Alouatta*, 15 *Cebus*, 8 *Ateles*, and 5 *Saimiri* groups (see Appendix 2 in [49]). However, after we applied the aforementioned discrimination criteria, only 37 datasets were included in the meta-analysis (Table 1, see also Appendix 4 in [49]).

Table 1. Studies on the diet of CR-NHP considered in the meta-analyses.

Ref[1]	**Species**[2]	S_{obs}[3]	**Site**[4]	**HLZ**[5]	**Habitat**[6]	**Suc.**[7]	**PS**[8]	**#G**[9]	**GS**[10]	**SM**[11]	**SE**[12]
1 (T)	*Ap*	57	1 (G)	TDF	mF	S	U	Pop	13-24	1, 2	2 (9)
2 (P)	*Ap*	21	2 (L)	TLRF	C	S	P	2	3/20	2	5 (10)
3 (P)	*Ap*	17	3 (G)	TDF	C	S	P	40	40	1, 2	2 (17)
4 (u)	*Ap*	75	4, 5 (G)	TDF	sF, LF	S	P	3	6/36/43	1, 2	2 (16)
5 (b)	*Ap*	94	6 (G)	TDF	sF	S	P	1	13	2	2 (7)
6 (b)	*Ap*	96	6 (G)	TDF	C	S	P	2	8/27	2	2 (14)
7 (T*)	*Ap*	45	3 (G)	TDF	C	S	P	4	6/24	2	1 (11)
8 (t)	*Ap*	41	7, 8 (G, P)	various	C	S	P	2	8/38	1, 2	1 (6)
9 (T*)	*Ap*	52	9 (P)	TRF	C	S	P	2	26/27	2	2 (24)
10 (P)	*Ap*	36	3 (G)	TDF	C	S	P	2	10/7	3	3 (12)
11 (T)	*Ap*	40	3 (G)	TDF	C	M	P	1	30	2	2 (12)
12 (u)	*Ap*	67	10 (P)	TWF	LF	M	P	2	—	2	2 (11)
13 (P)	*Ap*	22	6 (G)	TDF	sF	M	P	1	—	2	2 (10)
14 (T)	*Ap*	30	11 (A)	various	sF	S	U	4	9-15	1, 2	2 (8)

15 (u)	*Ap*	27	12 (G)	TDF	LF	S	P	1	—	2	3 (24)
16 (P)	*Ap*	111	13 (H)	TRF	C	M	P	2	12/23	2	2 (15)
17 (P)	*Ap*	100	10 (P)	TRF	LF	M	P	2	18/20	1	2 (12)
18 (P)	*Ap*	9	7 (G)	TDF	C	S	P	2	8/10	—	2 (7)
19 (P)	*Ap*	72	3 (G)	TDF	C	S	P	Pop	—	1, 2	37 (–)
3 (P)	*Ag*	13	3 (G)	TDF	C	S	P	1	—	1, 2	3 (24)
19 (P)	*Ag*	89	3 (G)	TDF	C	S	P	Pop	—	1, 2	37 (–)
20 (P)	*Ag*	33	3 (G)	TDF	C	M	P	1	20	2	2 (8)
21 (T)	*Ag*	86	10 (P)	TRF	LF	M	P	1	30	2	2 (12)
22 (P)	*Ag*	27	10 (P)	TRF	LF	M	P	1	31	2	2 (12)
23 (T*)	*Ag*	99	14 (P)	TRF	C	M	P	1	85	2, 4	2(17)
24 (P)	*Ag*	111	15 (P)	TRF	C	M	P	Pop	—	4, 5	2 (6)
3 (P)	*Ci*	7	3 (G)	TDF	C	S	P	1	26	1, 2	2 (17)
18 (P)	*Ci*	30	7 (G)	TDF	C	S	P	2	16/26	—	2 (7)
19 (P)	*Ci*	144	3 (G)	TDF	C	S	P	Pop	—	1, 2	37 (–)
25 (P)	*Ci*	40	3 (G)	TDF	C	M, S	P	3	16-26	2	3 (20)
26 (P)	*Ci*	5	3 (G)	TDF	C	M	P	1	24	2	4 (24)
27 (P)	*Ci*	13	3 (G)	TDF	C	M	P	Pop	—	2	3 (26)
28 (P)	*Ci*	112	3 (G)	TDF	C	M, S	P	6	8-35	1, 2	8 (22)
29 (T)	*Ci*	44	3 (G)	TDF	C	M	P	2	18/25	2	2 (7)
30 (P)	*Ci*	50	9 (P)	TRF	LF	S	P	2	20/22	1, 2	2 (24)
31 (P)	*Ci*	112	3 (G)	TDF	C	M	P	4	—	1, 2	2 (12)
32 (P)	*Ci*	9	3 (G)	TDF	C	M	P	1	72	2	1 (7)
33 (P)	*Ci*	59	2 (L)	TLRF	C	S	P	1	22	2	1 (12)
34 (T*)	*Soo*	67	14 (P)	TRF	LF	M	P	1	45	1, 2	2 (11)
35 (b)	*Soo*	25	16 (P)	TRF	C	S	P, U	22	9-28	4, 6	2 (9)
36 (u)	*Soo*	92	17 (P)	TRF	LF	M	P, U	Pop	28-99	2	2 (8)
37 (T)	*Soc*	33	18 (P)	TWF	LF	M	P, U	14	22-66	2	2 (10)

[1] References: 1 = Azofeifa-Rojas [40], 2 = Bolt *et al*. [86], 3 = Chapman [16], 4 = Chaves *et al*. [87], 5 = Glander [88], 6 = Glander [89], 7 = Larose [90], 8 = Martínez [91], 9 = McKinney [92], 10 = Melin et al [93], 11 = Morera [94], 12 = Riba-Hernández & Stoner [95], 13 = Rockwood & Glander [96], 14 = Sánchez-Porras [97], 15 = Stoner & Riba-Hernández [98], 16 = Stoner [99], 17 = Stoner *et al*. [100], 18 = Wehncke *et al*. [101], 19 = Melin *et al*. [35], 20 = Hiramatsu et al. [102], 21 = Riba-Hernández [103], 22 = Riba-Hernández et al. [104], 23 = Weghorst [105], 24 = Whitworth et al. [106], 25 = Chapman & Fedigan [107], 26 = Chapman [74], 27 = Chapman [108], 28 = Hogan et al. [109], 29 = McCabe [110], 30 = McKinney [21], 31 = Melin et al. [76], 32= Mosdossy et al. [75], 33= Mallot *et al.* [62], 34 = [102] Boinski [111], 35= Solano-Rojas [36], 36 = Solano-Rojas [112], 37 = Wong [113]. In parentheses the type of reference: P = paper in scientific journal, b = book chapter, T* = Ph.D. theses, T = M.Sc. theses, t = Degree theses, and u = unpublished data.

[2] Monkey species: Ap = Alouatta palliata palliata, Ag = Ateles geoffroyi, Ci = Cebus imitator, Soo = Saimiri oerstedii oerstedii, Soc = Saimiri oerstedii citrinellus.

[3] Observed number of plant species in diet.

[4] Study sites: 1 = Playa Hermosa Beach; 2 = La Suerte Biological Research Station; 3 = Santa Rosa National Park; 4 = Canopy de Tamarindo; 5 = Finca Josema; 6 = Hacienda La Pacífica; 7 = Santa Rosa National Park; 8 = Poza Lagarto site; 9 = Curú Wildlife Refuge; 10 = Punta Rio Claro Wildlife Refuge; 11 = Mina Moncada & Río Jesús sector; 12 = Sector Murciélago, Área de Conservación Guanacaste; 13 = La Selva Biological Station, 14 = Corcovado National Park; 15 = Osa Biological Station, Osa Peninsula; 16 = Puerto Jiménez, Osa Peninsula; 17 = Danta Lodge Reserve, Guadalupe, Osa Peninsula, 18 = Manuel Antonio National Park. In parenthesis the province: G=Guanacaste, L= Limón, P= Puntarenas, A= Alajuela, H= Heredia. .

[5] Holdridge Life Zones: TDF = Tropical Dry Forest, TRF = Tropical RainForest, TLRF = Tropical Lowland Rain Forest, TWF = Tropical Wet Forest.

[6] Type of habitat occupied by the study groups: sF = small fragment (<15 ha), mF = medium fragment (> 15-50 ha), LF = large fragment (>100-1000 ha), C = continuous forest (> 1000 ha).

[7] Successional status: S = secondary regeneration forest, M = mature forest.

[8] Protection status: P = protected by the state and/or the owners, U = unprotected.

[9] Number of study monkey groups. Pop = entire monkey population in the study area.

[10] Group size or range of group sizes studied.

[11] Sampling Method (SM): 1 = instantaneous group scans, 2 = focal animal, 3 = point-time method, 4 = *ad libitum* observations, 5 = fecal samples analysis, 6 = interviews.

[12] Sampling effort reported by the authors: number of study years and months (in parentheses).

2.3. Description of Field Data Collection Methods in the Literature Reviewed

Feeding behavior of howler monkeys *Alouatta palliata palliata* (hereafter *Ap*) were focused in the TDF of Guanacaste and TRF of Puntarenas provinces, throughout the Pacific coast of Costa Rica. Overall, 1-8 free-ranging monkey groups previously habituated to human presence were observed in each study. However, most authors did not indicate the exact diurnal period they monitored, or the number of hours sampled by day (see Appendix 1 in [49]). The most used sampling method for *Ap* was the focal animal method with behavioral samples of 10 min and instantaneous scan samples each 15 min [48], but some authors also used other methods such as *ad libitum* observations [48] or a combination of two different methods (Table 1, see also the Supplementary Material). The sampling effort varied largely between studies, ranging from 6 to 33 months (Table 1).

The diet of spider monkeys *Ateles geoffroyi* (hereafter *Ag*) was collected from three different HLZ (i.e. TDF, TRF, and TLRF) in 3 out of 7 provinces of the country (Table 1). In 83% of cases, authors used the focal animal method with focal samples ranging from 2 to 10 min, but instantaneous scan sampling or a combination of *ad libitum* method + collection of fecal samples were also used. Overall, the sampling effort by study varied from 6 to 36 months, but a study compiled data from 37 years in Santa Rosa National Park [35] (Table 1).

On the other hand, 82% of studies on the diet of the capuchin monkeys *Cebus imitator* (hereafter *Ci*) were performed in TDF (particularly Santa Rosa National Park) and the rest in TRF and TLF and the authors used the focal animal method or a combination of this method with group scans and the sampling effort ranged from 7 to 33 months (Table 1). The diet of the squirrel monkeys *Saimiri oerstedii* were studied in two regions in the central and southern Pacific coast of the country via a combination of field methods: *S. citrinellus* (hereafter *Soc*) was studied in a TWF (i.e. Manuel Antonio National Park) using focal and group scan methods, while *S. o. oerstedii* (hereafter *Soo*) was studied in Peninsula de Osa' TRF using the group scan method and *ad libitum* observations. For both squirrel monkey subspecies the sampling effort was ≤11 months (Table 1).

Because most studies included in this meta-analysis did not provide the number of feeding records or time devoted by each monkey group to the different food plant species, it was not possible to determine the 'top plant food species' in the diet of the CR-NHP (i.e. those species that together represent ≥ 80% of feeding records: [32]). Instead, we determined the 'plant species most frequently reported in diet' for each CR-NHP. For this, we arranged the final list of food plant species according to the total number of monkey groups/populations (considering all the study sites for each CR-NHP) that exploited each *i* plant species (see Appendix 5 in [49]). Finally, because the reviewed studies came from many researchers, most of which are not plant specialists but zoologists, and cover a wide time period (i.e. from 1972 to 2022), we detected diverse taxonomic inconsistencies, grammatical errors, and outdated classification with the reported plant scientific names (see Appendix 2 in [49]). Then, to prevent potential problems of over and/or underestimation of the plant species richness reported in each study, we standardized scientific names of the plants using the taxonomic name resolution service provided by Botanical Information and Ecology Network (https://bien.nceas.ucsb.edu/bien/tools/tnrs/), and the plant scientific names were updated using Tropicos plant database (https://www.tropicos.org/).

2.4. Statistical Analysis

2.4.1. Plant α-Diversity of Diet

We analyzed patterns of plant diversity in the diet of CR-NHP using Hill numbers (q), metrics that represent true diversities because they obey the replication principle [50]. Hill numbers are expressed in 'units of species' which can be plot in a single graph to compare the diversity profiles as a continuous function of the parameter q [50,51] and three different diversity orders can be analyzed: $q = 0$ represents the diversity of all species without overemphasizing their abundances (i.e. an equivalent of species richness), $q = 1$ is the exponential of Shannon's entropy and represents the diversity of 'common' species because it weights each species according to its abundance or frequency. Finally, the order $q = 2$ is the inverse of Simpson's index and represents the diversity of 'dominant' species in the community or, in this study, the assemblage of plant species that were frequently reported as food sources (i.e. rarely exploited plant species are ignored) in the different studies analyzed (Table 1).

To calculate the aforementioned diversity metrics and the sample completeness (i.e. the likelihood that the sample was sufficiently large to detect all the plant species used as food source by each primate species), we used the functions 'iNEXT', 'ChaoRichness', and 'estimateD' of the R package iNEXT [51]. With this same package, we also compared the species richness ($q = 0$) and the diversity of common ($q = 1$) and dominant species ($q = 2$) using rarefaction/extrapolation curves or R/E curves via the function 'ggiNEXT'. Rarefaction curves are necessary to make appropriate comparisons among communities where the sampling effort is unequal [52,53], as occurred in this study (i.e. the number of study groups was 5, 8, 15, and 33; Table 2). Using this procedure is possible to compute the expected species richness at a standardized sample size and performs precise extrapolations of the species richness as the bootstrap samples are added to a pool of previously encountered species [52]. Based on the R/E curves, we used 95% confidence intervals with the bootstrap procedure to compare the diversity orders between primate species. Non-overlapping confidence intervals at a particular number of samples indicate statistically significant differences [51,54]. We estimate the asymptotic α-diversity (i.e. the diversity expected when the R/E curve be asymptotic to the x-axis) using the iNEXT function. We used the aforementioned procedure to estimate the γ-diversity of plant species in the diet of CR-NHP. For this, we pooled the data for all the study groups and sites.

Finally, we compared the Shannon diversity indices for plant species in the diet of each primate species using the Hutchenson t-test [55]. For this, we used the function 'multiple_Hutcheson_t_test' of the R package ecolTest. Because of the large asymmetry in the sampling effort between the four primate species, we used the rarefaction approach to estimate the Shannon indices based on a standardized sample of 5 study groups per primate species.

Table 2. Observed and expected diversity of plant species in the diet of the four species of CR-NHP according to the available information on the topic.

Primate species	**Observed diversity (Hill numbers)**^{1}			# gen.	# fam.	#E^2	Expected diversity (Hill numbers)^3		
	0	**1**	**2**				**0**	**1**	**2**
Alouatta palliata	454 (33, 9000)	275	165	235	74	16	966 (864-1068)	436 (401-470)	189 (170-208)
Ateles geoffroyi	329 (8, 5190)	289	245	172	60	4	739 (608-870)	625 (547-702)	450 (398-501)
Cebus imitator	237 (15, 5679)	158	131	160	68	16	215 (191-240)	198 (184-211)	170 (155-184)
Saimiri oerstedii	183 (5, 806)	170	153	96	48	10	763 (563-963)	645 (509-780)	408 (314-503)
All	**868 (59, 20675)***	**496**	**290**	**348**	**91**	**28**	**1852 (1664-2041)**	**770 (717-823)**	**331 (305-357)**

[1] Diversity of species for each Hill' diversity order: 0= species richness, 1= exponential of Shannon entropy or diversity of common species, 2= inverse of Simpson or diversity of dominant species. In the case of species richness, the sampling effort is indicated in parenthesis (i.e. number of monkey groups sampled and total number of sampling hours considering all studies, see Table 1). *The observed species richness in diet were 881 species considering the datasets excluded from the analysis.

[2] Number of exotic and/or cultivated plant species used as a food source by each primate species.

[3] Asymptotic diversity estimates according to the non-parametric richness estimators described by [104]. The 95% C.I. for Hill numbers is indicated in parenthesis.

2.4.2. Plant β-diversity in Diet

We used the dissimilarities between the plant assemblages exploited by primates as indicators of β diversity. As differences between the plant communities can result from two main ecological processes named species turnover and nestedness , we estimated both β-diversity components as recommended by [56]. For this, we used the function 'beta-multi' and 'beta-sample' of the R program betapart [57]. In betapart, the species turnover is estimated via the Simpson dissimilarity index (hereafter β_{sim}), while the species nestedness is estimated as the nested component of Sørensen dissimilarity (hereafter β_{sne}) [56]. Then, we used the function 'pair-beta' to perform pairwise comparisons between the plant assemblages exploited by each primate species and the function 'hclust' to generate a hierarchical cluster of the pairwise dissimilarities for β_{sim} and β_{sne}.

2.4.3. Drivers of the Plant Assemblage in the Diet

To determine the influence of the primate species, HLZ, province, habitat type, forest disturbance level, study sampling effort (in months), and the interaction between primate species * HLZ on the plant assemblage in diet, we used a permutational multivariable analysis of variance (PERMANOVA), a non-parametric multivariable analysis of variance, as recommended for meta-analyses based in studies with disparate sampling efforts [58]. This method constructs ANOVA-like test statistics from a matrix of resemblances (distances, dissimilarities, similarities) calculated between the sample units and obtains p-values using random permutations of observations among the groups. Furthermore, contrary to traditional parametric multivariable analysis (e.g. MANOVA), PERMANOVA is unaffected by the correlation between variables and is less sensitive to heterogeneity in dispersion [58]. We ran the PERMANOVA via the function 'adonis2' of the R package vegan and we set the matrix of Euclidean distances with 999 permutations to estimate the p-value. Finally, to determine which levels of the predictor variables differ significantly, we ran pos-hoc contrasts using the function 'pairwise.perm.manova' of the R package RVAideMemoire (REF). All statistical analyses were performed in R v.4.1.2 [59] and the main R scripts used to run them are available online (see Appendices 6 and 7 in [49]).

3. Results

3.1. Alpha and Gamma Plant Species Diversity in the Diet of CR-NHP

Plant species richness in the diet of four CR-NHP varied noticeably across primate species and reviewed studies. It varied from 9 to 100 species in *Ap*, from 9 to 111 species in *Ag*, from 5 to 112 species in *Ci*, and from 25 to 92 species in *So* (Table 1). Overall, the total dietary plant species richness ranged from 183 species in *So* to 454 species in *Ap* (Table 2, see also Appendix 2 in [41]). The four CR-NHP also exploited food items of 28 exotic and/or cultivated plant species, ranging from 4 species in *Ag* to 16 species in *Ap* and *Ci* (Table 2). However, the sampling effort varied noticeably between species in terms of sampling years, sampling years, number of study groups. While *Ap* represented 54% of the 61 study groups *So* only 8% of them (Table 1). According to the rarefaction curves, the α-diversity of plant diet (i.e. diversity order q=0) was significantly higher in *Ag* than in the other three primate species, and higher in *So* than in *Ap* and *Ci* (Figure 2) even if we consider a standardized number of study groups (Hutcheson t-test ranged from 3.5 to 14.0, $p < 0.0005$ in all comparisons, see Supplementary Material). The same pattern was also true for the diversity of common and dominant species (Figure 2).

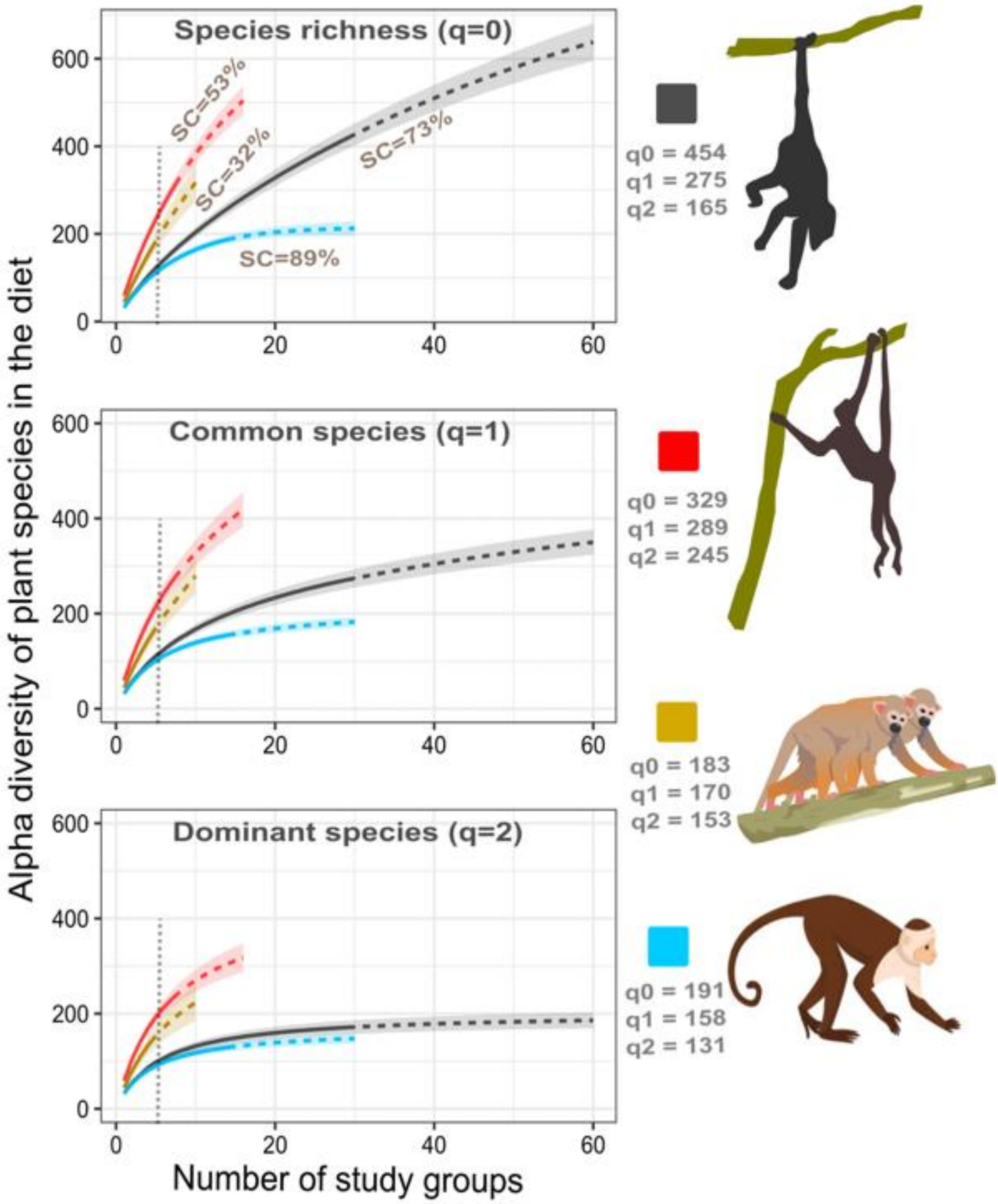


Figure 2. Rarefaction (solid line) and extrapolation (dashed line) curves with 95% confidence intervals comparing the alpha diversity of plant in diet of the four species of CR-NHP for diversity order q=0 (i.e. species richness, top panel), q=1 (i.e., Shannon diversity, middle panel), and q=2 (i.e. Simpson diversity, bottom panel). The reference samples were 33 for *Alouatta*, 8 for *Ateles*, 15 for *Cebus*, and 5 for *Saimiri*. Extrapolation curves are based in the double of the reference sample sizes.

Sampling completeness (SC) is indicated for the order q=0. The vertical dotted grey line indicates the rarified sample size (i.e. n = 5 groups for each primate species). The number of plant species exploited according to the diversity order is showed in the legend. Further details on the alpha diversity of plants are provided in Table 2. The 95% confidence intervals were obtained by bootstrap method based on 200 replications. Non-overlapped 95% C.I. indicate significant differences. See Methods for further details.

Furthermore, both the standardized plant species richness and the α-diversity of common species was similar between *Ap* and *Ci* but these diversities were higher in *Ap* than in *Ci* when the number of study groups was ≥ 7 (Figure 2). Conversely, the curve for the α- diversity of dominant species was flatter for *Ap* and *Ci* and no difference was detected for this diversity order (Figure 2). The sampling completeness (SC) of the plant species in diet differed between primate species (range = 32%-89%; Kruskal-Wallis test, $H = 13.6$, $p = 0.003$), and was higher in *Ci* than in *So* (contrast, $p < 0.05$) but not other significant difference was found between the other primate species (contrasts, $p > 0.05$ in all cases, Figure 2). The γ-diversity of plant species in the diet, i.e. pooling the data for the four CR-NHP, was 868 species (including trees, shrubs, palms, epiphytes, parasites, vines, lianas, and terrestrial herbs), distributed in 348 genera and 91 families (Table 2), but the sampling completeness was moderate (i.e. 76%, Figure 3). According to the asymptotic diversity estimates, the expected gamma diversity was 1852 species (range: 1664-2041, Table 2).

Finally, in addition to the plant foods, at least ten studies have reported the direct consumption of animals in *Ag, Ci,* and *So.* The consumption of animals was, apparently, frequent in *Ci* and *So* which preyed on small birds, mammals (including *Saimiri oerstedii* and *Sciurus variegatoides* in the case of *Ci* and *Artibeus watsonii, Uroderma billobatum* and *Vampyresa pusilla* for *So*), amphibians, reptiles, and a large number of non-identified invertebrates (Table S1). Conversely, the consumption of animals by *Ap* and *Ag* was extremely rare (Table S1).

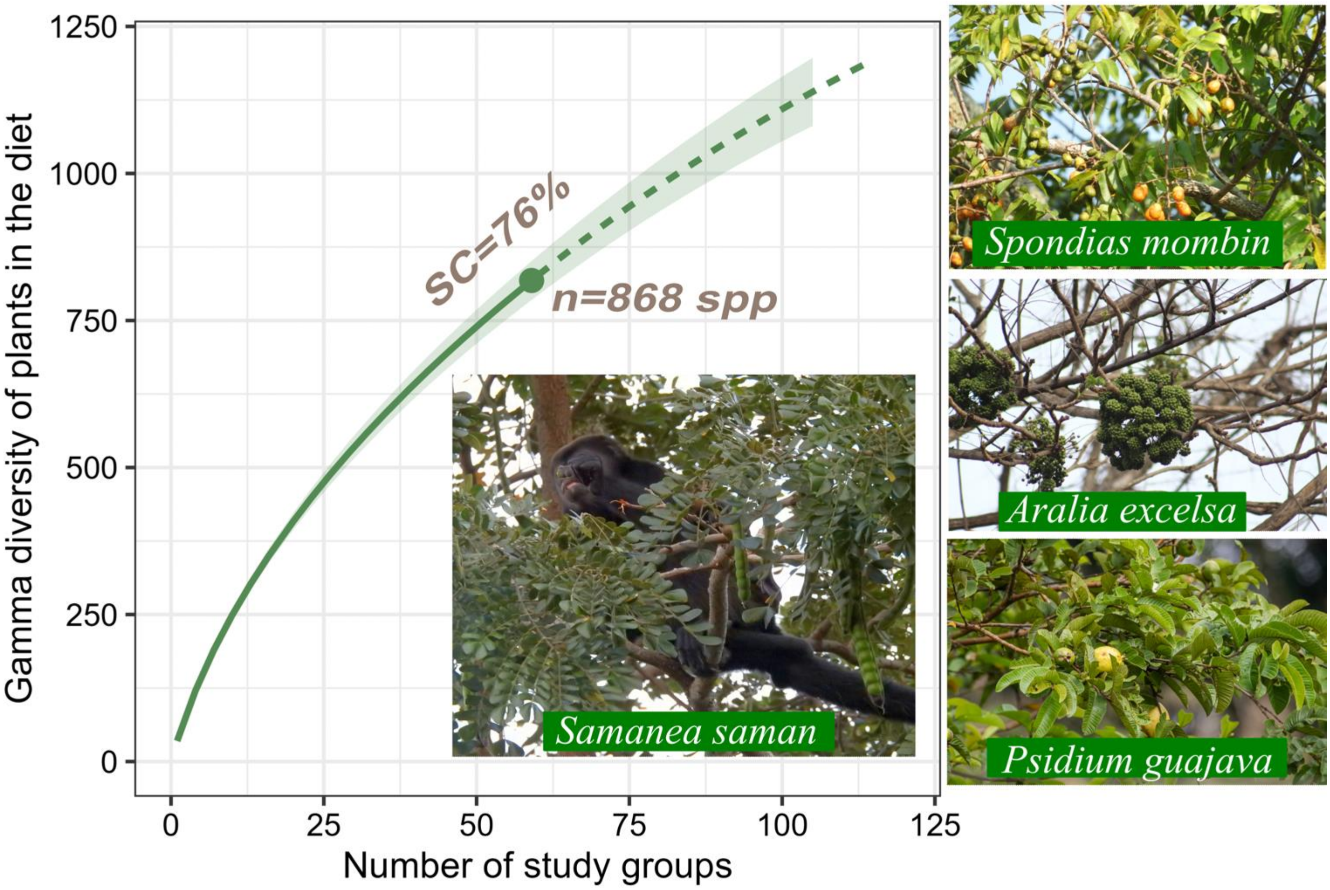


Figure 3. Rarefaction (solid line) and extrapolation (dashed line) curve with 95% confidence intervals for the gamma diversity of plants in diet of the four species of CR-NHP. To perform this diversity profile, the plant species richness ($q = 0$) consumed by the four primate species throughout the study sites were pooled. Extrapolation curve is based in the double of the reference sample size (i.e. 59 study groups). The 95% confidence intervals were obtained by bootstrap method based on 200 replications. Sampling completeness (SC) and the observed species diversity (n) are indicated in grey bold letters. Images of the top one food species for *Alouatta* (i.e. *S. saman*), *Ateles* (i.e. *S. mombin*), *Cebus* (i.e. *A. excelsa*), and *Saimiri* (i.e. *P. guajava*) are shown. Further details on the top food species for each species are provided in Table 2.

3.2. Most Important Plant Species in Diet

Overall, the three plant species most frequently reported in diet of CR-NHP were, in decreasing order, *Spondias mombin*, *Bursera simaruba*, and *Samanea saman*, while the most important genera were *Ficus*, *Inga*, and *Spondias* (see Appendix 5 in [49]). However, the composition of the top ten reported plant species in the diet of the CR-NHP varied noticeably between species (Table 3). The main top food plant species for *Ap* was *Samanea saman*, while for *Ag*, *Ci*, and *So* were, respectively, *Spondias mombin*, *Aralia excelsa*, and *Psidium guajava* (Table 3). Furthermore, 90% of the food plant species used by *Ap* were exploited by ≥ 3 food items (commonly mature and immature fruits and leaves), while in *Ag* and *Ci* 90% of these species were exploited by ≤ 2 food items and in *So* 50% of the food species were exploited by a single plant item and 50% by two food items (i.e. fruits and nectar, Table 3). Finally, the percentage of shared species ranged from 0% (*So* vs the other three primate species) to 30% (*Ap* vs *Ag*, Table 3).

Table 3. Top ten plant food species in diet of CR-NHP according to the total number of monkey groups in which each plant species was used as food source.

Primate species	**Plant species**[1]	**Family**	**GF**[2]	**Food items**[3]	**groups**[4]
Alouatta palliata	*Samanea saman*	Fabaceae	tree	L, l, lb, F, f, fl	24
	Enterolobium cyclocarpum	Fabaceae	tree	L, l, F, f, fl	22
	Andira inermis	Fabaceae	tree	L, I, lb, fl	20
	Spondias mombin	Anacardiaceae	tree	L, l, lb, F, f, fl	19
	Bursera simaruba	Burseraceae	tree	L, l, lb, F, f	18
	Brosimum alicastrum	Moraceae	tree	L, l, lb, F, f, fl	17
	Astronium graveolens	Anacardiaceae	tree	L, l, lb, F*, fl, p	16
	Maclura tinctoria	Moraceae	tree	L, l, lb, F, f, fl	16
	Sideroxylon capiri	Sapotaceae	tree	L, l, F, f, fl	16
	Inga edulis	Fabaceae	tree	l, F, f, fl	15
Ateles geoffroyi	*Spondias mombin*	Anacardiaceae	tree	F, fl	7
	Dilodendron costaricense	Sapindaceae	tree	F*	6
	Brosimum alicastrum	Moraceae	tree	L*, F*	5
	B. costaricanum	Moraceae	tree	F, f	4
	Bursera simaruba	Burseraceae	tree	l, F*	4
	Cecropia peltata	Urticaceae	tree	L, l, F*, fl	4
	Garcinia madruno	Clusiaceae	tree	F	4
	Manilkara chicle	Sapotaceae	tree	f	4
	Pouteria torta	Sapotaceae	tree	l, F	4
	Sideroxylon capiri	Sapotaceae	tree	F, f	4
Cebus imitator	*Aralia excelsa*	Araliaceae	tree	L*, F*	8
	Bursera simaruba	Burseraceae	tree	F*	8
	Ficus sp.	Moraceae	tree	L, l, F*	8
	Muntingia calabura	Muntingiaceae	tree	F*	8
	Sloanea terniflora	Elaeocarpaceae	tree	F*	8
	Vachellia collinsii	Fabaceae	shrub	F*	8
	Genipa americana	Rubiaceae	tree	F*	7
	Luehea candida	Malvaceae	tree	F*	7
	L. speciosa	Malvaceae	tree	F*	7
	Spondias mombin	Anacardiaceae	tree	F*	7

Saimiri oerstedii	***Psidium guajava***	Myrtaceae	tree	F, f	4
	Anacardium excelsum	Anacardiaceae	tree	F*	3
	Cecropia obtusifolia	Urticaceae	tree	F*	3
	Conostegia schlimii	Melastomataceae	tree	F*	3
	Miconia argentea	Melastomataceae	tree	F*	3
	Nephelium lappaceum	Sapindaceae	tree	F, f	3
	Ochroma pyramidale	Malvaceae	tree	F*, n	3
	Passiflora vitifolia	Passifloraceae	vine	F*, n	3
	Symphonia globulifera	Clusiaceae	tree	F*, n	3
	Vitex cooperi	Lamiaceae	tree	F*	3

[1] Plant species are arranged following a decreasing order of primate groups in which each species was exploited and then, by alphabetical order. The entire list of plant species used as food source by each monkey species is provided in the Appendix 5 [41].

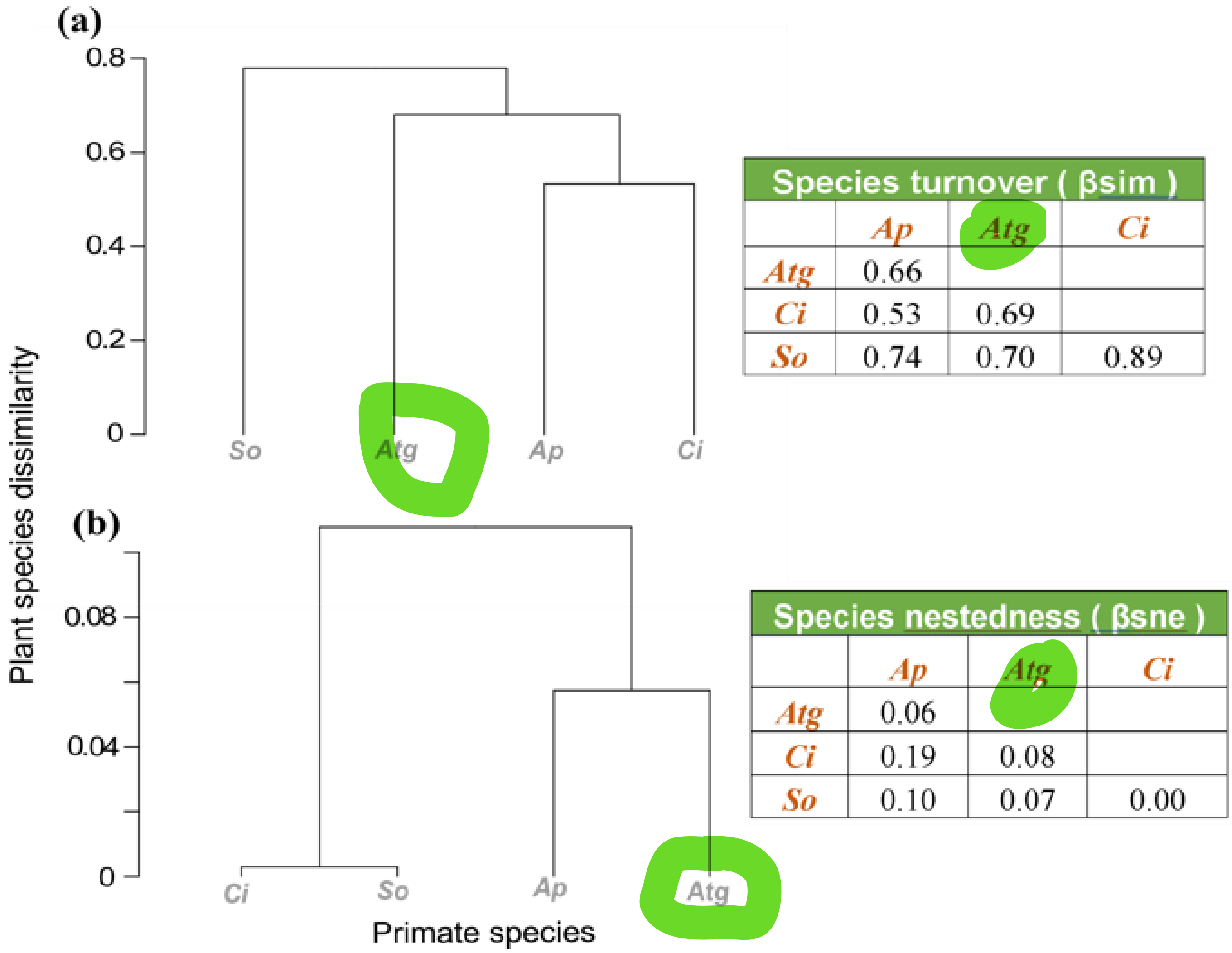
[2] Growth form: **tree** = tree > 4 m in height, **shrub** = trees < 4 m in height, **vine** = herbaceous climbers.
.

[3] Food items consumed by monkeys: **L**= mature leaves, **l** = immature leaves, **lb** = leaf buds, **F** = ripe fruits, **f** = unripe fruits, **fl** = flowers, **n** = nectar, **p** = petioles. The asterisk indicates that the maturity stage of the fruits or leaves is unknown.

[4] Number of monkey groups or populations where the consumption of the plant species was recorded.

3.3. Plant Species Assemblage Dissimilarity and β-Diversity Components

Overall, the number of non-shared plant species in diet ranged from 89 species in *Ap* and *Ci* to 373 species in *Ap* and *So*, while the number of shared species ranged from 18 in *So* and *Ci* to 97 in *Ap* and *Ag* (Table S2). Species turnover was the factor responsible for most of the dissimilarity in the plant species assemblages exploited by primates ($\beta_{sim} = 0.76$) with the species nestedness explained only a negligible fraction of the dissimilarity ($\beta_{sne} = 0.07$). Pairwise comparisons of plant β-diversity revealed that the largest species turnover occurred between *So* and *Ci* ($\beta_{sim} = 0.89$), while the largest species nestedness was observed between *Ap* and *Ci* ($\beta_{sne} = 0.19$, Figure 4).



Species turnover (βsim)

	Ap	*Atg*	*Ci*
Atg	0.66		
Ci	0.53	0.69	
So	0.74	0.70	0.89

Species nestedness (βsne)

	Ap	*Atg*	*Ci*
Atg	0.06		
Ci	0.19	0.08	
So	0.10	0.07	0.00

Figure 4. Clustering using average linkage of the β components of plant species dissimilarity between primate species. The component β_{sim} represent the dissimilarity in the plant assemblage due the species replacement or turnover **(a),** while the component β_{sne} represent the plant dissimilarity due the loss/gain of species or nestedness **(b)**. The pairwise comparison values for β_{sim} and β_{sne} are indicted in the tables.

3.4. Factors Affecting Plant Assemblages in Diet

The PERMANOVA revealed that three out of five predictor variables significantly influenced plant assemblages exploited by the primates (Table S3). Specifically, we found that the plant composition in the diet was strongly influenced by primate species (F= 1.6, d.f.=3, p = 0.001) and to a lesser degree, by HLZ (F= 1.2, d.f.=4, p = 0.019) and sampling effort (F= 1.2, d.f.=1, p = 0.035). However, the rest of variables (i.e. forest size, forest disturbance level, province, and the interaction between primate species and HLZ) did not affect the plant assemblages (Table S2). Most pairwise comparisons indicated that the plant composition in diet differed between primate species (contrasts tests, $p < 0.05$ in all cases), except for *So* and *Ag* ($p > 0.05$). Regards the influence of the HLZ, we only detect significant differences between Tropical Rain Forest and Tropical Dry Forest (p =0.005).

4. Discussion

4.1. Observed and Expected Diversity of Plants in Diet

We revealed through a comprehensive meta-analysis that the plant diet of CR-NHP is constituted by considerable species richness. Even if we consider the expected γ-diversity, the plant assemblage used by these primates was > 2000 plant species, which is consistent with the eclectic feeding behavior observed in other species of Atelidae (e.g. *Alouatta* spp.: [12,13,60], *Ateles* spp. [17,32]) and Cebidae (e.g. *Cebus* spp. [22,61,62], *Saimiri* spp.: [63,64], *Sapajus* spp. [11,65]). Overall, the eclectic feeding behavior of tropical NHP is frequently associated with three main factors. Firstly, no single food items can satisfy all nutritional demands that primates have, therefore, diet diversification (including diverse species of fruits, leaves, flowers, invertebrates, etc.) is a generalized behavioral strategy for acquiring the macronutrients that animals need [66,67]. Secondly, diet diversification contributes to diluting the potential negative effects of secondary metabolites present in many plant items (even in fruits) that animals ingest, which represent an efficient intoxication-avoiding strategy [68,69]. These eclectic feeding habits can also be a response to 'food shortage' in small or low-quality which often obligates animals to exploit a larger assemblage of fallback foods (e.g. leafy material of climbers growing in forest edges) to compensate the scarcity of their preferred plant foods [70]. Finally, the vegetative constituents of neotropical primate diets in human-modified landscapes includes not only a diverse array of native plants but also dozens of exotic and/or cultivated plants that they exploit opportunistically (see [9,21,22]), as we found in this study. Further studies are necessary to understand if the exploitation of some valuable crops by CR-NHP in the anthropogenic matrix, such as *Persea americana*, *Elaeis guineensis*, *Syzygium malaccense*, *Spondias purpurea*, and *Mangifera indica* (see Appendix 2 in [49]), result in relevant negative human-nonhuman primate interactions or if crop-raiding behavior is tolerated by the local inhabitants as have been reported for *Ap* and *Ag* in Gandoca community, Limon province [71].

In support of our prediction, the α-diversity of plants in diet of *Ag* was higher than in the other three CR-NHP, supporting the hypothesis that the dispersed and unpredictable distribution of fleshy fruits (i.e. the main food item in the diet of *Ag*: [72]) was an evolutionary stimulus to the cognitive adaptations and diet diversification in frugivorous primates [27]. However, the 37-y data compilation by Melin *et al.* [35], suggests that, at least in some TDFs, the diversity of plants in diet can be higher in *Ci* than in *Ag* (i.e. 144 vs 89 species) and that the diet of *Ci* is predominantly frugivorous despite they also consume a large variety of invertebrates. This highlights the importance of long-term studies to improving our understanding on the diet diversity and behavioral flexibility of the four CR-NHP. In addition, our findings was probably influenced, at least partially, by the fact that all analyzed studies with *Ag* were performed in continuous forests or large well-preserved fragments, while the studies on the of *Ap* and *So* were performed in continuous and unprotected secondary forest fragments of different sizes (see Table 1). Overall, larger and well-preserved forests are considered high-quality habitats for primates because they present a richer food plant assemblage compared with small or medium unprotected secondary forests [4, 73] and then, it is reasonable to expect that animal that plant diet diversity reflect these site-specific differences in food availability.

Finally, we believe that the experimental design of some of the studies we analyzed were not robust enough to allow an acceptable estimation of the diet diversity (see Table 1), which may influence the α-diversity patterns we obtained. For instance, Chapman [16] reported that in Santa Rosa National Park the diet of *Ap* after a 17-mo study period was only 17 plant species, which certainly is a gross underestimation of the real diet. Similarly, in another study with *Ci* the same author reported that, after a 24-mo study period , the diet richness of a group these animals was constituted by five species [74], and in the same study site Mosdossy *et al.* [75] reported a plant diet of nine species for a *Ci* group. These studies largely contrast with the plant diet reported for *Ci* in other studies in Santa Rosa National Park (i.e. 144 species [35], 112 species [76]).

4.2. *Most important Plant Species in Diet*

With the caveat that extrapolation of our findings must be considered with caution, due the lack of systematic feeding records on each plant food species and the scarcity of diet data (particularly in the case of *Ag* and *So*), our results concur with previous studies on the diet of Mesoamerican primates (e.g. [32,60,77,78]. We find that the most important genera in diet of these animals were represented by large forest trees such as *Ficus*, *Spondias* and *Brosimum*. The preference of the primates by species of these genera is not surprising because the high nutritional content of their fleshy fruits, immature leaves, and/or flowers, in addition to their abundance in most tropical forests (see [32,79]). However, the four CR-NHP shared a low percentage of important plant food species, which is probably explained, at least in part, by the features of the sites they inhabit, in particular the marked contrasts in the structure and composition of plant communities throughout the country [42]. Shifts in the assemblage of top food plant species can also occur due to the existence of particular idiosyncrasies or foraging cultures in some primate groups inhabiting human-modified landscapes as occurs with crop consumption in different Neotropical regions [9,21,22] and, our data suggest that this is also the case in CR-NHM. For instance, from the top ten reported plant species in diet of *So*, two ones can be classified as cultivated (Table 3). *Nephelium lappaceum* is a cultivated species exploited by fruits and *Psidium guajava* is a highly consumed fruit species frequently growth naturally (or cultivated in some gardens) in open areas throughout the forest edges and the anthropogenic matrix (Ó.M.C. pers. obs.). Even, these animals can be frequently observed foraging in secondary forests and in different elements of the anthropogenic matrix (e.g. subsistence gardens and small agriculture plantations) in Península de Osa, southern Costa Rica [36,78].

While our findings on the most reported plant species in diet of CR-NHM are preliminary, this plant list provides a useful scientific contribution to the conservation efforts of primates inhabiting severely disturbed and/or urbanized habitats throughout the country. For instance, this type of information has been recently used to elaborate management strategies that improve the connectivity (e.g. elaboration of biological corridors using top food plant species and protection of these tree species in the urban-forest interface) between urban forest remnants inhabiting by *Ap* in different highly tourist and urbanized areas of Guanacaste, Costa Rica [40,41,47, 80]. In this respect, the most promising food species to improve the forest connectivity are reforestation are likely rapid-growing and/or pioneer native species such as *Ficus* spp., *Spondias mombin*, *Bursera simaruba*, and *Muntingia calabura* (see Appendix 2 and 5 in [41] for further information on the plant food species). These strategies together with the installation of artificial bridges and environmental education can be powerful allies to prevent or mitigate the constant events of electrocution (and vehicle-collisions) of primates in Guanacaste and other regions of Costa Rica [41,47,80].

4.3. Plant β-diversity and Factors affecting the Plant Composition in Diet

As predicted, our findings strongly suggest that species turnover was the main mechanism responsible for the dissimilarities between the food plant assemblages in the diet among CR-NHP. Our findings also showed that the HLZ was the best predictor of plant assemblage in the diet of these animals. Overall, in many tropical forests, the β-diversity of tree species is mainly associated to species turnover because their well-recognized spatial variability in climatic and biotic conditions, which actively promote the plant species replacement from one forest to another due process such as dispersal limitation and speciation [5,81].

Even though the forest cover of Costa Rica (i.e. the main habitats of CR-NHP) is relatively small comparing to other most South American countries, the differences in the plant community composition tend to increase with distance, and remarkable changes in plant composition occurs from the northern Tropical Dry Forest to the southern Tropical RainForest [42] and even within a single region [82]. Therefore, due to the inter-site variations in plant composition, the CR-NHP must adjust their diets to the available plant foods [2,70,83], which result in a large plant species turnover in the diet. Finally, the contrasting foraging and digestive strategies observed between primates species (e.g. *Ap* vs *Ag*: [27,30]) may also influences the plant composition in diet of each CR-NHP. Overall, highly frugivorous primates such as *Ag* are able to digest a considerable number of fleshy fruits, in contrast, primates such as *Ap* that are specialized for fermentation-based digestion of leafy material [30].

5. Conclusions

Despite the scarcity of information on the topic (particularly for *So* and *Ag*) this meta-analysis supports the conclusion that CR-NHP have highly diverse and eclectic diets. Taken together these primates used >850 plant species (including at least 28 exotic and/or cultivated species). The rarefaction curves also confirmed the higher α-diversity of plants in the diet of *Ag* compared with the other three primate species, supporting previous studies on the importance of unpredictable availability of fleshy fruits as a selective pressure for diet diversification [27]. Similarly, we also find support that plant species turnover was the main ecological mechanism explaining the dissimilarity of plant assemblages in diet of the CR-NHP. This was largely expected, considering that vegetation assemblages (i.e. the food source available for primates) can vary drastically throughout the country [42,46]. Our compiled data will contribute to improve our understanding on the feeding ecology and the diet flexibility of CR-NHP and represent valuable scientific inputs to the design and implementation of management strategies based in plant menu in the diet of these animals.

At the same time, we recognize that most patterns in the diet diversity we reported here could change noticeably if we take in consideration the entire diet (i.e. considering both plant and animal items consumed by primates). Unfortunately, this type of analysis is not possible because to date, most records on animal items exploited by CR-NHP are anecdotic, extremely incomplete, and strongly biased to *Ci* and *So* (Table S1). Recent studies in Para state, Brazil, indicate that even in that even in two highly frugivorous *Ateles* species, the consumption of animal material occurs frequently because spider monkeys intentionally select larvae-infected fruits as possible strategy to satisfy the protein demand [84], and the same situation may be true in the CR-NHP (and in most of the 179 recognized Neotropical primates: [39]). Therefore, despite the multiple challenges associated to the study of animal consumption by primates (e.g. difficulty to determine the larvae content in the ripe fruits ingested, invertebrate complex taxonomy, and rarity of some hunting events on small and medium vertebrates), further studies on this topic are crucial to understand the real diet diversity of Neotropical primates. In this sense, we suggest the use of advanced molecular techniques, such as metagenomic analysis in fecal samples, to get a more complete picture of the diet, approaches that have been used with success in different Neotropical primates [62,81]. These techniques can also be useful to complement the observational analysis of plant diet, particularly when plant cannot be identified by the observers because the challenges to collect or identify they in the field.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/XXXX. Table S1: Animal taxa reported in the diet of CR-NHP; Table S2: Shared and non-shared plant species in the diet of the four Costa Rican non-human primates; Table S3: Results of the PERMANOVA.

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Data Availability Statement: All the datasets associated with this study are available here: .https://doi.org/10.6084/m9.figshare. Appendix 1: Detailed list of the studies on the diet of CR-NHP reviewed in this meta-analysis; Appendix 2: Database on the food species exploited by the four primate species; Appendix 3: PDFs of the papers reviewed in this study, Appendix 4: PDFs of the papers included in Table 1, Appendix 5: List of the main plant species, orders and families used by monkeys as food source; Appendix 6: R scripts on the analysis and main results of the diversity analysis in iNEXT; Appendix 7: R scripts and results of the PERMANOVA assessing the influence of the predictor variables on the food plant assemblage. These datasets are also cited in the text [41].

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