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UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
Departamento de Botânica
Programa de Pós-Graduação em Biologia Vegetal

UFMG

LISIEUX FRANCO FUZESSY

ECOLOGIA E EVOLUÇÃO DA DISPERSÃO DE SEMENTES POR PRIMATAS NEOTROPICAIS

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Doutor em Biologia Vegetal.

Área de Concentração Fisiologia Vegetal e Ecologia

BELO HORIZONTE – MG
2017

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“Nature is ever at work building and pulling down,
creating and destroying, keeping everything whirling and
flowing, allowing no rest but in rhythmical motion,
chasing everything in endless song out of one beautiful
form into another”
John Muir

“A Natureza está sempre trabalhando,
construindo e jogando ao chão, criando e destruindo,
mantendo tudo girando e fluindo, sem descanso, mas em
movimento rítmico, buscando em uma música infinita, de
uma forma bonita para outra”
John Muir

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RESUMO

O funcionamento e a dinâmica de florestas tropicais são, em grande parte, infuenciados pelo mutualismo entre frutos carnosos e vertebrados frugívoros, processo que promove consequências evolutivas e ecológicas fundamentais. Em troca do transporte de suas sementes para locais adequados para germinar e crescer, as plantas oferecem aos frugívoros uma recompensa nutricional. Assim, a ecologia alimentar e os padrões de atividade dos frugívoros determinam a efetividade do serviço oferecido como dispersores e este serviço está diretamente relacionado à probabilidade de sobrevivência, germinação de sementes e recrutamento de plântulas. Devido a este impacto na reprodução e *fitness*, as interações mutualísticas podem determinar a seleção e subsequente evolução de traços nas plantas. Primatas, juntamente com aves e morcegos, são os principais agentes dispersores em florestas tropicais. Seu corpo grande e hábito arbóreo, associados ao elevado consumo de frutos são o resultado de adaptações morfológicas, de locomoção e também sensoriais que se refletem em guildas alimentares. Buscando preencher lacunas no conhecimento acerca das consequências ecológicas e evolutivas da dispersão de sementes por primatas na região Neotropical, procuramos reunir, organizar e ampliar as informações disponíveis. Avaliamos, do ponto de vista ecológico e filogenético das plantas, as consequências das interações com primatas e testamos hipóteses acerca da ecologia e evolução da dispersão de sementes por diferentes guildas alimentares. O hábito alimentar generalista dos primatas não nos permitiu identificar consequências do mutualismo para a evolução da morfologia de frutos. Porém, a forte associação entre caracteres morfológicos apontou para existência de uma síndrome de dispersão primatocórica. Além disso, demonstramos que primatas dispersam grande diversidade de espécies de plantas, ingerem e dispersam sementes e frutos de variados tamanhos, tipos e cores, movem sementes para locais fora da área de influência do parental e favorecem a germinação após a passagem pelo trato digestivo. O papel dos primatas como dispersores é definido de acordo com as guildas alimentares, sendo o grau de frugivoria diretamente proporcional à qualidade do serviço oferecido.

ABSTRACT

The mutualism among fleshy fruits and fruit-eating vertebrates largely influence tropical forests functioning and dynamics, and promotes fundamental evolutionary and ecological consequences. During food handling, frugivores transport seeds to sutable sites to germinate and grow and, in turn, plants offer a nutritional reward. Thus, the frugivore feeding ecology and activity patterns determine its effectiveness as a disperser. Seed dispersal process establishes the probability of seed and seedling survival, seed germination and seedling recruitment. These impacts of mutualistic interactions on plant reproduction and fitness therefore influence selection and evolution of fruit traits. Primates, toghether with birds and bats, are the main disperser agents in tropical forests. A large body size associated with the arboreal habit and high fruit consumption are the outcome of sensorial, morphological and locomotor daptations, which reflects in feeding guilds. Here we gather, organize and expand available information about the ecological and evolutionary consequences of seed dispersal by primates in the Neotropical region aiming to fill knowledge gaps. We evaluate, from a plant ecological and phylogenetic point of view, the consequences of mutualistic interactions with Neotropical primates. We tested hypotheses on the ecology and evolution of seed dispersal by distinct feeding guilds. In terms of feeding ecology primates tend to be generalist and this fact prevented us to identify the consequences of mutualism to the evolution of fruit morphology. However, the strong association among morphological fruit traits in primate-dispersed species pointed to the existence of a dispersal syndrome. Also, we showed that primates are able to swallow and disperse a wide range of plant species, fruit colors, types and sizes, and move seeds to sites far from the zone of influence of the parent crown, and also promote germination after gut passage. The role of primates as seed dispersers is defined according to the feeding guilds, and the degree of frugivory modulates the quality of the service offered.

INTRODUÇÃO GERAL

O mutualismo entre frutos carnosos e vertebrados frugívoros promove várias consequências evolutivas e ecológicas fundamentais. Sem a frugivoria, a dinâmica das florestas tropicais seria bastante alterada (Fleming e Kress 2011). O consumo de frutos carnosos e a subsequente dispersão de suas sementes é um processo-chave na ecologia vegetal, uma vez que a deposição à certa distância da planta-mãe aumenta o fluxo gênico e as chances de colonização de novas áreas (Schupp et al. 2010). Em florestas Neotropicais, mais de 80% das plantas dependem de frugívoros dispersores para se reproduzir (Howe 2014). Em troca do transporte de suas sementes para locais adequados para germinar e crescer, as plantas oferecem uma recompensa nutricional e acabam assim por atrair diferentes grupos de vertebrados (Fleming e Kress 2011).

Os efeitos ecológicos da dispersão podem ser definidos em termos da quantidade de frutos e sementes removidos e da qualidade na manipulação e deposição das sementes. Assim, a ecologia alimentar e os padrões de atividade diários determinam a efetividade da dispersão de sementes, que está diretamente relacionada à probabilidade de sobrevivência, germinação de sementes e recrutamento de plântulas (Schupp et al. 2010, 2017). A quantidade de frutos e sementes removidos depende do tamanho do frugívoro e de seu requerimento nutricional, enquanto que o tratamento dado à semente é modulado pelo seu comportamento alimentar (Travesset e Verdú 2002). As condições do local de deposição estabelecem as chances de sobrevivência e estabelecimento pós-dispersão e são influenciadas principalmente pela distância do parental e de coespecíficos, pela composição da vizinhança (Schupp et al. 2010, 2017, Beckman e Rogers 2013) e pela microbiota presente no solo (Mangan et al. 2010, McCarthu-Neumann e Kobe 2010).

Primatas constituem grande parte da biomassa de vertebrados frugívoros em florestas tropicais, e são considerados, juntamente com aves e morcegos, os principais agentes dispersores (Fleming e Kress 2011, Eriksson 2016). São animais de corpo relativamente grande e hábito arbóreo, e reconecidos como grandes consumidores de frutos e sementes. Várias adaptações em termos de dentição, digestão, locomoção e também sensoriais permitem que primatas explorem frutos maturos e imaturos, com diversos tipos e tamanhos de sementes (Feagle 1999, Lucas et al. 2007). Estas adaptações se refletem em guildas alimentares, que definem o papel dos primatas como dispersores ou predadores de sementes, e portanto a eficiência de dispersão.

A ingestão de frutos está relacionada ao potencial de dispersão, mas a eficiência de um dispersor depende do seu impacto sobre a aptidão em produzir novos adultos. Um erro comum que dificulta o uso de estudos de dispersão de sementes na conservação é a suposição de que a utilização de frutos como recurso alimentar automaticamente implica em dispersão efetiva (Howe 2016). Embora alguns grupos de primatas ajam principalmente como predadores destruindo grande parte das sementes que consomem, estima-se que 58% dos primatas dispersem legitimamente as plantas das quais se alimentam, e o mutualismo com frutos carnosos seja uma característica fortemente conservada ao longo de sua filogenia (Gómez e Verdú 2012).

As interações ecológicas constituem num dos principais fatores que moldam a diversificação evolutiva das espécies (Thompson 2004, Lengyel et al. 2010, Guimarães Jr. et al. 2011, Nuismer et al. 2012). Porém, o significado evolutivo do mutualismo com primatas permanece desconhecido na história das plantas. As atividades de alimentação de qualquer dispersor em particular podem influenciar a evolução de traços da planta, ou resultar em uma relação coevolutiva recíproca (Thompson 2004, Lengyel et al. 2010). Em geral, os estudos de primatas Neotropicais como dispersores de sementes até o presente se concentraram em estudos restritos geográfica (Janson 1983, Lambert e Garber 1998) e taxonomicamente (Lomáscolo et al. 2008), mas não buscaram realizar sínteses para avaliar as consequências ecológico-evolutivas de tais processos.

Sabemos que a capacidade de dispersar sementes é um traço conservado ao longo da filogenia dos primatas (Gómez e Verdú 2012) e da importância evolutiva para este grupo (DeCasein et al. 2017). Porém, as conseqüências de tais interações permanecem pouco claras do ponto de vista filogenético da planta. Buscamos portanto, determinar a distribuição das espécies efetivamente dispersas ao longo de uma árvore filogenética, avaliando se existem atributos relacionados à primatocoria e se os mesmos são conservados ou não ao longo da filogenia das plantas.

Além disso, pretendemos sumarizar e ampliar o conhecimento acerca do mutualismo existente entre primatas e plantas para toda região neotropical, a região com a maior biodiversidade vegetal do planeta (Hughes et al. 2013). Focamos no componente qualitativo da eficiência de dispersão de sementes, comparando diferentes guildas alimentares em termos do tratamento fornecido durante a alimentação e manipulação dos frutos e das distâncias de dispersão. Como pouco se sabe sobre as chances de sobrevivência após a dispersão (Chapman et al. 2013, Bufalo et al. 2016), a distância que um frugívoro move sementes para longe da planta mãe associada às chances de germinação após a passagem pelo trato digestivo oferecem uma medida indicativa da probabilidade de produção de novos adultos (Comita et al. 2014). Consequentemente, consistem em uma medida da contribuição desses dispersores para a estrutura e dinâmica florestal.

Para avaliar as interações mutualísticas evolvendo primatas e plantas e as consequências ecológicas e evolutivas de tal processo, o presente trabalho foi dividido em quatro capítulos que buscaram testar hipóteses acerca da ecologia e evolução da dispersão de sementes por primatas.

No primeiro capítulo, a ser submetido ao periódico Evolutionary Ecology, buscamos descrever a existência de atributos de frutos associados à dispersão por primatas por meio de análises filogenéticas utilizando 749 espécies de planta dispersas por primatas. Apesar da grande diversidade de atributos funcionais identificados nos frutos dispersos, a forte associação entre eles nos permitiu descrever uma síndrome primatocórica e apontar uma prevalência de características particulares: frutos Neotropicais dispersos por primatas são em sua maioria bagas de tamanho médio ou grande e cor amarela ou laranja, em muitos casos protegidas por uma casca dura.

No segundo capítulo, a ser resubmetido ao periódico Biotrópica, buscamos demonstrar a influência do tamanho das sementes no comportamento de manipulação por primatas, e as consequências para a dispersão. Descobrimos que a grande maioria das sementes manipuladas por primatas são engolidas e passam intactas através de seu trato digestivo e comprovamos que sementes maiores tendem a ser mais engolidas por primatas frugívoros. Por outro lado, quando manipuladas por pequenos insetívoros, sementes grandes tendem a ser mais jogadas embaixo do parental. Apontamos também lacunas no conhecimento e a necessidade de aumentar o esforço de pesquisa para que se possa melhor compreender as relações mutualísticas envolvendo plantas e primatas.

No terceiro capítulo, publicado no peródico American Journal of Primatology (79:e22659, 2017) reunimos dados de 26 estudos sobre dispersão de sementes por primatas Neotropicais buscando estabelecer padrões e determinantes da distância de dispersão. Apresentamos um modelo preditor da distância e demontramos que os padrões de locomoção associados à morfologia das diferentes guildas alimentares definem o quão longe primatas são capazes de carregar sementes. Em geral, primatas neotropicais, especialmente frugívoros, movem sementes para locais mais distantes da zona de influência do parental.

No quarto capítulo, publicado no peródico Oikos (125: 1069–1080, 2016) avaliamos o efeito da passagem pelo trato digestivo de diferentes guildas alimentares de primatas na germinação de 156 espécies de planta, pertencentes a 48 famílias. Encontramos que, em geral, primatas exercem um efeito positivo, variável de acordo com a guilda alimentar, que chega a 75% de aumento na germinação em guildas que consomem mais frutos.

Por fim, reunimos as informações obtidas sobre atributos de frutos Neotropicais dispersos por primatas e os respectivios grupos de vertebrados que também agem como dispersores em uma coletânea ilustrada, onde plantas estão organizadas por famílias.

Link para download: https://www.dropbox.com/s/a5ygpxadtdxem8q/Fuzessy%20LF%20-%20ANEXO%20TESE%20-%20FRUIT%20DESCRIPTION.pdf?dl=0

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Saguinus fuscicollis, insectivore-frugivore Neotropical primate.
Illustration: Stephen D. Nash

CAPÍTULO 1:

Is there a strictly primate dispersed syndrome among Neotropical fruits?

Title: Is there a primate-dispersed syndrome among Neotropical fruits?

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Abstract

Ecological interactions are the major driver of trait diversification of plants and frugivores across the globe. The establishment of mutualism with plants increases speciation rates among primates, and mutualism is a strongly conserved character in primate phylogenetic history. However consequences of seed dispersal by Neotropical primates remain unclear from the plant phylogenetic point of view. Mutualistic interactions are the main process promoting evolutionary trait convergence, and association among traits with specific disperser groups, such as bats, birds or primates, defines dispersal syndromes. Here we used a phylogenetically-controlled approach to investigate the existence of a primate-dispersed syndrome (PDS). We hypothesized that a set of fruit traits, such as type, color, size, number of seeds per fruit and husk presence, define a PDS, and thus we expected a phenotypic integration among fruits dispersed by primates in Neotropics. Also, as dispersal syndromes are related to fruit-disperser specificity, we expected a low overlap on fruit consumption among primates, birds and bats. We found a great diversity among the 749 plant species in 82 families studied. Neotropical primates dispersed a variety of fruit colors, types and sizes, including species also sharing bats and birds as seed dispersers. Despite the diversity in fruits dispersed, a strong association among fruit traits allowed us to describe a PDS: primates tended to disperse mostly medium to large sized yellow or orange berries, protected by a husk. Here we showed that primates act as generalists in expanding mutualistic networks that involve a wide range of interacting species collectively favoring trait diversification among Neotropical plants.

Introduction

Ecological interactions have been recognized as a major driver of diversification of plant and frugivores across the globe (Thompson 2004; Lengyel et al 2010; Guimarães Jr. et al 2011; Nuismer et al 2012). Although facultative, the establishment of reciprocal positive interactions with plants is often related to an increase in geographic ranges and speciation rates among mutualistic primates over antagonistic ones, and mutualism is a strongly conserved character in primate phylogenetic history (Gómez and Verdú 2002).

Primates are a very well-studied vertebrate order in Neotropical forests, with most attention dedicated to feeding ecology (Hawes and Peres 2014). Although much is known about frugivory, seed dispersal and its ecological and evolutionary consequences have received much less attention (Howe 2016, but see Gómez and Verdú 2002). Fruit intake is clearly related to dispersal potential, and all primates across the Platyrrhini radiation routinely include fruits in their diets (Hawes and Peres 2014). However, the degree of frugivory and the role played in mutualistic interactions ranges widely across taxa (Hawes and Peres 2014; Fuzessy et al 2016, 2017, in prep.) and geographical region (Gómez and Verdú 2002). Neotropical primates therefore do not constitute a homogeneous group, mainly due to body size, movement patterns and handling behavior (Fuzessy et al. 2016, 2017, in prep).

Despite the pivotal importance to primate evolution (Gómez and Verdú 2002; DeCasien et al 2017), consequences of interactions with fruits remain unclear from the plant phylogenetic point of view. In general, seed dispersal mutualisms are characterized by a low degree of specialization: most plants interact with distinct groups of vertebrates and vice-versa (Bascompte and Jordano 2007; Donatti et al 2011). Recent studies suggest that mutualistic networks might be generated when an interaction evolves successfully, and more species can attach by evolutionary trait convergence (Bascompte and Jordano 2007; Guimarães Jr. et al 2011; Nuismer et al 2012). The consequence of such process would be the evolution of dispersal syndromes, i.e. nonrandom plant traits associated with specific disperser groups (van der Pijl 1969; Gautier-Hion et al 1985; Bascompte and Jordano 2007).

Many studies report the existence of seed dispersal syndromes, especially distinguishing bird-dispersed from primate-dispersed fruits (van der Pijl 1969; Janson 1983; Gautier-Hion et al 1985; Voigt et al 2004; Lomáscolo et al 2008), but the specificity of such syndromes remains a contentious issue (Flörchinger et al 2010). Most studies account for frugivory – and not effective seed dispersal – as indicative of mutualistic interactions and also do not consider phylogenetic influence. When syndromes were investigated under a phylogenetic-controlled point of view, the syndrome hypothesis was often not strongly supported (Herrera 1987; Fischer and Chapman 1993, Voigt et al. 2004), with exception for Lomáscolo et al (2008), evaluating evolution of traits among species of a single genus. Despite the difficult task, a series of analytical tools are currently available that allow us to evaluate if a primate-dispersed syndrome exists, and this information may shed light on the ecology and evolution of plant-primate interactions.

Here we aimed to investigate whether a combination of a set of fruit traits, such as color, type, size and husk presence influence primate choice, and thereby define a primate-dispersed syndrome (PDS) using a phylogenetic-explicit approach. Also, we tested whether fruit traits vary among plants dispersed by distinct primate families, and finally explored whether birds and bats overlapped their ability to disperse certain plant species with primates. We hypothesize that fruit traits define a PDS, and thus we expect a coordinated trait evolution (phenotypic integration), and also a low overlap on fruit consumption among primates, birds and bats.

Materials and methods

Database

We performed a comprehensive literature review, using both Web of Science (http://thomsonreuters.com/web-of-knowledge/) from 1945 to 2016, and Google Scholar (http://scholar.google.com) databases. Keywords used for search in Web of Science within the title, abstract and keywords of papers were: neotrop* AND (primate* OR monkey*) AND (seed* dispers*). Keywords used for search "anywhere in the article" in Google Scholar were: Neotropical primate seed dispersal "primate" OR "primates" OR "monkey" OR "monkeys". Our database was supplemented with studies cited in the reference lists of the articles surveyed. Because frugivory does not necessarily imply seed dispersal (Schupp et al 2010), sources for plant species included in our review comprised only studies that provided direct evidence of seed dispersal, i.e. seed survival after gut passage. The list of plant species dispersed by Neotropical primates was supplemented with data available in Bufalo et al (2016). The list of studies that provided information on plant species dispersed by Neotropical primates and met the criteria to inclusion in our review is available in Supplementary Material S1.

Dispersal Syndromes and Primate Families

To compare fruit traits among the most important families of seed dispersers in Neotropical primates (Gómez and Verdú 2002), we classified plants according to respective dispersers, into four families: Atelinae, Alouattinae, Cebinae and Callithrichinae. In many cases one plant species were dispersed by more than one primate family.

To assess overlapping in plant species and compare fruit traits among the most important seed dispersers in Neotropical forests (Fleming and Kress 2011), we surveyed the literature for other dispersers of plant species dispersed by Neotropical primates and classified plants into four categories: 1) species known to be exclusively primate-dispersed, 2) species known to be dispersed by primates and bats, 3) species known to be dispersed by primates and birds; and 4) species known to be dispersed by primates, bats and birds. Information on seed dispersal by bats and birds was collected from published literature, including a complete review from Lobova et al (2009) for seed dispersal by bats in Neotropics. The complete list of studies for bats and birds is available on Supplementary Material S2.

Fruit Traits

We evaluated five morphological fruit traits known to be related to food-selection by vertebrates (van der Pijl 1969; Gautier-Hion et al 1985; Herrera 2002) especially primates: fruit color, type, size (in terms of length and width), number of seeds per fruit and presence of husk (Janson 1983; Lambert and Garber 1998).

Categorical fruit traits, such as type and color, were classified according to functionality from disperser’s perspective (Janson 1983; Gautier-Hion et al 1985; Lambert and Garber 1998; Herrera 2002; Renoult et al 2014). Thus, as for fruit type we grouped aggregates and spadices with berries, since the consumed structure represent many small seeds swallowed within a matrix of pulp. Also, follicles and capsules were grouped into a single category, since both fruit types split along a seam to expose the inner seeds, pulp and/or arils (if present). Thus, fruit types were classified as: berry (B), drupe (D), capsule (C), legume (L) or multiple (M).

As for fruit color, yellow and orange ones, as well as black and purple, and also pink and red fruits are not easily distinguished during food selection (Janson 1983; Gautier-Hion et al 1985; Lambert and Garber 1998; Herrera 2002; Schmidt et al 2004), so they were grouped into single categories. Thus color categories were: yellow/orange (OR), black/purple

(BlP), red (R), green (G), brown (B) and white (W). To account for visual contrast possibly emerged from fruit structures (Schmidt et al 2004; Renoult et al 2014) we also considered the presence of more than one color in a single fruit (exposed pulp and/or arils, calyx and/or pedicels). The presence of any other color was identified as presence of contrast (C). Information on fruit traits was collected from published literature and online databases (see Supplementary Material S2).

Statistical and phylogenetic analyses

To explore the main pattern of association between fruit traits measured to species-level, we computed a global distance and applied a principal coordinated analysis (PCoA) to assess the two main axes of variation encompassed in the global distance matrix. First, continuous traits, such as fruit length, width and number of seeds per fruit were treated as ordinal variables. Fruit color was treated as a multichoice variable, which allowed us to account for more than one state when fruits presented more than one colored structures. To visualize the groups based on each variable, we plotted factorial maps (Pavoine et al 2009) with the package 'ade4' (Dray and Dufour, 2007) in the R environment (R Development Core Team, 2016). We then used chi-squared test to assess the association among morphological traits.

To assess whether phylogeny explain the evolution of traits related to fruit choice by primates in Neotropics, species dispersed by Neotropical primates were arrayed on a ultrametric phylogenetic tree (Supplementary Material S3). First, plant species were taxonomically and nomenclaturally updated (Boyle et al 2013, The Taxonomic Name Resolution Service) and species relationships were obtained using 'Phylomatic' (http://phylodiversity.net/phylomatic/). We then manually corrected and improved the ultrametric tree resolution in 'Mesquite' (http://mesquiteproject.org/) based on a number of recent studies of morphological and molecular phylogenies (Supplementary Material S4). To estimate branch lengths (i.e. time since divergence), we dated 143 nodes according to published literature (Supplementary Material S4) and positioned undated nodes evenly in the tree with the 'bladj' algorithm of Phylocom software (Webb et al, 2008).

To compare fruit choice among primate families and other seed dispersers (birds and bats), accounting for plant phylogeny, we fitted phylogenetically-adjusted regression models and performed Phylogenetic Generalized Least Squares analysis (PGLS) adjusting expected covariance under a Brownian model (Felsenstein 1985; Martins and Hansen 1997). We used the eigenvalues of PCoA axis 1 as dependent variable with the with the package 'nlme'. We performed Tukey HSD tests as post-hoc with primate families and other dispersers (birds and bats) as multi-level factor predictor variables, using 'multcomp' package (Hothorn et al 2008).

To assess the existence of a phylogenetic signal in the quantitative fruit traits (fruit length, fruit width and number of seeds per fruit) we used Blomberg's K test with 100,000 randomizations (Blomberg et al 2003; Munkemuller et al 2012) using the 'picante' package (Kembel et al, 2010). All the analyses were performed in the R environment (R Development Core Team 2016).

Results

Diversity of dispersed species

According to the information gathered from the 75 studies that matched our criteria, primates dispersed seeds of 749 plant species belonging to 82 families and 262 genera in Neotropics. The most dispersed family was Moraceae, with 73 species, followed by Sapotaceae (67 spp.) and Fabaceae (63 spp.) (Supplementary Materials S3 and S5).

Primates were the exclusive seed disperses of 547 species out of 749 species. Primates + birds dispersed 103 species, primates + bats 59 species, and the three vertebrate taxa dispersed 40 plant species.

Amongst families, Sapotaceae was the most exclusively primate-dispersed taxa, followed by Fabaceae. Note that we have not aimed to evaluate representativeness within families, i. e. data was reported in terms of absolute number of species dispersed, not weighted by total number of species in each family. Of the 67 Sapotaceae species found to be dispersed by primates, 63 were dispersed only by them, three were also dispersed by bats, one was also dispersed by birds and none were found to be dispersed by the three vertebrates together. Moraceae was the most common family dispersed by primates and bats, with 15 species. Salicaceae was the main shared family among primates and birds, with ten species dispersed, followed by Moraceae, Myrtaceae and Myristicaceae with seven species each (Fig. 1, Supplementary Material S3 and S5).

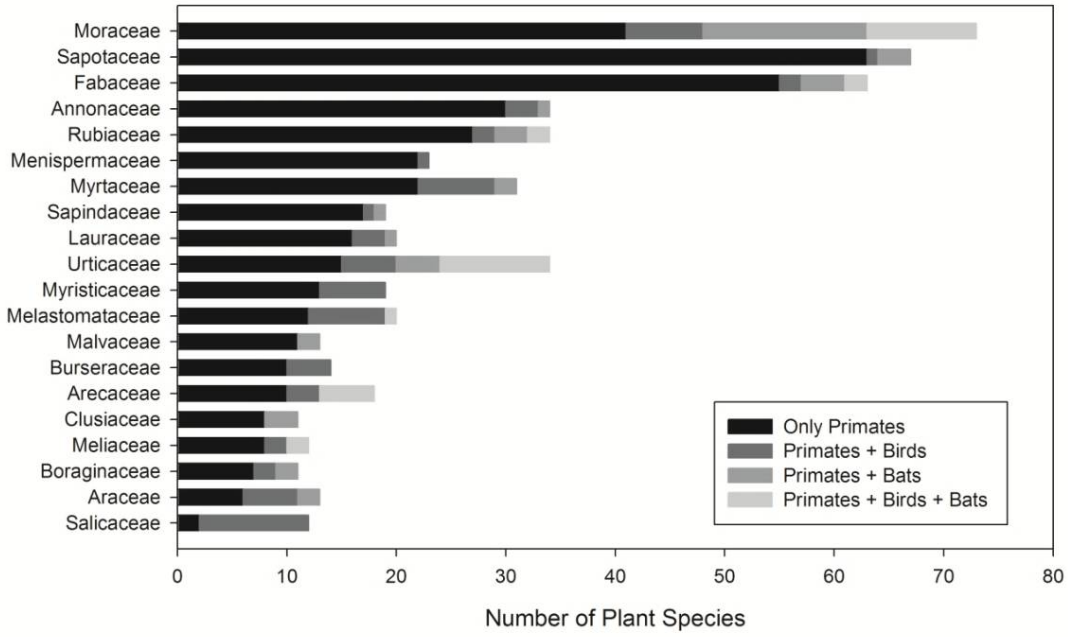

Figure 1 – Number of plant species per family dispersed by each syndrome provided for the 20 most dispersed families. Complete information is available in Supplementary Material S5

Trait diversity in fruit dispersed by Neotropical primates

Neotropical primates dispersed from very small rounded fruits (0.40 x 0.35cm) to very large and long (35.00 x 2.10cm) or rounded fruits (20.00 x 13.00cm) each containing from one to more than 100 seeds. Fruit length and width frequently respectively ranged between 1.0-5.00cm and 1.0-3.00cm (Supplementary Material S6). Berry was the most frequent fruit type dispersed (42%), followed by drupe (28.5%). This tendency was also true for the four categories of seed dispersers (Fig. 2).

We were able to classify husk status (presence or absence) in 738 plant species dispersed by primates. Husk was present in 41%, but percentages greatly varied among dispersal syndromes. Nearly half of the species dispersed exclusively by primates presented husk, while 40% of the species found to be dispersed by primates and bats had the structure. On the other hand, the very least proportion (about 2.5%) of the fruits shared with birds had the structure (Fig. 2).

We were able to classify fruit color in 720 plant species. Although primate-dispersed fruits varied among green, red, brown and white, the great majority (33%) was yellow/orange, followed by black/purple (19%). When considering syndromes, green was relevant in species sharing primates and bats as seed dispersers (29%). However, fruits dispersed by primates and birds were predominantly black/purple (32%). Brown and red were the most frequent color in fruits dispersed by the three taxa together (25% in each case). Overall, color contrast was present in less than 15% of the species, and this pattern was also true when considering primate-exclusive fruits and fruits dispersed by primates, birds and bats. Nearly a third (28%) of species shared among primates and birds presented contrast. On the other hand, the least proportion (less than 2%) of the fruits dispersed by primates and bats had contrast (Fig. 2).

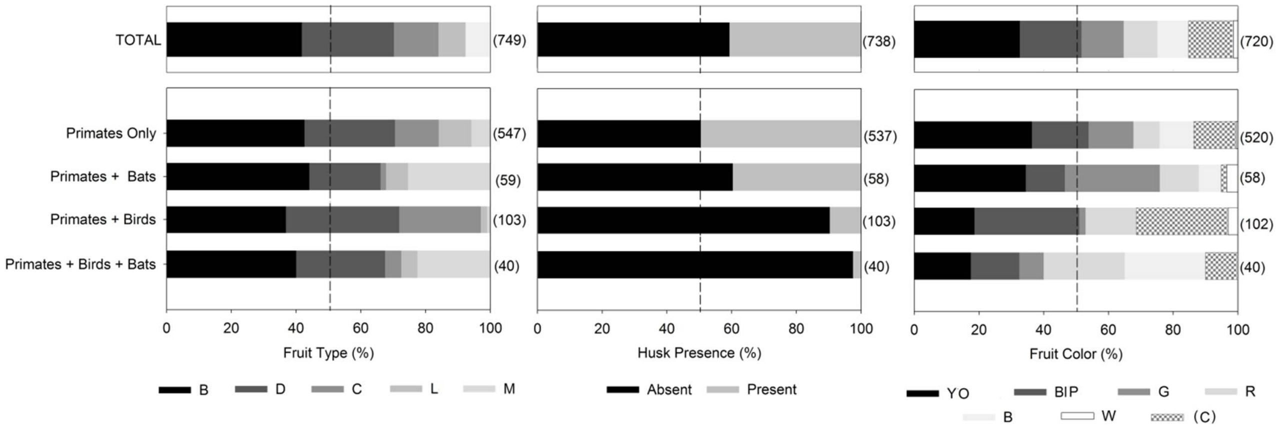

Figure 2 – Percentage of fruit types, husk presence and fruit colors in plants dispersed by primates in Neotropics (total) and among syndromes. Fruit types were classified into the following categories: B – berry, D – drupe, C – capsule, L – legume and M – multiple. Fruit colors were classified into the following categories: YO – yellow/orange, BlP – black/purple, G – green, R – red, B – brown, W – white and (C) – contrast.

Phenotypic integration of fruit traits

We were able to obtain complete trait information for 686 of the 749 plant species. The PCoA applied in the global trait distance computed highlighted a moderate association between these variables. The two main axes of the PCoA explained 47% of the total variance. The first axis separated fruits presenting husk from those with no protection and the second axis separated drupes from other fruit types (Fig. 3).

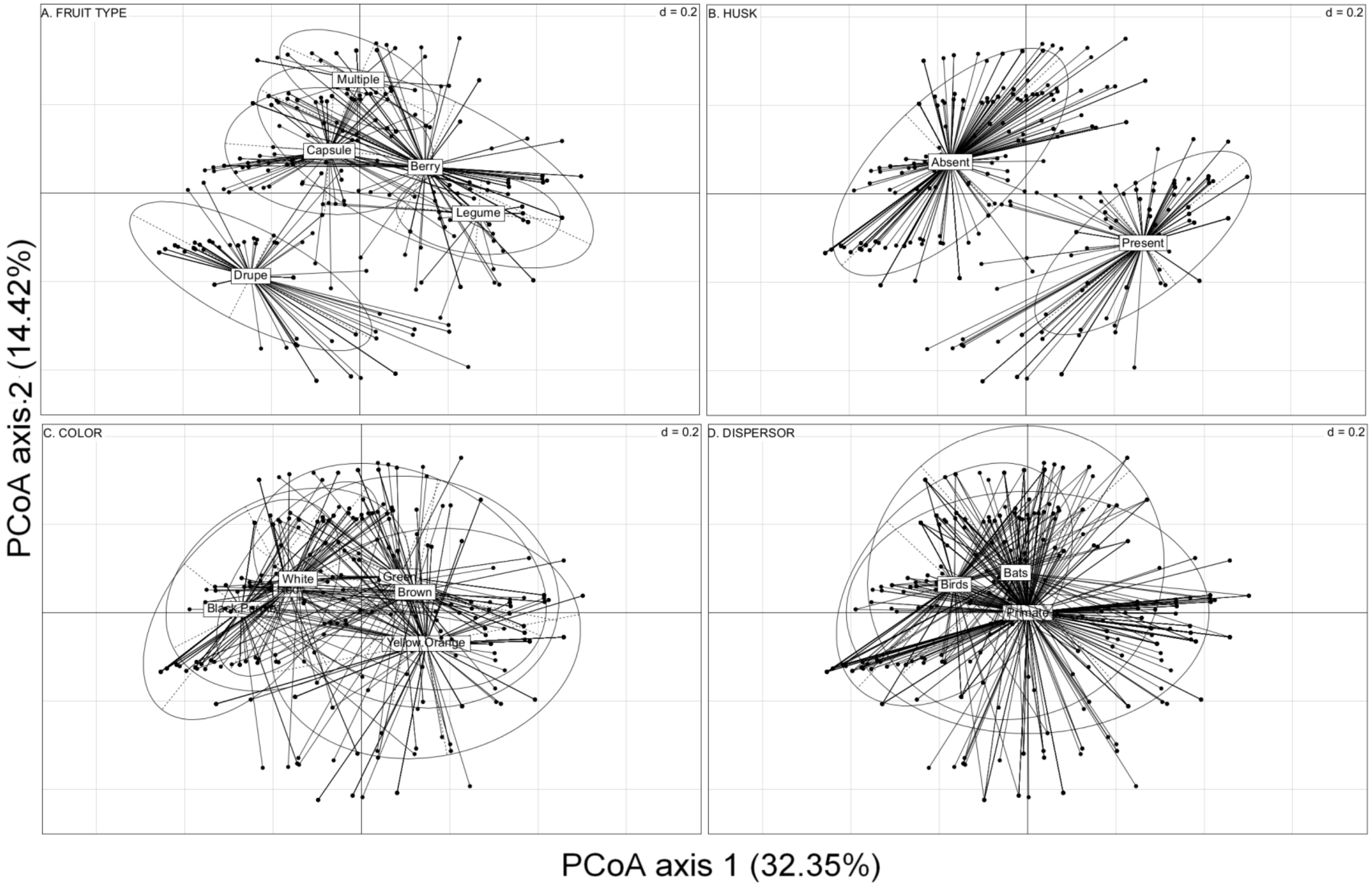

Figure 3. Principal coordinates analysis (PCoA) applied to the global Gower distance (Pavoine et al 2009) computed with fruit type and color as categorical traits, husk presence as discrete trait and fruit length and width as continuous traits.. Each panel shows a factorial plot representing the levels of each categorical variable and discrete variable at the centroid of species assigned to each level. Disperser panel (D) was built to visualize each seed dispersal syndrome spatial distribution. Contribution plot of each variable is available in Supplementary Material S6. The percentage of variation explained by each axis is shown in parentheses. Vertical and horizontal grid lines are separated by d=0.2 units at each axis scale.

According to Chi-squared analysis, fruit traits were strongly associated among each other (see Supplementary Material S7-A). Fruits dispersed by primates tended to be mainly medium to large yellow/orange berries with a husk (see Supplementary Material S7-B).

The PGLS analysis showed variation in fruit traits among disperser groups (F = 9.28, P < 0.0001). When accounting for plant phylogeny, fruits dispersed exclusively by primates were morphologically distinct from those dispersed either by primates and birds (Z = -4.8, P = <0.001), or by primates, bats and birds (Z = -2.73, P = 0.03) but not from fruits dispersed by primates and bats (Z = -1.7, P = 0.3). Fruits dispersed by primates and birds were similar from fruits dispersed by primates and bats (Z = -1.93, P = 0.2) as well as from fruits dispersed by primates, birds and bats (Z = -1.12, P = 0.7) ((Fig. 4A). Primate families did not differ in terms of fruits traits (F = 0.61, P = 0.8) (Fig. 4B).

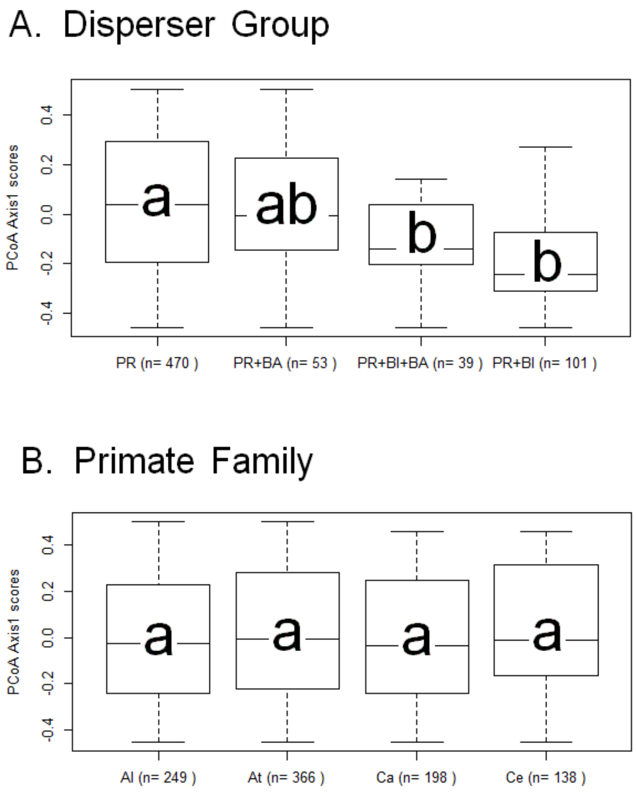

Figure 4 – Comparisons of PCoA axis 1 eigenvalues among dispersers (A) and primate families (B) accounting for plant phylogeny. Lowercase letters represent statistical difference among groups. Dispersal syndromes: PR – species dispersed exclusively by primates, PR+BA – species dispersed by primates and bats, PR+BI – species

dispersed by primates and birds, PR+BI+BA – species dispersed by the three taxa. Primate families: Al – Alouattinae, At – Atelinae, Ca – Callithrichinae, Ce – Cebinae. Total sample number = 686. Number of plant species in each group is represented in parenthesis. Note that one plant species can be dispersed by more than one primate family. Thus, the sum of values in parenthesis differs from 686.

We found a weak phylogenetic signal in fruit length (K=0.39, p=0.01) and fruit width (K=0.32, p=0.01), but a strong phylogenetic signal in number of seeds per fruit (K=0.92, p=0.01). Fruit size appears to have evolved multiple times along phylogeny of plants dispersed by Neotropical primates, unlike the number of seeds per fruit.

Discussion

The evolution of fruit traits underpinning a primate seed dispersal syndrome has been a long-lasting perennial issue in the ecology of fruit-primate interactions. To date, the identification of a specific primate-dispersal syndrome has been challenging due to the lack of an evolutionary ecology framework of fruit traits. In fact, we found great diversity on fruit traits among the 749 plant species studied. In terms of feeding ecology, primates tend to be generalists (Gomez and Verdú 2002, Howes and Peres 2014), and here we demonstrated that Neotropical primates disperse a variety of fruit colors, types and sizes. Despite this, there was a prevalence of particular features in relation to other disperser groups, such as birds and bats. In addition, the strong association among morphological fruit traits together with the very low overlap on plant species dispersed by primates and other dispersers, argue in favor of a characterization of a primate-dispersed syndrome (PDS). Thus, we were able to characterize a PDS as medium to large sized yellow/orange berries, in many cases protected by a husk.

Our results broadens the available information on fruit traits related to a PDS to the whole Neotropical region and partially corroborate previous findings from Lambert and Garber (1998) in South America and Janson (1983) in Peru, but point to a higher generality than previously thought. Also, here we show that, in spite of Neotropical primates largely vary in terms of body size and handling behavior (Fuzessy et al. in prep), fruits dispersed by distinct families did not vary in morphology.

As a consequence of an anatomical and sensorial constraint, we found a morphological distinction among fruits dispersed exclusively by primates and those shared with birds. Birds tend to be smaller and the absence of strong mandibular muscles and teeth restricts the consumption of large husked fruits (Lomáscolo and Schaefer 2010). Unlike primates, birds have a very complex vision system, which allows them to efficiently detect red and black fruits due to conspicuousness created to background foliage (Schmidt et al 2004, Ordano et al 2017).

On the other hand, we found a similarity among fruits dispersed exclusively by primates and those also dispersed by bats. Bats forage at night during flight and have simple color vision, as well as primate's vision system, which makes conspicuousness not important for fruit detection (Lobova et al 2009). In addition, primates and bats are both olfactory-dependent vertebrates, and another feature not examined here that may determine fruit choice is odor. Primate-dispersed (Nevo et al 2016) and also bat-dispersed fruits (Lobova et al 2009) significantly change their odor profiles upon ripening, which also distinguish them from most bird consumed fruits (Nevo et al 2016; Wenny et al 2016). However, the role of secondary metabolites in signaling ripeness to seed-dispersing vertebrates is not yet strongly supported (Nevo et al 2016). Future research should better address these questions, so studies examining traits related to fruit choice and consequently seed dispersal can incorporate odor as a potential predictor.

Despite it was not a primary purpose on our study, we were able to identify features often related to 'ornitochoric' and to 'chiropterochoric' fruits due to great diversity in traits among primate-dispersed species. Fruits eaten by birds are often red, blue or back, small-sized (less than 2cm), lacking outer rind and also lacking odor (van der Pijl 1969; Janson 1983; Gautier-Hion et al 1985; Voigt et al 2004; Lomáscolo et al 2008; Wenny et al. 2016, Ordano et al 2017). Here we found that one third of the fruits collectively dispersed by birds and primates were black or purple. Other 30% presented conspicuousness to the background or among fruit structures. Husk was present in only 10% of the fruits, and large sized-fruits were not dispersed by birds. Otherwise, bats tend to consume and disperse greenish or brownish small-seeded fruits gathered in infructescences or multiple-structures, which allow them to be taken in flight (van der Pijl 1969; Lobova et al. 2009). Here we found that less than 2% of plant species shared among primates and bats displayed color contrast, while about 30% were green. Also, a quarter of the fruits shared by bats with primates were multiple, and husk did not constrain bat participation as seed dispersers.

We found a weak phylogenetic signal in fruit length and width, suggesting a minor role of phylogeny in determining fruit size amongst primate-dispersed species in Neotropics. Those results concur with previous observations. Fruit size has been demonstrated to account for lower fractions of total phylogenetic variance in quantitative fruit traits, indicating that interaction with dispersers, which evolved many times in plant phylogenetic history, might influence evolution of fruit dimensions among angiosperms (Jordano 1995). On the other hand, the strong phylogenetic signal in number of seeds per fruit suggested a major role of phylogeny. Those results also concur with previous observations. Jordano (1995) has demonstrated that number of seeds per fruit is the main quantitative fruit trait which variation can be mostly accounted by angiosperm phylogenetic history across the globe, indicating a greater influence of early evolutionary history than pressures exerted by recent interactions with frugivores.

In conclusion, our study shows that mutualistic interactions and potential associations between fruit traits and primates define a primate-dispersed syndrome (PDS). It is important to note, however, that even the most exclusively primate-dispersed family, such as Sapotaceae, with large fruits, can also be dispersed by other frugivores (Snow 1981; Lobova et al 2009). Thus, seed dispersal mutualisms are rarely specialized, but expand networks involving generalists and a wide range of interacting species (Guimarães Jr. et al 2011; Nuismer et al 2012). Finally, to better understand the role of a broader range of interacting dispersers in selection upon fruit traits and vice-versa, future research should also incorporate fruits exclusively dispersed by other vertebrates.

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Supplementary Material S1

Autor(s)	Year	Title	Journal	Place	Country	Longitude	Latitude
Howe HF	1980	Monkey dispersal and waste of a Neotropical fruit	Ecological Society of America	Barro Colorado Island (BCI)	Panama	79° 51'W	9° 10'N
Estrada A and Coates-Estrada R	1984	Fruit eating and Seed Dispersal by Howling monkeys in the tropical rain forest of los Tuxtlas, Mexico	American Journal of Primatology	Los Tuxtlas Biological Reserve	Mexico	95,04°W	18,34°N
Estrada A, Coates-Estrada R, Vazquez-Yanes C	1984	Observations on Fruiting and Dispersers of *Cecropia obtusifolia* at Los Tuxtlas, Mexico	Biotropica	Los Tuxtlas Biological Reserve	Mexico	95,04°W	18,34°N
Garber PA	1986	The Ecology of Seed Dispersal in Two Species of Callitrichid Primates (*Saguinus mystax* and *Saguinus fuscicollis*)	American Journal of Primatology	Quebrada Blanco Biological Station	Peru	72°10' W	04°05' S
Chapman CA	1989	Primate seed dispersal: the fate of dispersed seeds	Biotropica	Santa Rosa National Park	Costa Rica	85°37' W	10°51' N
Estrada A and Coates-Estrada R	1991	Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas	Journal of Tropical Ecology	Los Tuxtlas Biological Reserve	Mexico	95,04°W	18,34°N
Moraes PLR	1992	Dispersão de sementes pelo monocarvoeiro (*Brachyteles arachnoides*) no Parque Estadual Carlos Botelho	Revista do Instituto Florestal	Carlos Botelho State Park	Brazil	47°50'W	24°45'S
Figueiredo RA	1993	Ingestion of *Ficus enormis* seeds by howler monkeys (Alouatta fusca) in Brazil: effects on seed germination	Journal of Tropical Ecology	Santa Genebral Reserve	Brazil	47°06'40"W	22°49'20"S
Galetti M, Pedroni F, Morellato LPC	1994	Diet of the brown howler monkey *Alouatta fusca* in a forest fragment in southeastern Brazil	Mammalia	Santa Genebral Reserve	Brazil	47°07'W	22°49'S
Galetti M, Pedroni F	1994	Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in southeast Brazil	Journal of Tropical Ecology	Santa Genebral Reserve	Brazil	47°07'W	22°49'S
Zhang SY, Wang LX	1995	Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana	Biotropica	Nouragues Biological Station	French Guiana	52°40'W	4°05' N
Nunes A	1995	Um teste de germinação em sementes dispersas por macacos-Aranha em Maracá, Roraima; Brasil	Studies on Neotropical Fauna and Environment	Maracá Ecologic Station	Brazil	61º40W	3º25'N
Julliot C	1996	Seed Dispersal by red Howling Monkeys (*Alouatta seniciculus*) in the tropical rain forest of French Guiana	International Journal of Primatology	Nouragues Biological Station	French Guiana	52°40’W	4°05’N

Julliot C	1996	Fruit choice by red Howler Monkeys (*Alouatta seniculus*) in a tropical rain forest	American Journal of Primatology	Nouragues Biological Station	French Guiana	52°40'W	4°05’N
Defler TR, Defler SB	1996	Diet of a group of *Lagothrix lagothricha* in Southeastern Colombia	International Journal of Primatology	Caparú Biological Station	Colombia	69°30'W	1°5'S
Julliot C	1997	Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understory of tropical rain forest	Journal of Ecology	Nouragues Biological Station	French Guiana	52°40’W	4°05’N
Garber PA, Kitron U	1997	Seed Swallowing in Tamarins: Evidence of a Curative Function or Enhanced Foraging Efficiency?	International Journal of Primatology	Barro Colorado Island (BCI)	Panamá	79°51’W	09°09'N
Knogge C, Heymann EW, Herrera ERT	1998	Seed dispersal of Asplundia peruviana (Cyclanthaceae) by the primate *Saguinus fuscicollis*	Journal of Tropical Ecology	Quebrada Blanco Biological Station	Peru	73°09'W	4°21'S
Andersen E	1999	Seed dispersal by monkeys and thef ate of dispersed Seeds in a Peruvian rain forest	Biotropica	Manu National Park	Peru	71°18'W	11°55'S
Feer F.	1999	Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest	Journal of Tropical Ecology	Nouragues Biological Station	French Guiana	52°40'W	4°05’N
Yumoto T, Kimura K, Nishimura A	1999	Estimation of the Retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagotricha*, in a Colombian forest	Ecological Research	Tinigua National Park	Colombia	74°10'W	2°40'N
Bravo SP and Zunino GE	2000	Germination of seeds from three species dispersed by black howler monkeys (*Alouatta caraya*)	Folia Primatol	Brasilera Island	Argentina	58°41'W	27°30'S
Oliveira ACM, Ferrari SF	2000	Seed dispersal by black-handed tamarins *Saguinus midas nige*r (Callitrichinae, Primates): implications for the regeneration of degraded forest habitats in eastern Amazonia	Journal of Tropical Ecology	Vitória Farm	Brazil	47°31' W	2°59' S
Stevenson PR	2000	Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: Dispersal Distance, germination rates, and dispersal quantity	American Journal of Primatology	Tinigua National Park	Colombia	74°10' W	2°40' N
Andersen E	2001	Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia	Journal of Tropical Ecology	BDFFP	Brazil	60° W	2°30' S
Stevenson PR, Castellanos MC, Pizarro JC, Garavito M	2002	Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia	International Journal of Primatology	Tinigua National Park	Colombia	74°10' W	2°40' N
Andersen E	2002	Primary seed dispersal by red howler honkeys and the effect of defecation patterns on the fate of dispersed seeds	Biotropica	BDFFP	Brazil	60°W	2°30'S

Wehncke EV, Hubbell SP, Foster RB, Dalling JW	2003	Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species	Journal of Ecology	Barro Colorado Island (BCI)	Panamá	79°51' W	9°10' N
Knogge C, Heymann EW	2003	Seed dispersal by sympatric tamarins *Saguinus mystax* and *Saguinus fuscicollis*: Diversity and characteristics of plant species	Folia Primatol	Quebrada Blanco Biological Station	Peru	73°09'W	04°21' S
Russo SE	2003	Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection	Plant Animal Interactions	Manu National Park	Peru	71°18'W	11°54'S
Knogge C, Herrera ERT, Heymann EW	2003	Effects of passage through tamarin guts on the germination potential of pispersed seeds	International Journal of Primatology	Quebrada Blanco Biological Station	Peru	73°09'W	04°21' S
Wehncke EV, Valdez CN, Dominguez CA	2004	Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: consequences for seed dispersal effectiveness	Journal of Tropical Ecology	Palo Verde National Park (PV)	Costa Rica	84°48′35″W	10°18′25″N
Russo SE and Augspurger CK	2004	Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*	Ecology Letters	Manu National Park	Peru	71°18' W	11°54' S
Righini N, Serio-Silva JC, Rico-Gray V, Martínez-Mota R	2004	Effect of Different Primate Species on Germination of *Ficus* (*Urostigma*) Seeds	Zoo Biology	-	-	-	-
Martinez-Mota R, Serio-Silva JC, Rico-Gray V	2004	The role of canopy ants in removing *Ficus perforata* seeds from howler monkey (*Alouatta palliafa mexicana*) feces at Los Tuxtlas, Mexico	Biotropica	Playa Escondida, Los Tuxtlas	Mexico	95°05'W	18°36'N
Estrada A, Coates-Estrada R	2004	Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico	Biotropica	Playa Escondida, Los Tuxtlas	Mexico	95°05'W	18°36'N
Stevenson PR, Link A, Ramírez BH	2005	Frugivory and seed fate in *Bursera inversa* (Burseraceae) at Tinigua Park, Colombia: Implications for primate conservation	Biotropica	Tinigua National Park	Colombia	74°10' W	2°40' N
Stevenson PR, Pineda M, Samper T	2005	Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park, Colombia	Oikos	Tinigua National Park	Colombia	74°10' W	2°40' N
Dew JL	2005	Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*	International Journal of Primatology	Yasuní National Park	Ecuador	75°28'W	0°42'S
Wehncke EV, Dalling JW	2005	Post-dispersal seed removal and germination selected tree species dispersed by *Cebus capucinus* on Barro Colorado Island, Panama	Biotropica	Barro Colorado Island (BCI)	Panamá	79°51' W	9°10' N
Link A and Di Fiori A	2006	Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity	Journal of Tropical Ecology	Yasuní National Park	Ecuador	76°W	1°S

Martins MM	2006	Comparative seed dispersal effectiveness of sympatric *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil	Biotropica	Barreiro Rico Farm	Brazil	48°06’W	22°41' S
Ponce-Santizo G, Andersen E, Cano E, Cuarón AD	2006	Dispersión primaria de semillas por primates y dispersión secundaria por escarabajos coprófagos en Tikal, Guatemala	Biotropica	Tikal National Park	Guatemala	89°35'5'' W	17°33'3"N
Domínguez-Domínguez LE, Morales-Mávil JE, Alba-Landa J	2006	Germinación de semillas de *Ficus insipida* (Moraceae) defecadas por tucanes (*Ramphastos sulfuratus*) y monos araña (*Ateles geoffroyi*)	Revista de Biología Tropical	Los Tuxtlas Biological Reserve	Mexico	-	-
Moura ACA, McConkey KR	2007	The capuchin, the howler, and the Caatinga: Seed dispersal by monkeys in a threatened brazilian forest	American Journal of Primatology	Serra da Capivara National Park	Brazil	42°45' W	8°54'S
Giraldo P, Gómez-Posada C, Martínez J, Kattan G	2007	Resource use and seed dispersal by red howler monkeys (*Alouatta seniculus*) in a Colombian Andean Forest	Neotropical Primates	Santuario Fauna and Flora Otún-Quimbaya	Colombia	75°28'W	04°43'N
Lapenta MJ and Procópio-de-Oliveira p	2008	Some aspects of seed dispersal effectiveness of golden lion tamarins (*Leontopithecus rosalia*) in a Brazilian Atlantic forest	Tropical Conservation Science	União Biological Reserve	Brazil	42°02’15”W	22°27’36”S
Lapenta MJ, Procópio-de-Oliveira P, Kierulff MCM, Motta-Junior JC.	2008	Frugivory and seed dispersal of golden lion tamarin (*Leontopithecus rosalia*) (Linnaeus, 1766)) in a forest fragment in the Atlantic Forest, Brazil	Brazilian Journal of Biology	União Biological Reserve	Brazil	42°02’15”W	22°27’36”S
Valenta K and Fedigan LM	2008	How much is a lot? Seed dispersal by white-faced capuchins and implications for disperser-based studies of seed dispersal systems	Primates	Santa Rosa National Park	Costa Rica	85°37' W	10°51' N
Martins MM	2008	Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparision of fruit type, color and seed size	Primates	Barreiro Rico Farm	Brazil	48°06’W	22°41' S
Felton AM, Felton A, Wood JT, Lindenmayer DB	2008	Diet and feeding ecology of *Ateles chamek* in a Bolivian semi-humid forest: The importance of *Ficus* as a staple food resource	International Journal of Primatology	Guarayos Forest Reserve	Bolivia	62°46'W	15°36'S
Bravo SP.	2009	Implications of behavior and gut passage for seed dispersal quality: The case of black and gold howler monkeys	Biotropica	Brasilera Island	Argentina	58°41'W	27°30'S
Catenacci LS, Vleeschouwer KM, Nogueira-Filho SLG	2009	Seed dispersal by golden-headed lion tamarins *Leontopithecus chrysomelas* in Southern Bahian Atlantic forest, Brazil	Biotropica	Una Biological Reserve	Brazil	39°03'W	15°10' S
Culot L, Huynen MC, Gérard P, Heymann EW	2009	Short-term post-dispersal fate of seeds defecated by two small primate species (*Saguinus mystax* and *Saguinus fuscicollis*) in the Amazonian forest of Peru	Journal of Tropical Ecology	Quebrada Blanco Biological Station	Peru	73°09'W	04°21' S
Valenta K and Fedigan LM	2009	Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*)	American Journal of Physical Anthropology	Santa Rosa National Park	Costa Rica	85°37' W	10°51' N

Valenta K, Klemens JA, Fedigan LM	2009	Sleep tree use by white-faced capuchins (*Cebus capuchinus*): Implications for differences in seedling composition	Neotropical Primates	Santa Rosa National Park	Costa Rica	85°37' W	10°51' N
Amato KR and Estrada A	2010	Seed dispersal patterns in howler monkey species (*Alouatta palliata* and *A. pigra*): A preliminary report of differences in fruit consumption, traveling behavior and associated dung beetle assemblages	Neotropical Primates	Los Tuxtlas Biosphere Reserve / Palenque National Park (PNP)	Mexico	95,04°W / 92°2′46.78″W	18,34°N / 17°29′2.32″N
Stevenson PR, Guzmán-Caro DC	2010	Nutrient transport within and between habitats through seed dispersal processes by woolly monkeys in north-western Amazonia	American Journal of Primatology	Tinigua National Park	Colombia	74°10' W	2°40' N
Culot L, Lazo JJM, Huynen MC, Poncin P, Heymann EW	2010	Seasonal variation in seed dispersal by tamarins alters seed rain in a secondary rain forest > APENDIX	International Journal of Primatology	Quebrada Blanco Biologic Station	Peru	73°09'W	04°21' S
Cardoso NA, Le Pendu Y, Lapenta MJ, Raboy BE	2011	Frugivory patterns and seed dispersal by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Una Biological Reserve, Bahia, Brazil	Mammalia	Una Biological Reserve	Brazil	39°03'W	15°10' S
Stevenson PR	2011	Pulp-seed attachment is a dominant variable explaining legitimate seed dispersal: a case study on woolly monkeys	Oecologia	Tinigua National Park	Colombia	74°10' W	2°40' N
Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A	2011	Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in Southern Mexico	International Journal of Primatology	Montes Azules Biosphere Reserve	Mexico	92°24' W	16°24′N
González-Di Pierro AM, Benítez-Malvido J, Méndez-Toribio M, Zermeño I, Arroyo-Rodríguez V, Stoner KE	2011	Effects of the physical environment and primate gut passage on the early establishment of *Ampelocera hottlei* Standley in rain forest fragments	Biotropica	Chiapas, Lacandona rainforest	Mexico	90°52'36''W	16°05'58''N
Ratiarison S, Forget PM	2011	Fruit availability, frugivore satiation and seed removal in 2 primate-dispersed tree species	Integrative zoology	Nouragues Biological Station	French Guiana	52°40'W	4°05'N
Anzures-Dadda A, Andresen E, Martínez ML, Manson RH	2011	Absence of howlers (*Alouatta palliata*) influences tree seedling densities in tropical rain forest fragments in Southern Mexico	International Journal of Primatology	Chiapas	Mexico	93°12′W	17°46′N
Bravo, SP	2012	The impact of seed dispersal by black and gold howler monkeys on forest regeneration	Ecological Research	Brasilera Island	Argentina	58°41'W	27°30'S
Levi T and Peres CA	2013	Dispersal vacuum in the seedling recruitment of a primate-dispersed amazonian tree	Biological Conservation	Tefé	Brazil	66°40'34"W	5°20'28" S
Feer F, Ponge JF, Jouard S, Gomez D	2013	APPENDIX - Monkey and dung beetle activities influence soil seed bank structure	Ecological Research	Nouragues Biological Station	French Guiana	52°40'W	4°05'N
Santos GASD, Bianchini E, Reis NR	2013	Seasonal variation of consumption of the species used as fruit source by brown howler monkeys (*Alouatta clamitans*) in southern Brazil	Biota Neotropica	Doralice Farm	Brazil	51°03'W	23°16'S

Ramírez MA, Galvis NF, Vargas SA, Léon JJ, Cifuentes EF, Stevenson PR	2014	Seed Dispersal by woolly monkeys in Cueva de los Guacharos National Park (Colombia): An Amazonian primate dispersing montane plants	High Altitude Primates, Developments in Primatology: Progress and Prospects	Los Guaracharos National Park	Colombia	76°06'W	1°36'N
González-Zamora A, Arroyo-Rodríguez V, Escobar F, Rös M, Oyama K, Ibarra-Manríquez G, Stoner KE, Chapman CA	2014	Contagious deposition of seeds in spider monkeys' sleeping tees limits effective seed dispersal in fragmented landscapes	Plos One	Chiapas, Lacandona rainforest	Mexico	90°56'W and 90°50'W	16°06'N and 16°15'N
Zárate DA, Andersen E, Estrada A, Serio-Silva JC	2014	Black howler monkey (*Alouatta pigra*) activity, foraging and seed dispersal patterns in shaded *Cocoa* plantations vs. rainforest in Southern Mexico	American Journal of Primatology	Chiapas, Lacandona rainforest	Mexico	90°53'40"W	16°8'58"N
Benitez-Malvido J, González-Di Pierro AM, Lombera R, Guillén S and Estrada A	2014	Seed source, seed traits, and frugivore habitats: implications for dispersal quality of two simpatric primates	American Journal of Botany	Chiapas, Lacandona rainforest	Mexico	90°52'36"W	16°05'58"N
Stevenson PR, Link A, González-Caro S, Torres-Jiménez MF	2015	Frugivory in canopy plants in a Western Amazonian forest: Dispersal systems, phylogenetic ensembles and keystone plants	Plos One	Tinigua National Park	Colombia	74°10'W	2°40'N
Nevo O, Heymann EW, Schulz S, Ayasse M	2016	Fruit odor as a ripeness signal for seed-dispersing Primates? A case study on four Neotropical plant species	Journal of Chemical Ecology	-	-	-	-

Supplementary Material S2 – Sources for dispersal syndromes and fruit traits

- Data for species dispersed **BY BATS** came from:

Charles-Dominique P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana, p. 119-135. *In* A. Estrada and T.H. Fleming (Eds). Frugivores and seed dispersal. Dordrecht, Dr. W. Junk Publ., 392p.

Galetti M et al 2011. Diversity of functional traits of fleshy fruits in a species-rich Atlantic rain forest. Biota Neotropica, 11: 181–193.

García-Estrada C et al 2012. Diets of frugivorous bats in montane rain forest and coffee plantations in Southeastern Chiapas, Mexico. Biotropica 44:394–401.

Estrada *et al* (1984) Comparison of frugivory by howling monkeys and bats in the tropical rain forest of Los Tuxtlas, Mexico. American Journal of Primatology. 7:3-13.

Lobova TA et al 2009. Seed dispersal by bats in the Neotropics, New York Botanical Garden Press.

Medellin RA and Gaona O. 1999. Seed dispersal by bats and birds in Chiapas, Mexico. Biotropica 31: 478–485.

Stevenson PR et al Guía de Frutos de los Bosques del Río Duda, Macarena, Colombia. Asociación Para la Defensa de La Macarena - IUCN. Bogotá, Colombia, 467 p.

- Data for species dispersed **BY BIRDS** came from:

Burns KC et al 2009. Geographic patterns in fruit color diversity: do leaves constrain the color of fleshy fruits? Oecologia 159: 337-343.

Charles-Dominique P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: Cecropia, birds and bats in French Guyana, p. 119-135. *In* A. Estrada and T.H. Fleming (Eds). Frugivores and seed dispersal. Dordrecht, Dr. W. Junk Publ., 392p.

Galetti MM et al 2011. Diversity of functional traits of fleshy fruits in a species-rich Atlantic rain forest. Biota Neotropica 11: 181–193.

Jordano P. 1983. Fig seed predation and dispersal by birds. Biotropica 15: 38-41

Kelly CK. 1995 Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia 102: 377-388.

Levey DJ et al 1994. Frugivory: an overview. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn (Eds) La Selva: ecology and natural history of a neotropical rain forest. Chicago press.

Martins VF et al 2014. Dispersal spectrum of four forest types along an altitudinal range of the Brazilian Atlantic forest. Biota Neotrop. 14.

Medellin RA and Gaona O. 1999. Seed dispersal by bats and birds in Chiapas, Mexico. Biotropica 31: 478–485.

Palmerim JM et al 1989. Trophic structure of a neotropical frugivore community: is there competition between birds and bats? Oecologia, Berlin, 79: 403-411.

Riba-Hernández, P., K. E. Stoner and P. W. Lucas. 2003. The sugar composition of fruits in the diet of spider monkeys (*Ateles geoffroyi*) in tropical humid forest in Costa Rica. Journal Tropical Ecology 19:709–716.

Skutch AF. 1980. Arils as food of tropical American birds. The Condor, Albuquerque 82: 31-42

Stevenson PR et al 2000. Guía de Frutos de los Bosques del Río Duda, Macarena, Colombia. Asociación Para la Defensa de La Macarena - IUCN. Bogotá, Colombia, 467pp.

Wheelwright NT. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808-818.

- Data for **FRUIT TRAITS** came from:

Barroso GM, Morim MP, Peixoto AL and Ichaso CLF. 1999. Frutos e sementes: morfologia aplicada à sistemática de dicotiledôneas. Viçosa: Editora UFV 443p.

Camargo J et al 2008. Guia de propágulos e plântulas da Amazônia. Editora INPA. Manaus, Brasil, 168pp.

Cornejo F and Janovec J. 2010. Seeds of Amazonian Plants. Princeton University Press. New Jersey, 192pp.

Esteves GL. 2005. Flora da Reserva Ducke, Amazonas, Brasil: Bombacaceae. Rodriguésia 56:115-124.

Galetti M et al 2011. Diversity of functional traits of fleshy fruits in a species-rich Atlantic rain forest. Biota Neotropica, 11: 181–193.

http://www.biotaneotropica.org.br/v11n1/en/abstract?article+bn02811012011.

Kuhlmann M. 2012. Frutos e sementes do cerrado atrativos para a fauna: Guia de campo. Rede de Sementes do Cerrado. Brasil, 360pp. Disponível em: http://www.frutosatrativosdocerrado.bio.br.

Link A and Stevenson PR. 2004. Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. Revista chilena de historia natural 77: 319-334.

Lobova TA et al 2003. *Cecropia* as food resource for bats in French Guiana and the significance of fruit structure in seed dispersal and longevity. American Journal of Botany 98: 388-403.

Lorenzi H. 1992. Árvores Brasileiras: manual de identificacao e cultivo de plantas arboreas nativas do Brasil vol. 1, 2 e 3. Editora Plantarum. Nova Odessa, 352pp.

Lorenzi H et al 2006. Frutas brasileiras e exóticas cultivadas (de consumo in natura). Editora Plantarum. Nova Odessa, São Paulo, 527pp.

Lorts et al 2008. Evolution of fruit types and seed dispersal: A phylogenetic and ecological snapshot. Journal of Systematics and Evolution 46:396-404.

Martins MM. 2008. Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparison of fruit type, color, and seed size. Primates 49:1-8.

Stevenson PR et al 2000. Guía de Frutos de los Bosques del Río Duda, Macarena, Colombia. Asociación Para la Defensa de La Macarena - IUCN. Bogotá, Colombia, 467pp.

van Roosmalen MGM and Garcia OMCG. 2000. Fruits of the Amazonian forest. Part II: Sapotaceae. Acta Amazonica 30:187-290.

van Roosmalen MGM. 1985. Fruits of Guianan Flora. Netherlands: Institute of Systematic Botany Utricht University, 463p.

Van Roosmalen MGM. 2003. Myristicaceae. Instituto Nacional de Pesquisas da Amazônia (INPA) 28p.

Wheelwright NT. 1985. Fruit size, gape width and the diets of fruit-eating birds. Ecology 66: 808-818.

Online Databases:

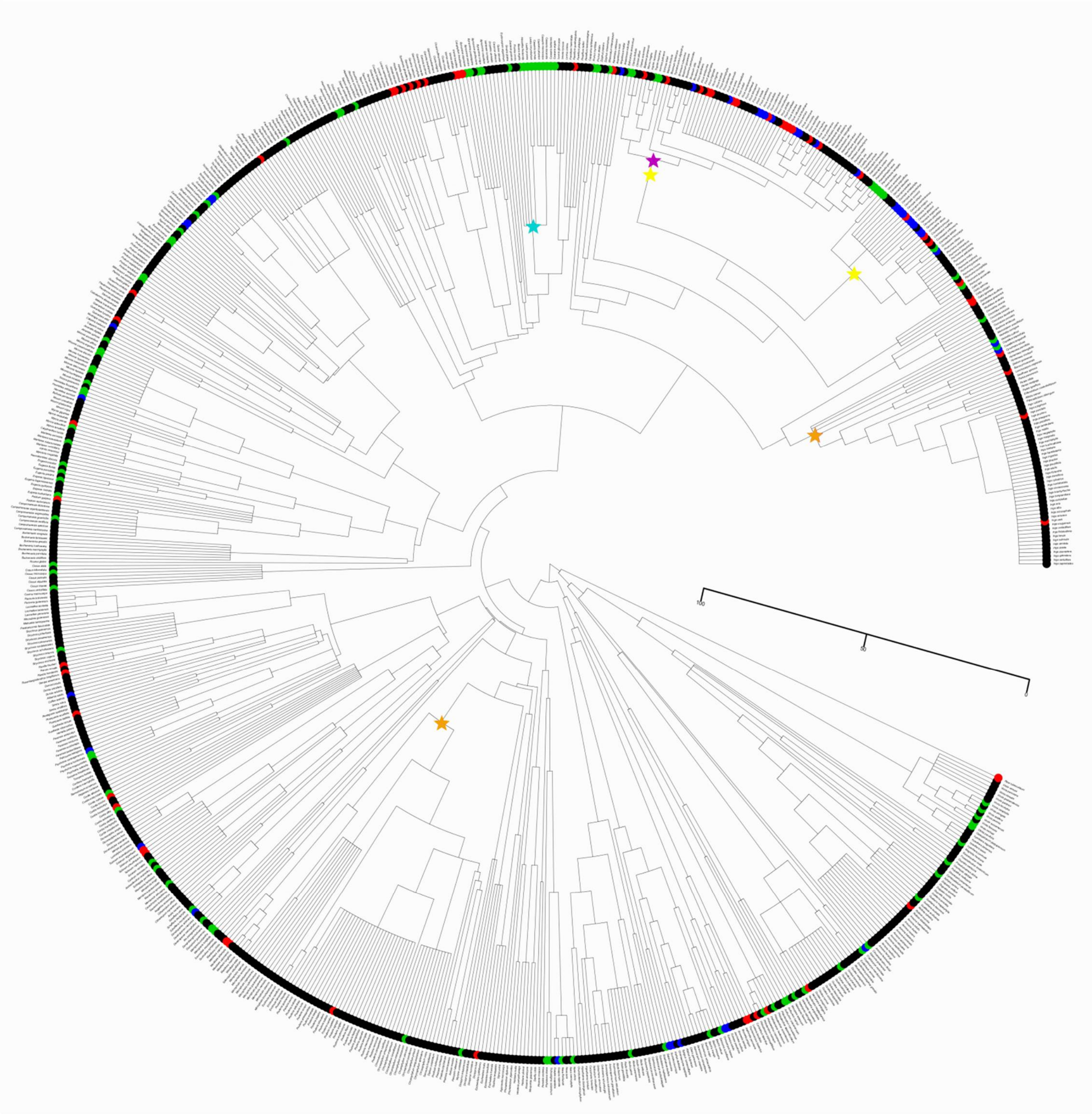
- Cambridge Database – Fruits From French Guiana: http://vision.psychol.cam.ac.uk/spectra/guiana/fruit.html
- Flora Digital do Rio Grande do Sul e Santa Catarina: http://www.ufrgs.br/fitoecologia/florars/
- FlorUSP: http://www.ib.usp.br/labtrop/guiamatinha/
- Frutos Atrativos do Cerrado: http://www.frutosatrativosdocerrado.bio.br/
- Los Charcos de Osa: www.osaresearch.org
- ManuPlants: http://biogeodb.stri.si.edu/bioinformatics/en/
- Neotropical Plants Image Database (Kew): http://www.kew.org/science/tropamerica/imagedatabase/

- Programa Flora Cristalino Kew Gardens:

  http://www.kew.org/science/tropamerica/cristalino.htm
- Projeto Flora de São Bento do Sul: https://sites.google.com/site/florasbs/home
- Smithsonian Tropical Research institute: http://biogeodb.stri.si.edu/bioinformatics/dfm/
- Useful Tropical Plants: http://tropical.theferns.info/

Supplementary Material S3 – Ultrametric tree generated for the 749 plant species dispersed by primates in Neotropics.

Tip colors represent dispersal syndromes: ●only primates; ●primates and birds; ●primates and bats; ●the three taxa. Stars represent the most dispersed families by each syndrome: ★only primates - Fabaceae (59Ma) and Neotropical Sapotaceae (55Ma); ★ primates and birds – Salicaceae (46Ma); ★primates and bats – Moraceae (23Ma) and Urticaceae (22Ma); ★ the three taxa – Moraceae (23Ma). Scale: 0_50_100 (Ma)



Supplementary Material S4 - Studies of morphological and molecular phylogeny used to corrected and improve the ultrametric tree resolution in 'Mesquite' and branch length estimation (i.e. time since divergence).

Table S3 – Node ages dated according to published literature

Node Label	Age (Ma)	Source
1	152.7	Mangallón (2009)
2	150.1	Magallón (2009)
3	147.9	Magallón (2009), Forest and Chase 2009d
4	143.9	Magallón (2009)
5	142	Forest and Chase 2009d
6	140.3	Mangallón (2009)
7	131	Forest and Chase 2009d
8	128	Bremer 2009
9	128	Anderson and Janben 2009
10	127	Bremer 2009
11	124	Forest and Chase 2009d
12	124	Anderson and Janben 2009
13	123	Bremer 2009
14	122	Forest and Chase 2009d
15	121	Forest and Chase 2009b
16	121	Bremer 2009
17	120	Anderson and Janben 2009
18	117	Forest and Chase 2009b
19	116.4	Berger 2016
20	114	Bremer 2009
21	113	Forest and Chase 2009d
22	113	Forest andChase 2009d
23	111	Forest and Chase 2009d
24	108	Bremer 2009
25	108	Bremer 2009
26	107	Armstrong et al 2014
27	107	Bremer 2009
28	107	Bremer 2009
29	106	http://www.timetree.org/
30	105	Forest and Chase 2009d
31	102.6	Berger 2016
32	102	Bremer 2009
33	100	Bremer 2009
34	100	Forest andChase 2009d
35	98	Forest and Chase 2009b
36	98	Bremer 2009
37	97	Wikström et al 2001
38	93	Pirie and Doyle 2012
39	91	Forest and Chase 2009b
40	90.4	Bremer and Erikson 2009
41	90	Forest and Chase 2009c
42	89	Forest and Chase 2009b
43	89	Zerega et al 2005
44	88	Bremer 2009
45	86	Forest and Chase 2009b
46	85	Forest and Chase 2009d
47	85	Berger 2016
48	84	Forest and Chase 2009d
49	82	Forest and Chase 2009c
50	81	Zerega et al 2005

51	81	Forest and Chase 2009b
52	79	Forest and Chase 2009b
53	78	Forest and Chase 2009b
54	78	Bremer 2009
55	77	Forest and Chase 2009b
56	76	Wikström et al 2001
57	76	Forest and Chase 2009b
58	74	Forest and Chase 2009b
59	74	Forest and Chase 2009b
60	73.1	Bremer and Erikson 2009
61	73.1	Bremer and Erikson 2009
62	73	Pirie and Doyle 2012
63	72	Zerega et al 2005
64	70.7	Richardson et al 2015
65	69	Forest and Chase 2009b
66	68.1	Forest and Chase 2009d
67	68	Forest and Chase 2009b
68	68	Bremer 2009
69	68	Forest and Chase 2009b
70	67	Bremer 2009
71	66	Forest and Chase 2009b
72	65	Wikström et al 2001
73	65	Anderson and Janben 2009
74	64.5	Berger 2016
75	64	Bremer 2009
76	64	Pirie and Doyle 2012
77	63	Bremer 2009
78	62	Forest and Chase 2009b
79	62	Forest and Chase 2009b
80	61	Forest and Chase 2009c
81	61	Bartish et al 2011
82	60	Forest and Chase 2009b
83	60	Forest and Chase 2009b
84	60	Weeks et al 2005
85	59	Zerega et al 2005
86	59	Bartish et al 2011
87	58.6	Lavin et al (2005)
88	58	Forest and Chase 2009b
89	57	http://www.timetree.org/
90	56	Forest and Chase 2009c
91	56	Weeks et al 2005
92	55	Wikström et al 2001
93	55	Bartish et al 2011
94	55	Forest and Chase 2009b
95	52.5	Weeks et al 2005
96	52	Wikström et al 2001
97	51	Forest and Chase 2009c
98	50	http://www.timetree.org/
99	49	Zerega et al 2005
100	48	Zerega et al 2005
101	47.5	Terra-Araujo 2015
102	47	Forest and Chase 2009c
103	46	Forest and Chase 2009b
104	45	Forest and Chase 2009b
105	45	Wikström et al 2001
106	45	Forest and Chase 2009b
107	44.8	Terra-Araujo 2015
108	43	Wikström et al 2001
109	42	Forest and Chase 2009b
110	42	Zerega et al 2005
111	41	Weeks et al 2005

112	41	Forest and Chase 2009b
113	41	Forest and Chase 2009b
114	40.5	Muschner et al 2012
115	40	Forest and Chase 2009c
116	36	Wikström et al 2001
117	34	Wikström et al 2001
118	33	Wikström et al 2001
119	33	Wikström et al 2001
120	31	Pirie and Doyle 2012
121	28	Wikström et al 2001
122	27	Weeks et al 2005
123	27	Pirie and Doyle 2012
124	27	Pirie and Doyle 2012
125	26	Bremer 2009
126	24	Pirie and Doyle 2012
127	23.9	Lavin et al 2005
128	23	Weeks et al 2005
129	23	Wikström et al 2001
130	23	Wikström et al 2001
131	22	Wikström et al 2001
132	20	Wikström et al 2001
133	18	Armstrong et al 2014
134	18	Pirie and Doyle 2012
135	18	Wikström et al 2001
136	16	Pirie and Doyle 2012
137	14	Wikström et al 2001
138	13	Wikström et al 2001
139	11.7	Terra-Araujo 2015
140	11.6	Richardson et al 2015
141	11.1	Terra-Araújo 2015
142	10	Loss-Oliveira et al 2016
143	8.7	Terra-Araujo 2015

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Supplementary Material S5 – Plant families, number of species per family dispersed by primates in Neotropics (total) and number of species dispersed by each syndrome.

	TOTAL	**Primates Only**	**Primates + Birds**	**Primates + Bats**	**Primates + Birds + Bats**
Moraceae	**73**	41	7	15	10
Sapotaceae	**67**	63	1	3	0
Fabaceae	**63**	55	2	4	2
Annonaceae	**34**	30	3	1	0
Rubiaceae	**34**	27	2	3	2
Urticaceae	**34**	15	5	4	10
Myrtaceae	**31**	22	7	2	0
Menispermaceae	**23**	22	1	0	0
Lauraceae	**20**	16	3	1	0
Melastomataceae	**20**	12	7	0	1
Myristicaceae	**19**	13	6	0	0
Sapindaceae	**19**	17	1	1	0
Arecaceae	**18**	10	3	0	5
Burseraceae	**14**	10	4	0	0
Araceae	**13**	6	5	2	0
Malvaceae	**13**	11	0	2	0
Meliaceae	**12**	8	2	0	2
Salicaceae	**12**	2	10	0	0
Boraginaceae	**11**	7	2	2	0
Clusiaceae	**11**	8	0	3	0
Celastraceae	**10**	10	0	0	0
Apocynaceae	**9**	9	0	0	0
Chrysobalanaceae	**9**	6	0	3	0
Loganiaceae	**9**	8	1	0	0
Anacardiaceae	**8**	5	1	0	2
Combretaceae	**8**	8	0	0	0
Polygalaceae	**8**	7	1	0	0
Solanaceae	**8**	4	1	2	1
Araliaceae	**7**	5	1	0	1
Vitaceae	**7**	4	3	0	0
Acanthaceae	**6**	5	1	0	0
Convolvulaceae	**6**	6	0	0	0
Malpighiaceae	**6**	2	4	0	0
Nyctaginaceae	**6**	3	2	0	1
Euphorbiaceae	**5**	3	2	0	0
Lecythidaceae	**5**	5	0	0	0
Olacaceae	**5**	5	0	0	0
Passifloraceae	**5**	4	0	1	0
Cannabaceae	**4**	2	0	2	0
Cyclanthaceae	**4**	2	0	2	0
Ebenaceae	**4**	3	0	1	0
Marcgraviaceae	**4**	2	2	0	0
Rhamnaceae	**4**	2	1	1	0
Bromeliaceae	**3**	3	0	0	0
Hypericaceae	**3**	1	0	2	0
Linaceae	**3**	3	0	0	0
Primulaceae	**3**	2	1	0	0
Ulmaceae	**3**	2	0	0	1
Violaceae	**3**	3	0	0	0

Capparaceae	**2**	2	0	0	0
Caricaceae	**2**	1	1	0	0
Dichapetalaceae	**2**	2	0	0	0
Dilleniaceae	**2**	2	0	0	0
Phyllanthaceae	**2**	1	1	0	0
Phytolaccaceae	**2**	0	2	0	0
Rosaceae	**2**	0	2	0	0
Santalaceae	**2**	2	0	0	0
Simaroubaceae	**2**	2	0	0	0
Verbenaceae	**2**	2	0	0	0
Achariaceae	**1**	1	0	0	0
Aquifoliaceae	**1**	0	1	0	0
Cactaceae	**1**	1	0	0	0
Calophyllaceae	**1**	0	0	1	0
Canellaceae	**1**	0	1	0	0
Cardiopteridaceae	**1**	1	0	0	0
Caryocaraceae	**1**	1	0	0	0
Cucurbitaceae	**1**	1	0	0	0
Erythroxylaceae	**1**	1	0	0	0
Goupiaceae	**1**	0	1	0	0
Humiriaceae	**1**	1	0	0	0
Lamiaceae	**1**	1	0	0	0
Magnoliaceae	**1**	1	0	0	0
Muntingiaceae	**1**	0	0	0	1
Ochnaceae	**1**	1	0	0	0
Opiliaceae	**1**	1	0	0	0
Piperaceae	**1**	0	0	1	0
Putranjivaceae	**1**	1	0	0	0
Rutaceae	**1**	0	1	0	0
Schlegeliaceae	**1**	0	1	0	0
Siparunaceae	**1**	0	0	0	1
Stemonuraceae	**1**	1	0	0	0
Styracaceae	**1**	1	0	0	0
Total Families	**82**	**71**	**40**	**23**	**14**
Total spp.	**749**	**547**	**103**	**59**	**40**

Supplementary Material S6 – Fruit size

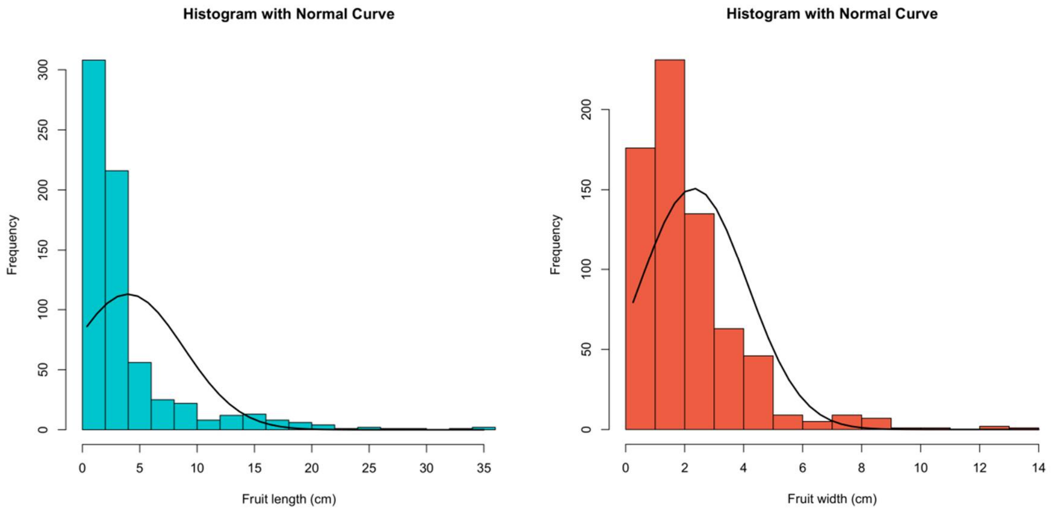


Figure S6 - A – Histogram and normal curves of length and width (in centimeter) of the 749 species dispersed by primates.

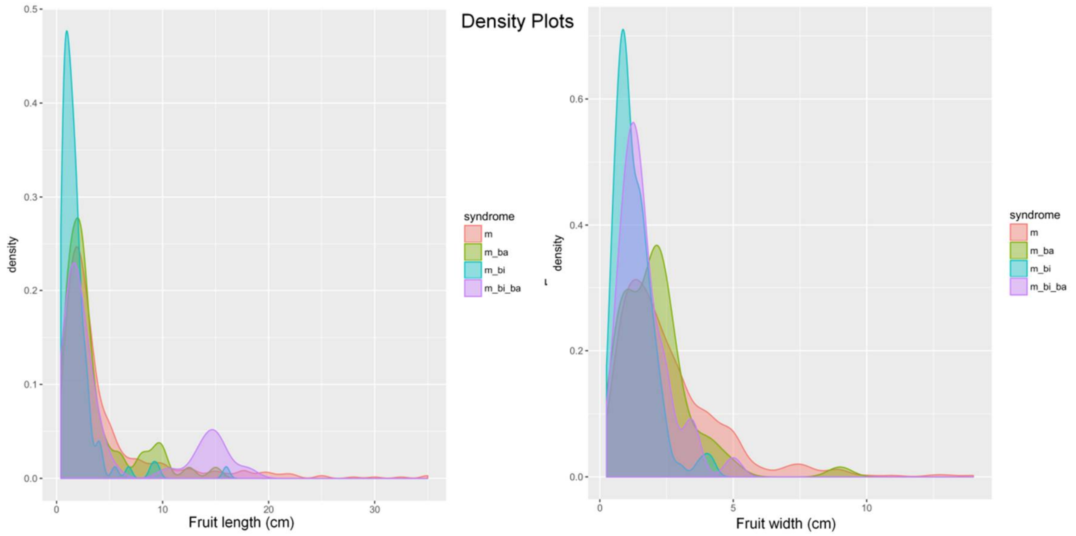


Figure S6 - B – Density plots of length and width of fruits (in centimeter) dispersed by each syndrome. m – only primates; m_ba – primates and bats; m_bi – primates and birds; m_bi_ba – the three taxa.

Supplementary Material S7 – Principal coordinates (PCoA) and trait association analyses

Table S7.A – Chi-squared values and significance (α=0.05)

	Fruit Color	Fruit Type	Husk Presence	Fruit Length	Fruit Width	N seeds/fruit
Fruit Color	-	663.71	213.45	260.02	172.7	105.79
Fruit Type	P<0.001	-	163.39	214.52	107.97	545.74
Husk Presence	P<0.001	P<0.001	-	118.39	124.68	57.20
Fruit Length	P<0.001	P<0.001	P<0.001	-	499.8	90.38
Fruit Width	P<0.001	P<0.001	P<0.001	P<0.001	-	92.59
N seeds/fruit	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	-

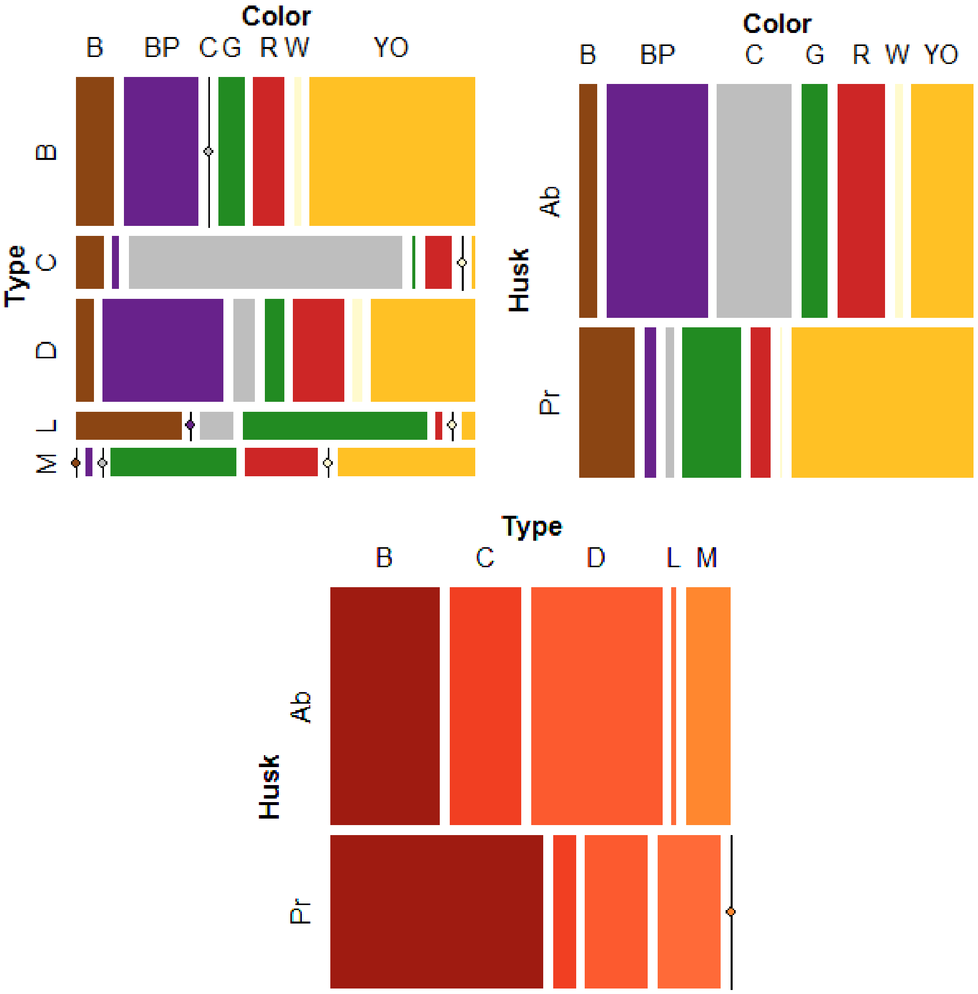


Figure S7.B – Mosaic plots showing strong association among categorical fruit traits.

Type – M=multiple, L=legume, D=drupe, C=capsule and B=berry; **Color** – B=brown, BP=black/purple, C=contrast, G=green, R=red, W=white and YO=yellow/orange; **Husk** – Pr=present and Ab=absent.

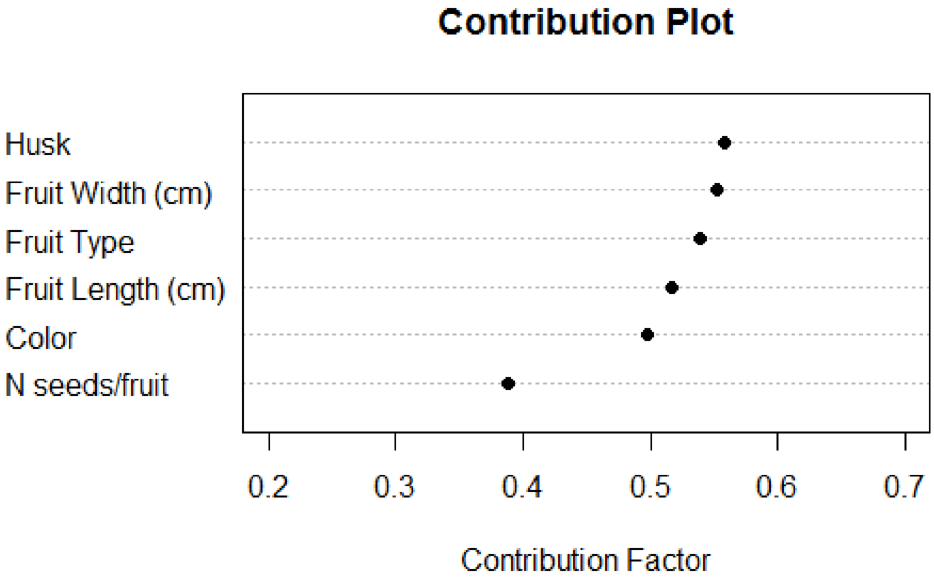


Figure S7.C – Contribution plot showing each morphological fruit trait contribution to distances in PCoA analysis

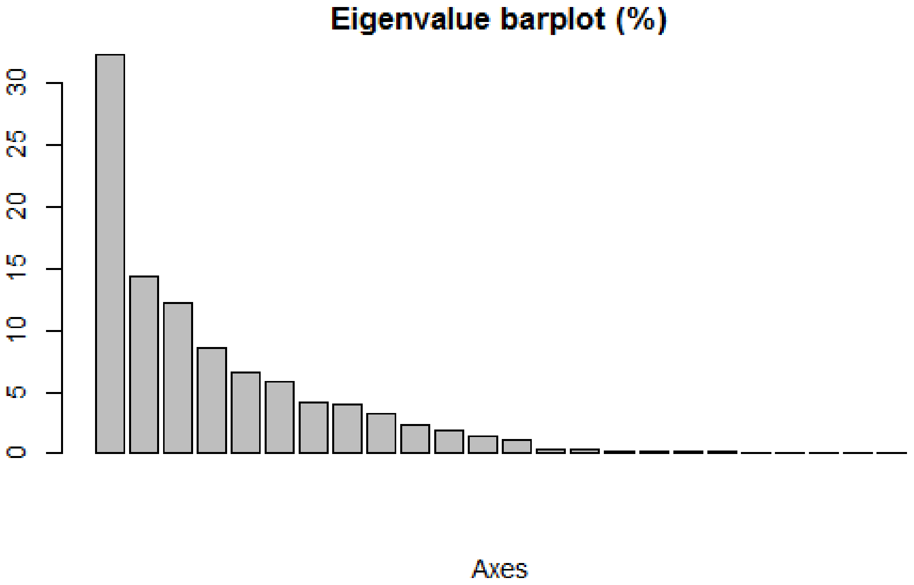
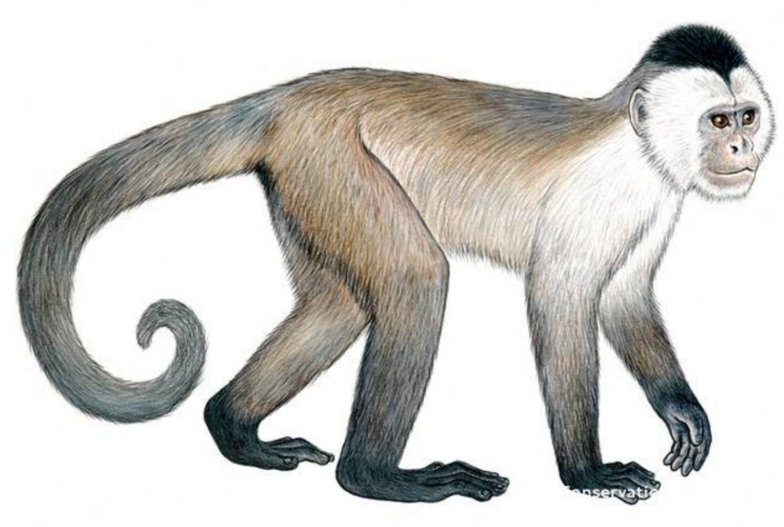


Figure S7.D – Bar plot showing explanation power of each axis (in percentage of the total variance)



Cebus kaapori, frugivore-insectivore Neotropical primate.
Illustration: Stephen D. Nash

CAPÍTULO 2:

Size does matter: Effects of seed size and frugivory degree on dispersal by Neotropical primates

Title: Size does matter: Effects of seed size and frugivory degree on dispersal by Neotropical primates

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ABSTRACT

Mutualistic interactions between primates and plants have positive impacts on plant community dynamics. Despite the increasing number of studies on primate frugivory we are still not able to disentangle the real contribution of seed dispersal by primates to Neotropical forest functioning. The use of fruit resources does not imply effective seed dispersal and many variables, such as seed size and animal diet, may influence the outcome of the plant-animal interaction. Here, we performed a comprehensive literature search on seed dispersal by primates in Neotropics to disentangle their role as seed dispersers, hypothesizing frugivory degree and seed size as main factors affecting fruit handling behavior and the diversity of seeds dispersed. We found that the great majority of seeds manipulated by Neotropical primates were swallowed and passed intact through their gut and that larger seeds had a tendency of being ingested exclusively by primates when accounting for other major vertebrate dispersers. Furthermore, feeding guild had a great influence on the number and sizes of seeds dispersed, as primarily frugivores dispersed more seeds and had higher probabilities of ingesting larger seeds when compared to folivorous and insectivorous. Although folivores were shown to have the least contribution to seed dispersal, publication is biased towards this group, which may compromise our currently understanding of primates as seed dispersers. Organizing available knowledge and identifying the main gaps allowed us to evaluate more accurately the role played by primates in ecosystems, and ultimately the outcomes for conservation.

KEY WORDS: endozoochory; feeding guild; frugivory; mutualism; plant-animal interaction; seed handling; taxonomic bias

RESUMO

Interações mutualísticas entre primatas e plantas tem um impacto positivo na dinâmica de comunidades vegetais. Apesar do número crescente de estudos sobre frugivoria, ainda não conseguimos desvendar a real contribuição da dispersão de sementes por primatas para o funcionamento de florestas neotropicais. O uso de frutos como recurso não implica em dispersão efetiva e variáveis como tamanho de sementes e dieta podem influenciar o resultado da interação planta-animal. Aqui, realizamos uma pesquisa bibliográfica abrangente sobre a dispersão de sementes por primatas no Neotrópico para desvendar seu papel como dispersores. Hipotetizamos que o grau de frugivoria e o tamanho das sementes são os principais fatores que afetam a manipulação de frutos e a diversidade de sementes dispersas. Destacamos que sementes maiores tenderam a ser ingeridas exclusivamente por primatas quando comparamos primatas e outros vertebrados. Além disso, a guilda alimentar teve uma grande influência sobre o número e tamanhos de sementes dispersas. Primatas primariamente frugívoros dispersaram maior diversidade de sementes e apresentaram maiores probabilidades de ingerir sementes grandes quando comparados a folivoros e/ou insetívoros. Embora primatas folívoros tenham mostrado menor contribuição para a dispersão, a informação disponível na literatura é tendenciosa em relação a este grupo, o que pode comprometer a nossa compreensão do real papel desempenhado por primatas como dispersores. A organização do conhecimento disponível e a identificação das principais lacunas podem nos permitir avaliar com maior precisão o papel desempenhado pelos primatas nos ecossistemas e, em última instância, as consequencias para a conservação.

FRUGIVORES ARE KEY ELEMENTS OF MUTUALISTIC INTERACTIONS WITH PLANTS AND THUS PLAY AN important role for forest dynamics, regeneration and conservation in the face of the emerging threats (Fleming & Kress 2011, Vidal *et al.* 2013). In Neotropical forests the great majority of woody species depend on vertebrates for seed dispersal, and frugivores contribute to restoration and management of degraded habitats (Howe 2014). Many plant species are likely to experience changes in recruitment and survival as a result of declines in frugivore populations (Bueno *et al*. 2013, Galetti *et al*. 2013), and as a consequence, losses of frugivore functional diversity via defaunation have been profoundly affecting forests dynamics and community composition (Dirzo *et al.* 2007, Stevenson 2011, Beckman & Rogers 2013). In turn, because large frugivores tend to be especially sensitive to habitat fragmentation and hunting, long-term maintenance of fruiting plants becomes challenging, even though central, to ensure ecosystem functioning and dynamics (Dirzo *et al.* 2007, 2014, Bufalo *et al.* 2016).

Primates have been increasingly recognized as having a potential impact on forest regeneration and plant community dynamics. They are able to remove great amount of fruits, ingest a large range of seeds sizes and often move them for long distances, a result of their long daily travel distances, often-extensive home ranges and moderately long transit times (González & Stevenson 2014, Fuzessy *et al.* 2017). Although much is known about primate frugivory in the Neotropics, a common error hampering the use of seed dispersal studies in tropical conservation is the assumption that use of fruit resources by fruit-eating animals implies effective seed dispersal (Howe 2016). Fruit intake is clearly related to dispersal potential, but the effectiveness of a disperser depends on its impact on parental plant fitness, which itself is the product of qualitative and quantitative components including the number of seeds removed, per-seed survival and germination success, seedling survival and growth, and sapling survival (Schupp *et al.* 2010).

In the last decades there has been a striking increase in the number of studies on primate frugivory and seed dispersal in the Neotropics, although research is geographically and taxonomically uneven (Hawes *et al.* 2013, Bufalo *et al.* 2016). Knowledge biases prevent us from assessing the real contribution of seed dispersal by primates to Neotropical forests. Recently, Bufalo *et al.* (2016) reviewed the potential of primates to disperse seeds, tested the link between primate body size and the size of dispersed seeds, and highlighted knowledge gaps in primate seed dispersal research in the Atlantic forest. Although this paper advanced our understanding of primate seed dispersal, there are also some key facets that remain unexplored.

For example, primates vary in their degree of frugivory ranging from species almost exclusively depending on fruits to species including fruits sporadically in their diets (Hawes & Peres 2014). Unfortunately, we still lack comparative information on fruit handling behavior and diet breadth among different guilds of primates. In addition, seed size has also been shown to be an important plant trait determining the probability of ingestion and thus the diversity of consumers, as well as allegedly driving gut passage times (Schleuning *et al.* 2016, Sebástian-González 2017). To date we are unaware of any study addressing how seed size modulates the probability of ingestion in primates and how it differs between seed dispersed by primates *versus* other dispersers. Altogether, these unexplored facets of seed dispersal mutualisms are relevant to determine seed dispersal effectiveness relative to other vertebrates. This combined information may allow us to evaluate more accurately the role played by primates as keystone mutualists, and ultimately the implications for conservation. Organizing available knowledge and identifying the main gaps become fundamental to guide and optimize future research.

Here, we broaden the analyses of seed dispersal by primates conducted by Bufalo et al. (2016) to the whole Neotropical realm with the goal of developing a general understanding of overlooked aspects of seed dispersal by primates. Specifically, we 1) compared fruit handling behavior and the number of species dispersed by different feeding guilds considering the degree of frugivory for all species in seed dispersal studies; 2) compared seed size in terms of plant species between swallowed vs spitted/dropped seeds and between species dispersed exclusively by primates *versus* species dispersed by multiple vectors; and 3) explored the relationships between the number of fecal samples and number of plant species dispersed by different guilds. Finally, we demonstrate publication bias and stress knowledge gaps in order to orient future research. We believe the results presented here will be useful for steering the research agenda of seed dispersal in the Neotropics that would, in turn, lead to a better understanding of the ecology and evolution of mutualistic interactions.

METHODS

THE DATABASE – We performed a comprehensive literature review, using Web of Science and Google Scholar databases (1945–2015). We searched electronically for the following terms within the title, abstract and keywords of papers: primate seed dispersal, monkey seed dispersal, primate seed fate and primate seed handling. The literature list was supplemented with studies cited in the reference lists of the articles surveyed. Because frugivory does not necessarily imply seed dispersal (Schupp et al 2010), sources for Neotropical primates included in our review comprised only studies that provided direct evidence of primate seed dispersal (*sensu* Bufalo et al 2016), i.e. intact seeds in feces. Although defecating intact seeds does not indicate effective seed dispersal, it is the best available proxy at this scale in the absence of more detailed information on seed survival and seedling establishment. We also recorded the number of studies and sampling effort in each study (total number of hours spent in the field).

To compare seed dispersal among primate functional groups we used the ecospecies classification from Peres & Janson (1999) adapted by Hawes & Peres (2014). Ecospecies are functional groups defined based on body size, group size, foraging behavior, food handling and diet (Peres & Janson 1999). Dietary type is a key factor determining the quality of treatment given to the seeds during gut passage (Fuzessy et al 2016). Thus, we grouped ecospecies into feeding guilds based on frugivory level according to data available (see further details on the next section). Data on feeding guild and ecospecies classification of the primate species included in our study are available in Table 1.

TABLE 1 – Feeding guild, ecospecies classification, IUCN conservation status and body size (mass, in g) for the 20 primate species (ten ecospecies) included in the study

Subfamily	**Feeding Guild**	**Ecospecies**	**Primate species**	**IUCN status**[a]	**Body mass**[b]
Atelinae	FO	Al	*Alouatta caraya*	LC	5.38
	FO	Al	*Alouatta guariba*	LC	5.54
	FO	Al	*Alouatta palliata*	LC	6.58
	FO	Al	*Alouatta pigra*	EN	8.93
	FO	Al	*Alouatta seniculus*	LC	6.46
	FO	Br	*Brachyteles arachnoides*	EN	10.79
	FR	At	*Ateles belzebuth*	EN	8.32
	FR	At	*Ateles chamek*	EN	9.37
	FR	At	*Ateles geoffroyi*	EN	7.16
	FR	La	*Lagothrix lagotricha*	VU	6.27
	FR	La	*Lagothrix lugens*	CR	*
Cebinae	FI	Cf	*Cebus capucinus*	LC	3.51
	FI	Ca	*Sapajus apella*	LC	2.65
	FI	Ca	*Sapajus nigritus*	NT	*
Callitrichinae	FI	Sxf	*Saguinus fuscicollis*	LC	0.37
	FI	Sxf	*Saguinus mystax*	LC	0.54
	FI	Sm	*Saguinus niger*	VU	*
	FI	So	*Saguinus geoffroyi*	LC	0.61
	FI	Le	*Leontopithecus chrysomelas*	EN	0.58
	FI	Le	*Leontopithecus rosalia*	EN	0.63

[a] IUCN Red List status categories: LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

[b] Adult body mass. Data from Ford & Davis (1992) and Smith & Jungers (1997).

* Information not available

FO = folivores, FI = Insectivore-frugivores and FR = primarily frugivores

CORRELATES OF FRUGIVORY DEGREE AND SEED DISPERSAL – As a measure of frugivory degree, we considered the average percentage of time each ecospecies spent feeding on fruits or the percentage of the feeding records during data collection in the field as proxies of the amount of fruits included in the diet. We labeled primate diet specializations using the following criteria: the first label corresponds to the food type constituting 45% or more of the diet, while the second label (if present) relates to the food type comprising 20-45% of the diet (Chivers & Hladik 1980). By these criteria, species were divided into three dietary categories: folivores (FO), frugivore-insectivores (FI) and primarily frugivores (FR). Data on frugivory degree, ecospecies classification and feeding guilds is available on Table S2.

Three ecospecies could not be categorized based on data available in the studies: *Saguinus niger*, *Saguinus geoffroyi* and *Leontopithecus*. Data for Sm came from only one study on a single small group of *Saguinus niger* at an isolated and small disturbed forest fragment of eastern Amazonia (Oliveira & Ferrari 2000), which may imply an altered and atypical behavior as a consequence of a human-altered landscape. Data for *Saguinus geoffroyi* and *Leontopithecus* were not available. Thus, to ensure consistency of our dataset, frugivory classification for those three ecospecies was based on previous knowledge on feeding habits available on Hawes & Peres (2014).

To compare primate handling behavior of plant species, we calculated the percentage of fruits of each species that were dropped and/or scattered without seed consumption, apparently digested (damaged in feces or seen swallowed but not found in feces) and found intact in feces, according to information provided in the studies. To compare the richness of plant species dispersed by each guild, we performed an ANCOVA using sampling effort as a covariate to test whether distinct functional groups differ in number of plant species found apparently intact in feces, controlled by the time researcher spent in the field (in hours).

SEED SIZE EFFECTS – To compare seed size between species swallowed *vs.* spitted/dropped by primates, we obtained two distinct measures of seed size: dry seed weight (in grams) and largest length (in mm). Despite seed weight being the most readily available measure of seed size, we opted to maintain the two size measures even though they are correlated, because frugivore gullet size may constrain ingestion of very large, but not necessarily heavy, seeds (Wheelwright 1985).

To control for Neotropical primate ecospecies variation in seed residence time in the gut, we calculated two indexes (for more detailed information, see Supplementary Material S4-A):

- Average transit time index (TTI): single plant species average transit time divided by the average transit time of all plant species passed through the gut of a certain primate ecospecies;
- First appearance index (FAI): single plant species time to first appearance in feces divided by the average time to first appearance in feces of all plant species passed through the gut of certain primate ecospecies.

We log-transformed seed sizes measures and then performed linear regressions to assess seed size effects on Neotropical primate gut transit time. We then separated seeds into two categories: swallowed and dropped. We performed a Wilcoxon Mann-Whitney test to compare seed sizes between swallowed and dropped seeds, since data distribution was not properly adjusted to any family in generalized linear models. In addition, we fitted generalized linear models with a logit link function and binomial distribution to test whether seed size category determines handling behavior. The adjusted logistic model was tested for the goodness of fit by checking whether the residual deviance was large relative to the degrees of freedom of the model and whether or not the observed event rates matched expected event rates in subgroups of the model population (Hosmer & Lemeshow 2013).

Finally, to compare seed size effects on disperser groups, we classified plant species dispersed by Neotropical primates into two categories: 1) exclusively primate-dispersed and 2) species known to be dispersed by primates and other dispersers (bats and birds). Information on seed dispersal by bats and birds was collected from published literature (see Supplementary Material S4-D). To compare seed sizes among disperser groups, we performed a Wilcoxon Mann-Whitney test, since data distribution was not properly adjusted to any family in generalized linear models. To test whether chances of being dispersed exclusively by primates increases with increasing seed sizes, we fit generalized linear models with a logit link function and binomial distribution. The adjusted logistic model was also tested for the goodness of fit.

Most data on seed weight came from the Royal Botanic Gardens Kew's Seed Information Database (http://www.rbgkew.org.uk/data/sid/). Additional data on seed weight and data on greatest dimension of the seed came from the studies surveyed, Janson CH (unpublished data), and published literature (e.g. Lorenzi 1998, Galetti *et al.* 2011). When data on seed size were not available, we used the average of available data for other congeneric species, given that seed size is a conservative trait across plant phylogeny (Moles et al. 2005).

PUBLICATION BIAS – To supplement the results found by Bufalo et al. (2016) for seeds dispersed by primates in the Brazilian Atlantic Forest and to extend the knowledge to the entire Neotropical region, we evaluated the consequences of sampling effort on the reliability of the seed dispersal effectiveness (SDE) data available in literature. We estimated the effects of observation time on the number of fecal samples and also, the effects of the number of fecal samples on the diversity of plant species found in feces. The assessment was made through linear regression models. All statistical analyses were performed in R version 3.2.5 (R Core Team 2016) using the additional package *psych* (Revelle 2017).

RESULTS

THE DATABASE – The list of the 73 studies that conformed to our search and provided frugivory degree, seed handling behavior and/or the characterization of the dispersed species by Neotropical primates is available in Table S1.

Studies surveyed covered 20 species (10 ecospecies) of Neotropical primates, dispersing about 665 current plant species in 85 families.

CORRELATES OF FRUGIVORY DEGREE AND SEED DISPERSAL – Fruit comprised 8-87% of the diet of Neotropical primates (for criteria and individual data, see Table S2). *Alouatta* (Al) and *Brachyteles* (Br) were classified as folivores. *Sapajus* (Ca), *Cebus* (Cf), *Saguinus* (Sxf, Sm and So) and *Leonthopithecus* (Le) were classified as frugivore-insectivores. *Lagothrix* (La) and *Ateles* (At) were classified as primarily frugivores (Fig. 1).

Primate species varied widely in the diversity of plants dispersed. The folivore Al dispersed only 8 up to 87 plant species per study, whereas the highest diversity (165 and 166 plant species dispersed) was shown by the frugivore La and the frugivore-insectivore Sxf, respectively (Table S3). Among feeding guilds, frugivore and frugivore-insectivores primates dispersed a larger number of species than did folivores when controlling by sampling effort (F-value = 15.25, p<0.001, Fig. 2).

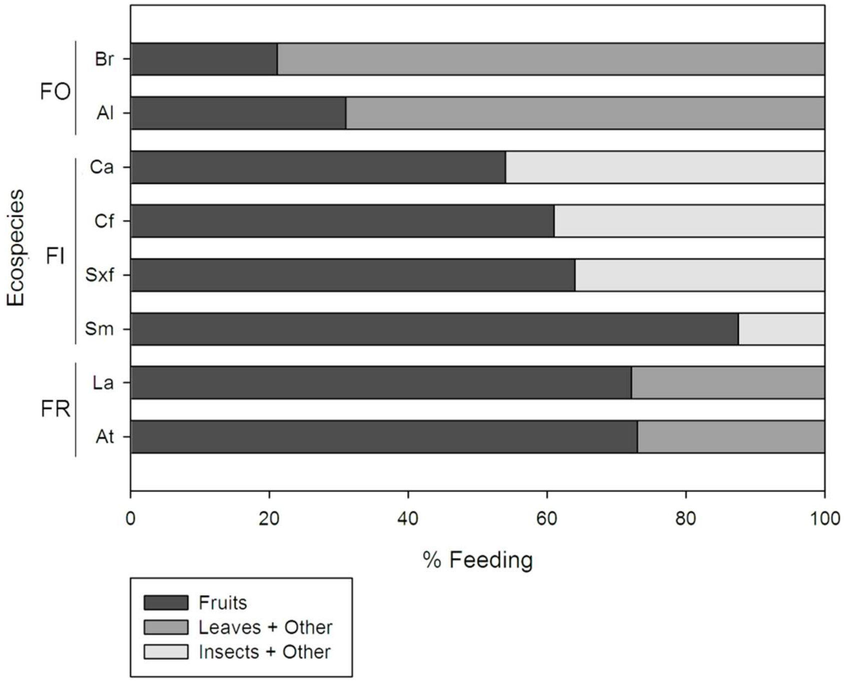

FIGURE 1: Frugivory level for each Neotropical primate ecospecies included in our review. Data available for eight ecospecies: Al = *Alouatta*, Br = *Brachyteles,* At = *Ateles*, La = *Lagothrix*, Cf = *Cebus*, Ca = *Sapajus*, Sxf = *Saguinus mystax* and *Saguinus fuscicolis* (grouped into one single ecospecies due to studies carried out with mixed groups of both species), Sm = *Saguinus nigritus*.

FO = folivore-frugivores, FI = frugivore-insectivores and FR = primarily frugivores

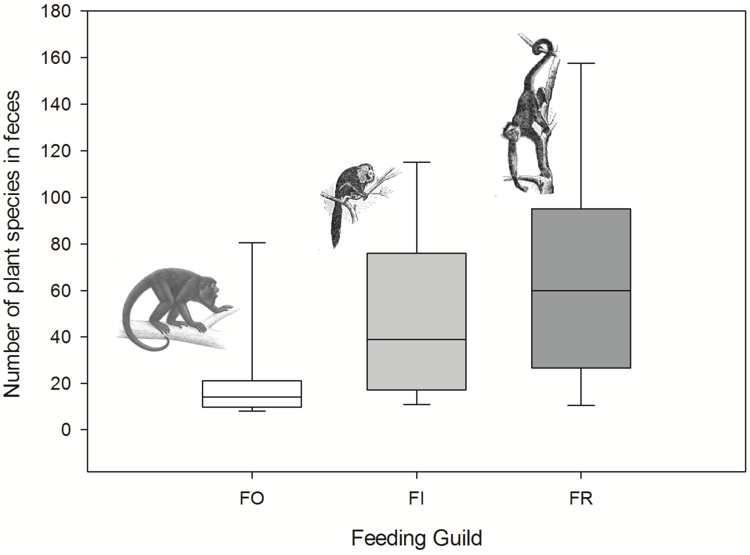

FIGURE 2: Boxplots (median and percentiles) showing richness of seeds found intact in feces of primates across feeding guilds. FO = folivores, FI = Frugivore-insectivores and FR = primarily frugivores

As for handling behavior, the great majority of seeds consumed were found intact in feces, regardless of ecospecies or feeding guild (Fig. 3). However frugivore-insectivore primates tended to drop or spit more seeds during feeding behavior compared to the other guilds: from 4% to 33% of the handled species were dropped and/or spit. In contrast, folivores and frugivores defecated from about 50% to 100% of the seeds intact. Apparently digested seed species accounted for about 0%-30% in folivores and frugivore-insectivores, and only 0-18% in primarily frugivores (for detailed information see Table S3).

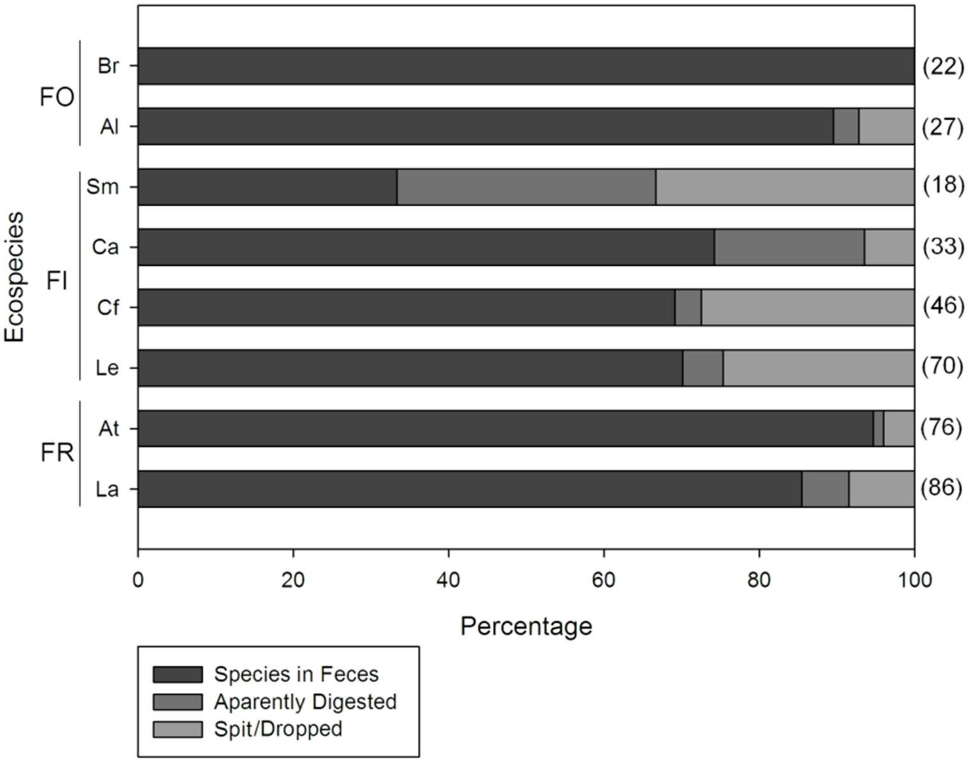

FIGURE 3: Handling behavior among Neotropical primate feeding guilds. Bars represent percentage of plant species in each category. Numbers in parentheses stand for total number of plant species handled. Data available for 8 ecospecies: Al = *Alouatta*, Br = *Brachyteles*, At = *Ateles*, La = *Lagothrix*, Cf = *Cebus*, Ca = *Sapajus*, Le = *Leothopithecus*, Sm = *Saguinus nigritus*.

FO = folivores, FI = Insectivore-frugivores and FR = primarily frugivores

SEED SIZE EFFECTS – Seed size had no significant effect on gut transit time, but whether the seed is swallowed or dropped by a Neotropical primate was dependent on both seed mass and seed size. The chances of a seed being dropped instead of swallowed increased with increasing seed sizes (see Supplementary Material S4_A-C).

Seeds dispersed exclusively by primates tended to be larger both in terms of mass and length. Larger seeds tended to be dispersed exclusively by primates rather than by bats or birds as well (see Supplementary Material S4_D)

PUBLICATION BIAS – Of 24 ecospecies for which frugivory data are available (Hawes & Peres 2014), information on seed dispersal was available only for ten. We detected varying levels of study effort both for the number of studies (Fig. 4) as well as observation time in the field (Fig. 4). Al was the most studied ecospecies, followed by At, Sxf, La, Cf, and trailed by the poorly understood Le, Ca, Br, So e Sm.

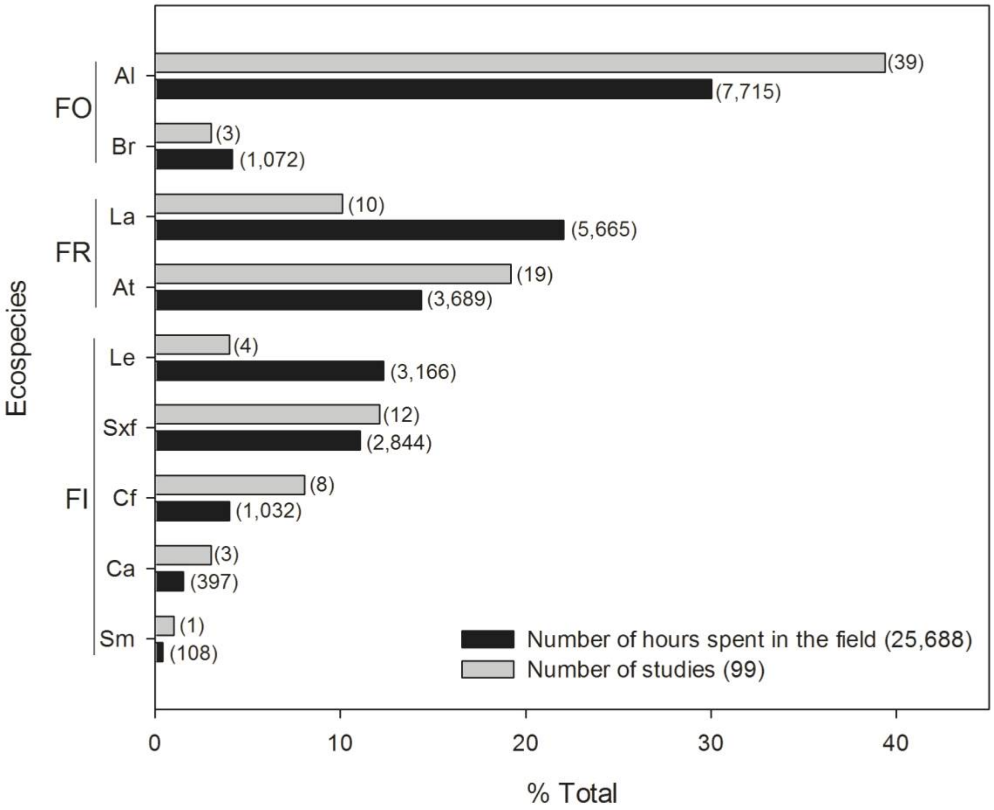

FIGURE 4: Publication bias in terms of number of studies including each ecospecies and time spent in the field for each ecospecies (in hours). Few studies included more than one ecospecies, so we considered one seed dispersal system as each ecospecies analyzed in one study. Total of studies surveyed = 73; total of seed dispersal systems = 99. Data were available for ten ecospecies. Numbers in parenthesis represent the absolute number of studies and hours spent in the field. Neotropical primate ecospecies: Al = *Alouatta*, Br = *Brachyteles*, At = *Ateles*, La = *Lagothrix*, Cf = *Cebus*, Ca = *Sapajus*, Le = *Leothopithecus*, Sxf = *Saguinus mystax* and *Saguinus fuscicolis* (grouped into one single ecospecies due to studies carried out with mixed groups of both species), So = *Saguinus geoffroyi*, Sm = *Saguinus nigritus*. FO = folivores, FI = Insectivore-frugivores and FR = primarily frugivores

Observation time spent in the field positively influenced the number of fecal samples collected (Fig. 5A), and the more fecal samples were collected, the larger the number of plant species found in feces (Fig. 5B). This outcome was also true at the level of the feeding guild (Fig. 5C-E).

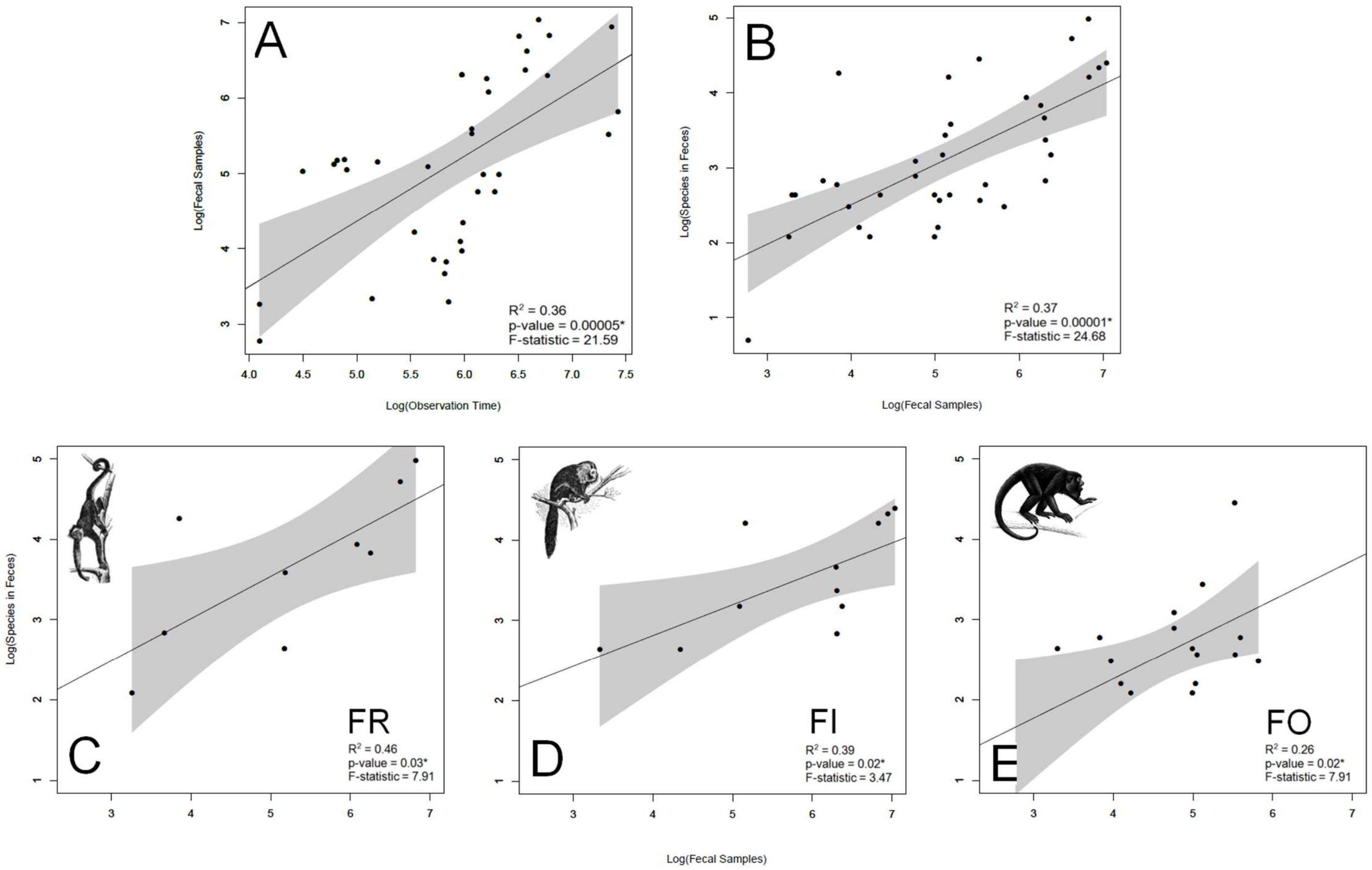

FIGURE 5: A – Linear regression showing a strong relationship between observation time in the field (hours) and number of fecal samples collected (log-transformed values). B - Linear regression demonstrating a strong relationship between number of fecal samples collected and the number of plant species found intact on feces (log-transformed values). C,D,E - Linear regression between the number of fecal samples collected and the number of plant species found intact in feces for FR = frugivores, FI = frugivore-insectivores, FO = folivores, respectively (log-transformed values).

DISCUSSION

Our study showed that, regardless of the frugivory degree, the great majority of seeds manipulated by Neotropical primates is swallowed and passes intact through their gut. We highlight the fact that frugivorous species disperse the greatest diversity of plants among Neotropical primates, and that seed size strongly affects handling behavior. Seeds dispersed exclusively by primates tend to be larger than those dispersed by more diverse sets of animals. In addition, the larger the seed, the greater the chances of being dispersed exclusively by primates rather than by bats or birds as well. These results expand knowledge on seed dispersal in Neotropics, and also elaborate the role of primates as seed dispersers in contributing to the first step towards effective seed dispersal.

FRUGIVORY AND CONSERVATION – Our assessment of primate feeding guild based on fruit intake strongly supports the categories of dietary adaptation proposed by Chivers and Hladik (1980) based on the morphology of the gastrointestinal tract. Folivores, such as *Alouatta* and *Brachyteles* showed the lowest frugivory degree among ecospecies included in our review. They provide a moderate quality of treatment inside the gut (Fuzessy et al. 2016) but they offer the worst service among Neotropical primates in terms of the distance deposited away from the parent crown, as a result of their short movement rates (Fuzessy et al. 2017). In addition, they exhibited the least diversity of plant species in feces. Nevertheless, howler monkeys play an important role in seed dispersal in fragmented areas. Because of their lower dependence on fruits, a high dependence on widely available resources such as leaves, and flexibility in species used as fruit sources, numerous howler populations exhibit small spatial requirements, and are able to inhabit degraded non-optimal ecosystems (Santos *et al.* 2013, Arroyo-Rodríguez *et al.*

2015). As a result of ecological flexibility, they are the least threatened among the Neotropical primates: only *Alouatta pigra* was classified as endangered (IUCN 2016), while the other species were least concern (Table 1). Species of the genus *Alouatta* occupy a large geographic range and occur in both evergreen and deciduous forest, from sea level to high elevations (Peres & Janson 1999).

Small primates that include a significant fraction of insects in the diet, but still consume at least 45% of fruits (frugivore-insectivore), such as *Saguinus* (Sxf, So and Sm), *Leontopithecus* (Le), *Cebus* (Cf) and *Sapajus* (Ca) include a high diversity of plant species as fruit sources (Hawes & Peres 2014). The outcome is a relatively weak selection pressure on fruit traits, due to a low dispersal quality in terms of treatment in the gut (Fuzessy et al. 2016). Nevertheless, their highly active lifestyle enables them to move seeds to sites far from the zone of influence of the parent crown, contributing to reduced chances of density-dependent mortality (Fuzessy et al. 2017). Moreover, here we show that those small frugivore-insectivores disperse a high diversity of plant species in their feces, a likely consequence of their generalist feeding behavior. *Leontopithecus* is the most endangered ecospecies of this group (Table 1) and is of considerable importance for rain forest regeneration (Lapenta & Procópio de Oliveira 2008). Although conservation efforts have been successfully establishing growing populations, permanent deforestation and habitat reduction, added to the introduction of exotic primates still represents a raised concern (Kierulff *et al.* 2012, Johnson *et al*. 2017).

Relative to other feeding guilds, predominant frugivores, such as *Lagothrix* and *Ateles* dispersed a large diversity of intact seeds. At the same time, these large-bodied primates are all included in some category of conservation threat (Table 1, Estrada *et al.* 2017). Unlike large folivorous and small insectivorous primates, *Lagothrix* and *Ateles* are often restricted to mature forests and thus are vulnerable to habitat disturbance, mainly due to their strict feeding habits (Di Fiore & Campbell 2007). These species are at once among the most effective seed-dispersing primates in the Neotropics, yet face the worst pressures from a variety of conservation threats (Jerusalinsky *et al.* 2011). Thus, conservation efforts towards forest composition and species preservation are fundamental in maintaining ecosystem functioning and dynamics.

HANDLING BEHAVIOR AND SEED SIZE EFFECTS – Neotropical primates swallow most of the seeds in fruits that they feed on. A low percentage of swallowed seeds are digested or destroyed inside the gut regardless of the primate's ecospecies or feeding guild (Figure 3). Most of the ingested seeds appear intact in feces and then tend to germinate more and faster after gut passage (Fuzessy *et al.* 2016). These trends yield very positive and complementary outcomes of seed handling by Neotropical primates.

Feeding behavior strongly affects seed handling. As a consequence of their diverse and highly generalist diet, small insectivores/omnivores tend to open some fruits looking for insects and drop them without any consumption under the feeding plant (Wehncke *et al.* 2003). Although small frugivore-insectivores tend to spit out or drop more seed species than larger-bodied folivores and frugivores, only a small percentage of consumed species are left under the feeding plant. The only exception seems to be *Saguinus niger* (Sm), but, as already mentioned before, data for Sm came from a possible altered and odd feeding behavior as consequence of a disturbed landscape.

In addition to high quality treatment of seeds in the gut, Neotropical primates contribute importantly to movement of seeds away from sources of high mortality. Gut transit times in Neotropical primates vary from a couple of hours to one day, depending on gut complexity and diet. Long daily travel distances within a home range associated with retention of the food inside their guts allow them to bring seeds to a variety of suitable sites to germinate (Fuzessy *et al.* 2017). Dropping or scatting seeds under the feeding tree could imply high density competition with conspecifics, high predation risk above the soil and exposure to enemies within the soil (negative plant-soil feedback) due to proximity to the parent plant (Mangan *et al.* 2010, McCarthy-Neumann & Kobe 2010, Comita *et al.* 2014).

Seed size represents, in addition to the trade-off between offspring number and size, a combined balance between requirements for dispersal and establishment (Foster & Janson 1985, Moles *et al.* 2005): broad dispersal would favor evolution of small seeds (Fenner & Thompson 2005) whereas successful establishment would favor large seeds (Jurado & Westoby 1992, Lloret *et al*. 1999, Kidson & Westoby 2000). However, we have shown that seed size affects handling behavior in Neotropical primates. Very large seeds tend to be dropped instead of swallowed more often than small seeds. That could mean large-seeded plants might benefit less from the services provided by Neotropical primates. Nonetheless, we also show that, regardless of seed size, a very small percentage of seeds is dropped during manipulation and the vast majority are swallowed and pass intact though primate guts.

Seed size varies between disperser groups. Primates, bats and birds are the main extant seed dispersers in Neotropics, but they often target different plant species (Eriksson 2016). For instance, a medium-sized seed dispersed by a Neotropical primate may be too large for a small frugivorous bat or bird, so large-seeded plants must often rely on large frugivores, such as primates and large fruit-eating birds (Wotton & Kelly 2012). As consequence of a body size constraint, there is a trend for large-seeded plants to have smaller numbers of dispersers than small seeds (Stevenson 2002). Here we confirmed the trend for larger seeds to be dispersed mainly by large vertebrates, such as primates, while smaller seeds are also dispersed by birds and/or bats.

PUBLICATION BIAS AND FUTURE RESEARCH DIRECTIONS – We found relatively more study effort devoted to *Alouatta*, measured both as the number of studies as well as observation time in the field. Together with the poorly studied *Brachyteles* (Bufalo *et al.* 2016), they form the folivore feeding guild and were included in 42% of the seed dispersal systems included in our review. This emphasis towards folivores was also reported by Hawes & Peres (2014) reviewing the feeding ecology on Neotropical primates. Possible explanations for this emphasis are their lower metabolic rates and subsequent shorter and slower travel paths, which make them an easier target to observe and follow in the field, as well as their extensive distribution throughout the Neotropics. The skewed study coverage toward *Alouatta* may influence our current perception of seed dispersal by Neotropical primates.

Ateles was the second best studied ecospecies in terms of number of studies while *Lagothrix* was the second best sampled ecospecies in terms of observation time. Together, they constitute the major seed disperser group in the Neotropics. Although together they were included in 29% of seed dispersal studies, they had considerable field sampling effort (36.5% of the total observation time). Frugivore-insectivores also contributed to 29% of the publications on Neotropical primate seed dispersal, but many species were understudied with both few studies and also low sampling effort in the field, such as *Saguinus niger*, *Saguinus geoffroyi* and *Sapajus nigritus*.

We found an intuitive and strong relationship between the time which an observer spends in the field and the number of fecal samples collected. Also, the number of fecal samples collected strongly determined the number of plant species found in feces. Therefore, sampling effort may influence conclusions about quantity and diversity of seeds dispersed by Neotropical primates. Although sampling effort varied at the level of feeding guild, at a similar sampling effort proxy (log-transformed fecal sample number), primarily frugivore primates still showed greater amount of plant diversity in their feces, followed by insectivores and, finally, folivores.

Current knowledge on publication bias on Neotropical primate feeding behavior suggests that up to now all primate ecospecies, even the broadly studied howlers, have been insufficiently sampled and it is not possible to confirm that the full breadth of fruits in their diet has been uncovered (Hawes & Peres 2014). That can be extended to seed dispersal as well, since we showed that diversity in fruit intake reflects diversity of seeds found intact on feces.

Although still incomplete, our information revealed likely contributions from Neotropical primates to plant population and community dynamics. We stress the benefits of primate seed manipulation to plant reproduction and reinforced their high functional diversity in traits influencing dispersal processes (Chapman & Russo 2005). We uncovered neglected aspects underlying primate-plant mutualism, such as the role of seed size, handling behavior and degree of frugivory. One of the richest environments in the world, Neotropical forests are a complex interacting system of plants and animals depending on each other. Even though Neotropical primates vary in their effectiveness as seed dispersers according to functional groups, even folivorous species provide valuable seed dispersal services in fragments that they inhabit.

It is important to stress the need to increase research effort to cover current gaps in our knowledge. Studies on seed dispersal must be improved to be useful in conservation efforts (Howe 2016). Elucidating how changes in primate populations affect plant communities in the Neotropics has the potential to deliver valuable results of immediate ecological and conservation outcomes. Documenting primates as effective dispersal agents via seed dispersal remains difficult (Bueno *et al.* 2016), in part because of knowledge gaps and biases as revealed here. For instance, seed fate after defecation has received much less attention than other aspects of dispersal. Association with secondary dispersers, especially dung beetles, has been described as a positive and additional advantage (Andresen 2002, Andresen & Feer 2005, Vulinec *et al.* 2006) but information on direct post-dispersal survival and establishment have been strongly neglected (but see Valenta *et al.* 2009, Bravo 2012, Chaves *et al.* 2015). We suggest that future studies on seed dispersal by Neotropical primates need to consider feeding guild-dependence when describing seed dispersal effectiveness, and post-dispersal seed fates should be extensively addressed to fully understand primate roles in connecting forest fragments and structuring plant communities.

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DATA AVAILABILITY STATEMENT

The data used in this study are available in Supplementary Material (Table S2, Table S3 e Table S4_A)

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Supplementary Material S1 – Studies included in the review

Code	Title	Authors *Journal* (volume)	Year	Country	Study Area (ha)	Observation time (h)	Primate Species
1	Seed dispersal patterns in howler monkey species (*Alouatta palliata* and *A. pigra*): A preliminary report of differences in fruit consumption, traveling behavior and associated dung beetle assemblages	Amato KR & Estrada A *Neotrop Primates* (17)	2010	Mexico	155000	135	*Alouatta palliata*
1	Seed dispersal patterns in howler monkey species (*Alouatta palliata* and *A. pigra*): A preliminary report of differences in fruit consumption, traveling behavior and associated dung beetle assemblages	Amato KR & Estrada A *Neotrop Primates* (17)	2010	Mexico	1800	120	*Alouatta pigra*
2	Implications of behavior and gut passage for seed dispersal quality: The case of black and gold howler monkeys	Bravo SP *Biotropica* (41)	2009	Argentina	280	1680	*Alouatta caraya*
3	Seed dispersal by red howling monkeys (*Alouatta seniciculus*) in the tropical rain forest of French Guiana	Julliot C *Int J Pimatol* (17)	1996	French Guiana	160	1540	*Alouatta seniculus*
4	Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: Consequences for seed dispersal effectiveness	Wehncke EV, Valdez CN, Dominguez CA *J Trop Ecol* (20)	2004	Costa Rica	20000	253	*Alouatta palliata*
4	Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: Consequences for seed dispersal effectiveness	Wehncke EV, Valdez CN, Dominguez CA *J Trop Ecol* (20)	2004	Costa Rica	20000	287.5	*Cebus capucinus*
5	Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest	Andersen E *Biotropica* (31)	1999	Peru	1532806	348	*Alouatta seniculus*
5	Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest	Andersen E *Biotropica* (31)	1999	Peru	1532806	303	*Ateles chamek*
6	Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas	Estrada A & Coates-Estrada R *J Trop Ecol* (7)	1991	Mexico	155000	NA	*Alouatta palliata*
7	Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity	Link A & Di Fiore A *J Trop Ecol* (22)	2006	Ecuador	982	670	*Ateles belzebuth*
8	Seed dispersal by golden-headed lion tamarins *Leontopithecus chrysomelas* in Southern Bahian	Catenacci LS, Vleeschouwer KM, Nogueira-Filho SLG	2009	Brazil	18500	710	*Leontopithecus chrysomelas*

	atlantic forest, Brazil	*Biotropica* (41)					
9	Some aspects of seed dispersal effectiveness of golden lion tamarins (*Leontopithecus rosalia*) in a Brazilian Atlantic forest	Lapenta MJ & Procópio-de-Oliveira p *Trop Cons Sci* (1)	2008	Brazil	2400	1583.9	*Leontopithecus rosalia*
10	Frugivory and seed dispersal of golden lion tamarin (*Leontopithecus rosalia* (Linnaeus, 1766)) in a forest fragment in the Atlantic Forest, Brazil	Lapenta MJ, Procópio-de-Oliveira P, Kierulff MCM, Motta-Junior JC. *Braz J Biol* (68)	2008	Brazil	2400	871.9	*Leontopithecus rosalia*
11	Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species	Wehncke EV, Hubbell SP, Foster RB, Dalling JW *J Ecol* (91)	2003	Panamá	1560	180	*Cebus capucinus*
12	Effects of seed dispersal by three Ateline monkey species on seed germination at Tinigua National Park, Colombia	Stevenson PR, Castellanos MC, Pizarro JC, Garavito M *Int J Primatol* (23)	2002	Colombia	201875	720	*Lagothrix lagotricha*
12	Effects of seed dispersal by three Ateline monkey species on seed germination at Tinigua National Park, Colombia	Stevenson PR, Castellanos MC, Pizarro JC, Garavito M *Int J Primatol* (23)	2002	Colombia	201875	NA	*Ateles belzebuth*
12	Effects of seed dispersal by three Ateline monkey species on seed germination at Tinigua National Park, Colombia a	Stevenson PR, Castellanos MC, Pizarro JC, Garavito M *Int J Primatol* (23)	2002	Colombia	201875	900	*Alouatta seniculus*
13	Seed dispersal by black-handed tamarins, *Saguinus midas niger* (Callitrichinae, Primates): Implications for the regeneration of degraded forest habitats in eastern Amazonia	Oliveira ACM & Ferrari SF *J Trop Ecol* (16)	2000	Brazil	210	108	*Saguinus niger*
14	Comparative seed dispersal effectiveness of sympatric *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil	Martins MM *Biotropica* (38)	2006	Brazil	1450	555	*Alouatta guariba*
14	Comparative seed dispersal effectiveness of sympatric *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil	Martins MM *Biotropica* (38)	2006	Brazil	1450	534	*Brachyteles arachnoides*
15	Short-term post-dispersal fate of seeds defecated by two small primate species (*Saguinus mystax* and *Saguinus fuscicollis*) in the Amazonian forest of Peru	Culot L, Huynen MC, Gérard P, Heymann EW *J Trop Ecol* (25)	2009	Peru	120	NA	*Saguinus fuscicollis* *Saguinus mystax*
16	Dispersão de sementes pelo mono carvoeiro no Parque Estadual carlos Botelho	Moraes *Revista IF* (4)	1992	Brazil	37797	81.88	*Brachyteles arachnoides*
17	The ecology of seed dispersal in two species of Callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*)	Garber PA *Am J Primatol* (10)	1986	Peru	120	NA	*Saguinus fuscicollis* *Saguinus mystax*

18	Frugivory patterns and seed dispersal by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Una Biological Reserve, Bahia, Brazil	Cardoso NA, Le Pendu Y, Lapenta MJ, Raboy BE *Mammalia* (75)	2011	Brazil	18500	NA	*Leontopithecus chrysomelas*
19	Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity	Stevenson PR *Am J Primatol* (50)	2000	Colombia	201875	720	*Lagothrix lagotricha*
20	Primate seed dispersal: The fate of dispersed seeds	Chapman CA *Biotropica* (21)	1989	Costa Rica	108	171	*Cebus capucinus*
20	Primate seed dispersal: The fate of dispersed seeds	Chapman CA *Biotropica* (21)	1989	Costa Rica	108	394	*Alouatta palliata*
20	Primate seed dispersal: The fate of dispersed seeds	Chapman CA *Biotropica* (21)	1989	Costa Rica	108	335	*Ateles geoffroyi*
21	Nutrient transport within and between habitats through seed dispersal processes by woolly monkeys in North-western Amazonia	Stevenson PR & Guzmán-Caro D *Am J Primatol* (72)	2010	Colombia	201875	NA	*Lagothrix lagothircha*
22	Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*)	Valenta K & Fedigan LM *Am J Phys Anthropol* (138)	2009	Costa Rica	108	393.5	*Cebus capucinus*
23	Pulp-seed attachment is a dominant variable explaning legitimate seed dispersal: a case study on woolly monkeys	Stevenson PR *Oecologia* (166)	2011	Colombia	201875	1140	*Lagothrix lagotricha*
24	Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in Southern Mexico	Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A, *Int J Primatol* (32)	2011	Mexico	1170.4	504	*Ateles geoffroyi*
24	Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in Southern Mexico	Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A, *Int J Primatol* (32)	2011	Mexico	331000	496	*Ateles geoffroyi*
25	How much is a lot? Seed dispersal by white-faced capuchins and implications for disperser-based studies of seed dispersal systems	Valenta K & Fedigan LM *Primates* (49)	2008	Costa Rica	108	393.5	*Cebus capucinus*
26	Seasonal variation in seed dispersal by tamarins alters seed rain in a secondary rain forest	Culot L, Lazo JJM, Huynen MC, Poncin P, Heymann EW *Int J Primatol* (31)	2010	Peru	120	2303	*Saguinus fuscicollis* *Saguinus mystax*
27	The capuchin, the howler, and the Caatinga: Seed dispersal by monkeys in a threatened Brazilian forest	Moura ACA, McConkey KR *Am J Primatol* (69)	2007	Brazil	100000	NA	*Alouatta caraya*

27	The capuchin, the howler, and the Caatinga: Seed dispersal by monkeys in a threatened Brazilian forest	Moura ACA, McConkey KR *Am J Primatol* (69)	2007	Brazil	100000	397	*Sapajus libidinosus*
28	Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparision of fruit type, color and seed size	Martins MM *Primates* (49)	2008	Brazil	1450	480	*Alouatta guariba*
28	Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparision of fruit type, color and seed size	Martins MM *Primates* (49)	2008	Brazil	1450	456	*Brachyteles arachnoides*
29	The impact of seed dispersal by black and gold howler monkeys on forest regeneration	Bravo, SP *Ecol Res* (27)	2012	Argentina	280	NA	*Alouatta caraya*
30	Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park, Colombia	Stevenson PR, Pineda M, Samper T *Oikos* (110)	2005	Colombia	201875	NA	*Lagothrix lagotricha*
31	Um teste de germinação de sementes dispersas por macaco-aranha em Maracá, Roraima, BR	Nunes A *Stud Neotrop Fauna E* (30)	1995	Brazil	100000	NA	*Ateles belzebuth*
32	Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest	Julliot C *Am J Primatol* (40)	1996	French Guiana	2400	1540	*Alouatta seniculus*
33	Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*	Dew JL *Int J Primatol* (26)	2005	Ecuador	982	457.45	*Ateles belzebuth*
33	Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*	Dew JL *Int J Primatol* (26)	2005	Ecuador	982	429.45	*Lagothrix lagotricha*
34	Diet of a group of *Lagothrix lagothricha* in Southeastern Colombia	Defler TR, Defler SB *Int J Primatol* (17)	1996	Colombia	NA	2400	*Lagothrix lagotricha*
35	Sleep tree use by white-faced capuchins (*Cebus capuchinus*): Implications for differences in seedling composition	Valenta K, Klemens JA, Fedigan LM *Neotrop Primates* (16)	2009	Costa Rica	108	NA	*Cebus capucinus*
36	Post-dispersal seed removal and germination selected tree species dispersed by *Cebus capucinus* on Barro Colorado Island, Panama	Wehncke EV, Dalling JW *Biotropica* (37)	2005	Panamá	1560	NA	*Cebus capucinus*
37	Monkey and dung beetle activities influence soil seed bank structure	Feer F, Ponge JF, Jouard S, Gomez D *Ecol Res* (28)	2013	French Guiana	100000	NA	*Alouatta seniculus*
38	Absence of howlers (*Alouatta palliata*) Influences tree seedling densities in tropical rain forest fragments in Southern Mexico	Anzures-Dadda A, Andresen E, Martínez ML, Manson RH *Int J Primatol* (32)	2011	Mexico	12500	NA	*Alouatta palliata*

39	Diet and feeding ecology of *Ateles chamek* in a bolivian semi-humid forest: The importance of *Ficus* as a staple food resource	Felton AM, Felton A, Wood JT, Lindenmayer DB *Int J Primatol* (29)	2008	Bolivia	100000	863	*Ateles chamek*
40	Diet of the brown howler monkey *Alouatta fusca* in a forest fragment in southeastern Brazil	Galetti M, Pedroni F, Morellato LPC *Mammalia* (58)	1994	Brazil	250	NA	*Alouatta guariba*
41	Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in southeast Brazil	Galetti M, Pedroni F *J Trop Ecol* (10)	1994	Brazil	250	NA	*Sapajus nigritus*
42	Seed dispersal by woolly monkeys in Cueva de los Guacharos National Park (Colombia): An Amazonian primate dispersing montane plants	Ramírez MA, Galvis NF, Vargas SA, Léon JJ, Cifuentes EF, Stevenson PR *Developments in Primatology: Progress and Prospects* 44	2014	Colombia	9000	132	*Lagothrix lugens*
43	Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest	Feer F *J Trop Ecol* (15)	1999	French Guiana	100000	NA	*Alouatta seniculus*
44	Resource use and seed dispersal by red howler monkeys (*Alouatta seniculus*) in a Colombian Andean Forest	Giraldo P, Gómez-Posada C, Martínez J, Kattan G *Neotrop Primates* (14)	2007	Colombia	489	388.3	*Alouatta seniculus*
45	Seed dispersal by sympatric tamarins *Saguinus mystax* and *Saguinus fuscicollis*: Diversity and characteristics of plant species	Knogge C, Heymann EW *Folia Primatol* (74)	2003	Peru	120	888	*Saguinus mystax*
45	Seed dispersal by sympatric tamarins *Saguinus mystax* and *Saguinus fuscicollis*: Diversity and characteristics of plant species	Knogge C, Heymann EW *Folia Primatol* (74)	2003	Peru	120	804	*Saguinus fuscicollis*
46	Fruit eating and seed dispersal by howling monkeys in the tropical rain forest of los Tuxtlas, Mexico	Estrada A & Coates-Estrada R *Am J Primatol* (6)	1984	Mexico	155000	NA	*Alouatta palliata*
47	Estimation of the retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagotricha*, in a Colombian forest	Yumoto T, Kimura K, Nishimura A *Ecol Res* (14)	1999	Colombia	201875	89.7	*Alouatta seniculus*
47	Estimation of the retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagotricha*, in a Colombian forest	Yumoto T, Kimura K, Nishimura A *Ecol Res* (14)	1999	Colombia	201875	123.53	*Lagothrix lagotricha*
48	Dispersión primaria de semillas por primates y	Ponce-Santizo G, Andersen	2006	Guatemala	57600	60	*Alouatta pigra*

	dispersión secundaria por escarabajos coprófagos en Tikal, Guatemala	E, Cano E, Cuarón AD *Biotropica* (38)					
48	Dispersión primaria de semillas por primates y dispersión secundaria por escarabajos coprófagos en Tikal, Guatemala	Ponce-Santizo G, Andersen E, Cano E, Cuarón AD *Biotropica* (38)	2006	Guatemala	57600	60	*Ateles geoffroyi*
49	Seasonal variation of consumption of the species used as fruit source by brown howler monkeys (*Alouatta clamitans*) in southern Brazil	Santos GASD, Bianchini E, Reis NR *Biota Neotrop* (13)	2013	Brazil	100	340	*Alouatta guariba*
50	Effects of passage through tamarin guts on the germination potential of dispersed seeds	Knogge C, Herrera ERT, Heymann EW *Int J Primatol* (24)	2003	Peru	120	804	*Saguinus fuscicollis* *Saguinus mystax*
51	Seed swallowing in tamarins: Evidence of a curative function or enhanced foraging efficiency?	Garber PA, Kitron U *Int J Primatol* (18)	1997	Panamá	4500	NA	*Saguinus geoffroyi*
51	Seed swallowing in tamarins: Evidence of a curative function or enhanced foraging efficiency?	Garber PA, Kitron U *Int J Primatol* (18)	1997	Peru	500	NA	*Saguinus mystax*
52	Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds	Andersen E *Biotropica* (34)	2002	Brazil	800	NA	*Alouatta seniculus*
53	Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico	Estrada A, Coates-Estrada R *J Trop Ecol* (7)	1991	Mexico	155000	NA	*Alouatta palliata*
54	Contagious deposition of seeds in spider monkeys’ sleeping trees limits effective seed dispersal in fragmented landscapes	González-Zamora A, Arroyo-Rodríguez V, Escobar F, Rös M, Oyama K, Ibarra-Manríquez G, Stoner KE, Chapman CA, *PlosOne* (9)	2014	Mexico	176200	NA	*Ateles geoffroyi*
54	Contagious deposition of seeds in spider monkeys’ sleeping trees limits effective seed dispersal in fragmented landscapes	González-Zamora A, Arroyo-Rodríguez V, Escobar F, Rös M, Oyama K, Ibarra-Manríquez G, Stoner KE, Chapman CA *PlosOne* (9)	2014	Mexico	330000	NA	*Ateles geoffroyi*
55	Black howler monkey (*Alouatta pigra*) activity, foraging and seed dispersal patterns in shaded cocoa plantations vs. rainforest in Southern	Zárate DA, Andersen E, Estrada A, Serio-Silva JC *Am J Primatol* (76)	2014	Mexico	120	432	*Alouatta pigra*

	Mexico						
55	Black howler monkey (*Alouatta pigra*) activity, foraging and seed dispersal patterns in shaded cocoa plantations vs. rainforest in Southern Mexico	Zárate DA, Andersen E, Estrada A, Serio-Silva JC *Am J Primatol* (76)	2014	Mexico	2000	432	*Alouatta pigra*
56	Germination of seeds from three species dispersed by black howler monkeys (*Alouatta caraya*)	Bravo SP & Zunino GE *Folia Primatol* (71)	2000	Argentina	280	NA	*Alouatta caraya*
57	Ingestion of *Ficus enormis* seeds by howler monkeys (*Alouatta fusca*) in Brazil: effects on seed germination	Figueiredo RA *J Trop Ecol* (9)	1993	Brazil	250	NA	*Alouatta guariba*
58	Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia	Andersen E *J Trop Ecol* (17)	2001	Brazil	10000	NA	*Alouatta seniculus* *Ateles chamek*
59	Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*	Russo SE & Augspurger CK *Ecol Lett* (7)	2004	Peru	1532806	NA	*Ateles chamek*
60	Dispersal vacuum in the seedling recruitment of a primate-dispersed Amazonian tree	Levi T & Peres CA *Biol Cons* (163)	2013	Brazil	1600	NA	*Ateles chamek* *Sapajus apella* *Cebus albifrons* *Lagothrix cana* *Saguinus fuscicollis* *Saguinus mystax* *Saimiri ustus*
61	Frugivory and seed fate in *Bursera inversa* (Burseraceae) at Tinigua Park, Colombia: Implications for primate conservation	Stevenson PR, Link A, Ramírez BH *Biotropica* (37)	2005	Colombia	201875	NA	*Ateles belzebuth* *Lagothrix lagotricha*
62	Monkey dispersal and waste of a Neotropical fruit	Howe HF *Ecology* (61)	1980	Panamá	1560	NA	*Alouatta palliata* *Cebus capucinus*
63	Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana	Zhang SY, Wang LX *Biotropica* (27)	1995	French Guiana	100000	NA	*Ateles paniscus* *Sapajus apella*
64	Effects of the physical environment and primate gut passage on the early establishment of *Ampelocera hottlei* Standley in rain forest fragments	González-Di Pierro AM, Benítez-Malvido J, Méndez-Toribio M, Zermeño I, Arroyo-Rodríguez V, Stoner KE *Biotropica* (43)	2011	Mexico	300000	NA	*Alouatta pigra*

65	Fruit availability, frugivore satiation and seed removal in 2 primate-dispersed tree species	Ratiarison S, Forget PM *Integr Zool* (6)	2011	French Guiana	100000	NA	*Alouatta seniculus*
66	Effect of different primate species on germination of *Ficus* (*Urostigma*) seeds	Righini N, Serio-Silva JC, Rico-Gray V, Martínez-Mota R, *Zoo Biol* (23)	2004	NA	Captivity	NA	NA
67	Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understory of tropical rain forest	Julliot C *J Ecol* (85)	1997	French Guiana	100000	NA	*Alouatta seniculus*
68	Germinación de semillas de *Ficus insipida* (Moraceae) defecadas por tucanes (*Ramphastos sulfuratus*) y monos araña (*Ateles geoffroyi*)	Domínguez-Domínguez LE, Morales-Mávil JE, Alba-Landa J, *Rev Biol Trop* (54)	2006	Mexico	Captivity	NA	*Ateles geoffroyi*
69	Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection	Russo SE *Oecologia* (136)	2003	Peru	1532806	NA	*Ateles chamek*
70	Observations on fruiting and dispersers of *Cecropia obtusifolia* at Los Tuxtlas, Mexico	Estrada A, Coates-Estrada R, Vazquez-Yanes C *Biotropica* (16)	1984	Mexico	155000	NA	*Alouatta palliata*
71	Seed dispersal of *Asplundia peruviana* (Cyclanthaceae) by the primate *Saguinus fuscicollis*	Knogge C, Heymann EW, Herrera ERT *J Trop Ecol* (14)	1998	Peru	120	NA	*Saguinus fuscicollis*
72	The role of canopy ants in removing *Ficus perforata* seeds from howler monkey (*Alouatta palliata mexicana*) feces at Los Tuxtlas, Mexico	Martinez-Mota R, Serio-Silva JC, Rico-Gray V *Biotropica* (36)	2004	Mexico	40	NA	*Alouatta palliata*
73	Seed source, seed traits, and frugivore habitats: implications for dispersal quality of two sympatric primates	Benitez-Malvido J, González-Di Pierro AM, Lombera R, Guillén S & Estrada A *Am J Bot* (101)	2014	Mexico	330000	NA	*Alouatta pigra* *Ateles geoffroyi*

Supplementary Material S2 – Individual data on frugivory degree among ecospecies available in surveyed studies.

Source Code[a]	**Primate species**	**Guild**	**Ecospecies**	**Frugivory degree**	**Source type**
28	*Alouatta guariba*	FO	Al	8	%of the feeding records
40	*Alouatta guariba*	FO	Al	15	%of the feeding bouts
49	*Alouatta guariba*	FO	Al	14	%of the feeding records
1	*Alouatta palliata*	FO	Al	23.87	%of the feeding time
20	*Alouatta palliata*	FO	Al	28.5	%of the feeding time
1	*Alouatta pigra*	FO	Al	42.9	%of the feeding time
55	*Alouatta pigra*	FO	Al	26.9	%of the feeding time
55	*Alouatta pigra*	FO	Al	28.9	%of the feeding time
5	*Alouatta seniculus*	FO	Al	44	%of the feeding time
12	*Alouatta seniculus*	FO	Al	39	%of the feeding time
32	*Alouatta seniculus*	FO	Al	25.5	%of the feeding records
44	*Alouatta seniculus*	FO	Al	45.1	%of the feeding records
47	*Alouatta seniculus*	FO	Al	69	%of the feeding time
28	*Brachyteles arachnoides*	FO	Br	21.1	%of the feeding records
11	*Cebus capucinus*	FI	Cf	53	%of the feeding time
20	*Cebus capucinus*	FI	Cf	81.2	%of the feeding time
25	*Cebus capucinus*	FI	Cf	49	%of the feeding time
45	*Saguinus fuscicollis*	FI	Sx	59.8	%of the feeding records
50	*Saguinus fuscicollis*	FI	Sx	59.8	%of the feeding records
45	*Saguinus mystax*	FI	Sx	69.6	%of the feeding records
50	*Saguinus mystax*	FI	Sx	69.6	%of the feeding records
13	*Saguinus niger*	FI	Sm	87.5	%of the feeding time
41	*Sapajus nigritus*	FI	Ca	53.9	%of the feeding bouts
12	*Ateles belzebuth*	FR	At	72	%of the feeding time
33	*Ateles belzebuth*	FR	At	87	%of the feeding records
5	*Ateles chamek*	FR	At	80	%of the feeding time
39	*Ateles chamek*	FR	At	82	%of the feeding time
20	*Ateles geoffroyi*	FR	At	77.9	%of the feeding time
24	*Ateles geoffroyi*	FR	At	54.1	%of the feeding time
24	*Ateles geoffroyi*	FR	At	57	%of the feeding time
33	*Lagothrix lagotricha*	FR	La	73	%of the feeding records
34	*Lagothrix lagotricha*	FR	La	78.9	%of the feeding records
47	*Lagothrix lagotricha*	FR	La	81.5	%of the feeding time
12	*Lagothrix lagotricha*	FR	La	55	%of the feeding time

[a] Detailed information on supplementary material S1

Supplementary Material S3 – Individual data on handling behavior among ecospecies available in surveyed studies

Source Code[a]	Primate Species	Guild	Ecospecies	Feeding species	Apparently Digested	%[b]	Spit/ dropped	%[c]	Species in feces	%[d]
7	*Ateles belzebuth*	FR	At	152	4	3	2	1	146	96
33	*Ateles belzebuth*	FR	At	73	0	0	1	1	72	99
39	*Ateles chamek*	FR	At	63	0	0	3	5	60	95
5	*Ateles chamek*	FR	At	75	0	0	4	5	71	95
20	*Ateles geoffroyi*	FR	At	36	NA	NA	NA	NA	17	47
24	*Ateles geoffroyi*	FR	At	73	NA	NA	NA	NA	46	63
24	*Ateles geoffroyi*	FR	At	61	NA	NA	NA	NA	51	84
33	*Lagothrix lagotricha*	FR	La	104	9	9	16	15	79	76
47	*Lagothrix lagotricha*	FR	La	17	3	18	0	0	14	82
34	*Lagothrix lagotricha*	FR	La	177	9	5	3	2	165	93
42	*Lagothrix lugens*	FR	La	46	0	0	10	22	36	78
20	*Cebus capucinus*	FI	Cf	41	NA	NA	NA	NA	14	34
22	*Cebus capucinus*	FI	Cf	27	1	4	9	33	17	63
11	*Cebus capucinus*	FI	Cf	95	0	0	28	29	67	71
25	*Cebus capucinus*	FI	Cf	39	5	13	5	13	29	74
4	*Cebus capucinus*	FI	Cf	30	0	0	6	20	24	80
18	*Leontopithecus chrysomelas*	FI	Le	57	11	19	13	23	33	58
10	*Leontopithecus rosalia*	FI	Le	57	0	0	18	32	39	68
9	*Leontopithecus rosalia*	FI	Le	97	0	0	21	22	76	78
45	*Saguinus fuscicollis*	FI	Sxf	124	NA	NA	NA	NA	81	65
26	*Saguinus fuscicollis Saguinus mystax*	FI	Sxf	307	NA	NA	NA	NA	166	54
50	*Saguinus fuscicollis Saguinus mystax*	FI	Sxf	124	NA	NA	NA	NA	81	65
13	*Saguinus midas*	FI	Sm	18	6	33	6	33	6	33
45	*Saguinus mystax*	FI	Sxf	130	NA	NA	NA	NA	67	52
27	*Sapajus libidinosus*	FI	Ca	25	7	28	1	4	14	56
41	*Sapajus nigritus*	FI	Ca	40	5	13	3	8	32	80
2	*Alouatta caraya*	FO	Al	13	0	0	1	8	12	92

40	*Alouatta guariba*	FO	Al	20	2	10	1	5	18	90
49	*Alouatta guariba*	FO	Al	16	0	0	0	0	16	100
28	*Alouatta guariba*	FO	Al	8	NA	NA	NA	NA	8	100
46	*Alouatta palliata*	FO	Al	19	NA	NA	1	5	9	47
20	*Alouatta palliata*	FO	Al	19	NA	NA	NA	NA	12	63
1	*Alouatta palliata*	FO	Al	18	NA	NA	NA	NA	13	72
6	*Alouatta palliata*	FO	Al	35	0	0	7	20	28	80
53	*Alouatta palliata*	FO	Al	35	0	0	7	20	28	80
4	*Alouatta palliata*	FO	Al	9	1	11	0	0	8	89
55	*Alouatta pigra*	FO	Al	14	0	0	1	7	13	93
55	*Alouatta pigra*	FO	Al	17	0	0	1	6	16	94
1	*Alouatta pigra*	FO	Al	33	NA	NA	NA	NA	31	94
44	*Alouatta seniculus*	FO	Al	14	4	29	1	7	9	64
47	*Alouatta seniculus*	FO	Al	11	2	18	0	0	9	82
3	*Alouatta seniculus*	FO	Al	97	1	1	3	3	86	89
5	*Alouatta seniculus*	FO	Al	15	0	0	1	7	14	93
32	*Alouatta seniculus*	FO	Al	90	1	1	2	2	87	97
28	*Brachyteles arachnoides*	FO	Br	22	0	0	0	0	22	100

[a] Detailed information in supplementary material S1
[b] Percentage of feeding species apparently digested
[c] Percentage of feeding species spitted and/or dropped
[d] Percentage of feeding species found intact in feces

Supplementary Material S4 – Seed size effects

A – Seed size effects on transit time

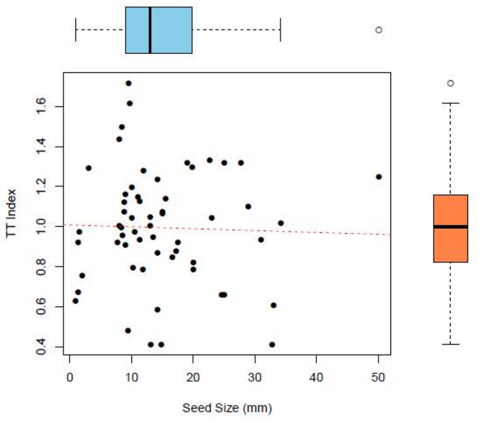
In order to weigh each ecospecies effects on Transit Time, we calculated two indexes of gut retention times: average transit time index (TTI) and first appearance index (FAI) (also see the following table with raw data) and evaluated seed size effects on them.

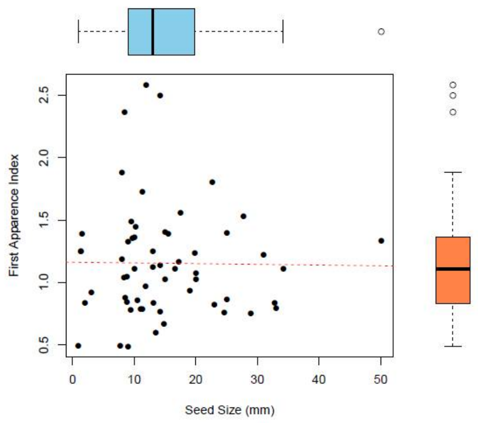
TTI = average time taken to certain plant species travel through certain ecospecies gut (in minutes) divided by the average time taken to all plant species travel through certain ecospecies gut (in minutes)

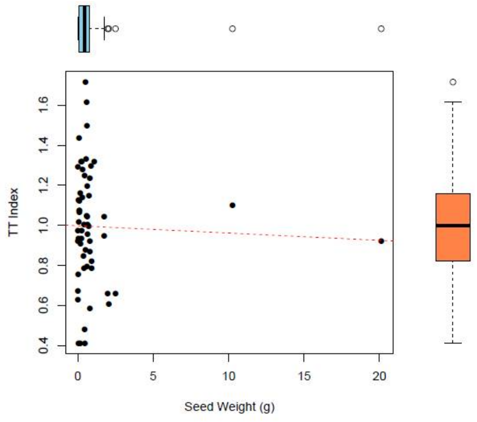
FAI = average time taken to the first seed of certain plant species appear in certain ecospecies feces (in minutes) divided by the average time taken to the first seed of all plant species appear in certain ecospecies feces (in minutes)

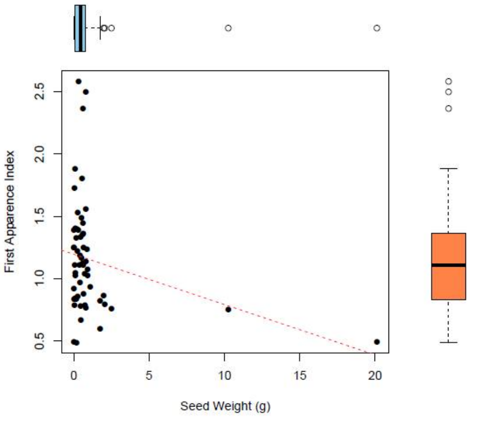
```
Formula = average transit time index ~ seedsz * seedwg
Coefficients:
                Estimate Std. Error t-value  p-value
seedsz        -8.473e-04  4.481e-03  -0.189    0.851
seedwg        -3.260e-03  2.320e-02  -0.140    0.889
seedsz:seedwg -1.855e-05  1.588e-03  -0.012    0.991

Residual standard error: 0.2951 on 54 degrees of freedom
Multiple R-squared:  0.002178,  Adjusted R-squared:  -0.05326
F-statistic: 0.03929 on 3 and 54 DF,  p-value: 0.9895
```

```
Formula = first appearance index ~ seedsz * seedwg
Coefficients:
                Estimate Std. Error t-value  p-value
seedsz         0.001709   0.006698   0.255    0.800
seedwg        -0.023992   0.034685  -0.692    0.492
seedsz:seedwg -0.001379   0.002374  -0.581    0.564

Residual standard error: 0.4412 on 54 degrees of freedom
Multiple R-squared:  0.07457,   Adjusted R-squared:  0.02315
F-statistic:  1.45 on 3 and 54 DF,  p-value: 0.2384
```









Source code[a]	Primate ecospecies	Plant species	Longer length (mm)	Weight (g)	Individual 1st appearance (min)	Individual Average (min)	FAI (Individual 1st appearance / Average 1st appearance)	TTI (Individual Average / Total Average)
47	Al	*Castilla ulei*	11.500	0.620	NA	1146.00	NA	0.97
47	Al	*Coccoloba densifrons*	9.000	0.260	NA	1200.00	NA	1.02
47	Al	*Perebea mollis*	11.200	0.570	NA	1128.00	NA	0.96
47	Al	*Perebea xanthochyma*	10.500	0.250	NA	1182.00	NA	1.00
47	Al	*Pourouma bicolor*	12.500	0.700	NA	1278.00	NA	1.08
47	Al	*Pseudolmedia laevis*	7.500	0.435	NA	1146.00	NA	0.97
					Average 1st appearance: NA	**Total Average:** 1180.00		
7	At	*Abuta* sp.	19.800	0.860	246.00	338.00	1.24	1.30
7	At	*Alibertia hadrantha*	9.000	0.170	97.00	236.00	0.49	0.91
7	At	*Annona helosioides*	15.000	0.100	279.00	279.00	1.40	1.07
7	At	*Annona pittieri*	15.000	0.100	204.00	277.00	1.03	1.06
7	At	*Cayaponia* sp.	8.000	0.076	374.00	374.00	1.88	1.44
7	At	*Cissus biformifolia*	8.800	0.094	208.00	292.00	1.05	1.12
7	At	*Cissus* sp.	8.800	0.094	168.00	279.00	0.85	1.07
7	At	*Clarisia racemosa*	24.600	2.500	151.00	172.00	0.76	0.66
7	At	*Cupania* sp.	11.000	0.740	157.00	299.00	0.79	1.15
7	At	*Eugenia* sp.	9.500	0.508	296.00	447.00	1.49	1.72
7	At	*Ficus* sp.	0.900	0.002	98.00	164.00	0.49	0.63
7	At	*Guarea kunthiana*	25.000	0.200	277.00	343.00	1.39	1.32
7	At	*Guarea purusana*	20.000	0.903	204.00	204.00	1.03	0.78
7	At	*Guarea* sp.	20.000	0.903	214.00	214.00	1.08	0.82
7	At	*Guatteria* sp.	16.600	0.365	220.00	220.00	1.11	0.85
7	At	*Hyeronima alchorneoides*	2.000	0.007	166.00	196.00	0.84	0.75
7	At	*Inga oerstediana*	14.180	0.79	226.00	226.00	1.14	0.87
7	At	*Inga* sp.	14.180	0.79	152.00	152.00	0.76	0.58
7	At	*Matisia cordata*	NA	NA	177.00	275.00	0.89	1.06
7	At	*Naucleopsis glabra*	10.000	0.610	220.00	311.00	1.11	1.19
7	At	*Naucleopsis ulei*	10.000	0.610	271.00	271.00	1.36	1.04
7	At	*Neea* sp.	9.000	0.148	264.00	302.00	1.33	1.16
7	At	*Perebea xanthochyma*	10.500	0.250	170.00	253.00	0.86	0.97
7	At	*Porcelia* sp.	NA	NA	150.00	214.00	0.75	0.82
7	At	*Prunus debilis*	9.700	0.575	269.00	421.00	1.35	1.62
7	At	*Pseudomalmea diclina*	8.300	0.721	207.00	259.00	1.04	0.99

7	At	*Sapotaceae* sp1	NA	NA	223.00	223.00	1.12	0.86
7	At	*Sapotaceae* sp2	NA	NA	184.00	207.00	0.93	0.80
7	At	*Spondias mombin*	33.000	2.047	158.00	158.00	0.79	0.61
7	At	*Talisia novagranata*	19.000	1.075	186.00	343.00	0.94	1.32
7	At	*Tapirira guianensis*	11.300	0.026	156.00	243.00	0.78	0.93
7	At	*Trichilia laxipaniculata*	11.800	0.393	192.00	205.00	0.97	0.79
7	At	*Trichilia* sp.	8.000	0.393	236.00	261.00	1.19	1.00
7	At	*Virola flexuosa*	25.000	1.962	171.00	171.00	0.86	0.66
7	At	*Virola obovata*	13.500	1.742	118.00	246.00	0.59	0.94
7	At	*Virola pavonis*	23.000	1.742	163.00	271.00	0.82	1.04
7	At	*Vitex* sp.	NA	0.341	138.00	275.00	0.69	1.06
7	At	*Ziziphus cinnamomum*	NA	0.469	163.00	272.00	0.82	1.04
					Average 1st appearance: 198.76	**Total Average:** 260.34		
47	La	*Castilla ulei*	11.500	0.620	NA	870.00		2.32
47	La	*Clarisia racemosa*	24.600	2.500	NA	120.00		0.32
47	La	*Pourouma petioulata*	11.500	0.56	NA	276.00		0.73
47	La	*Strychnos schultesiana*	20.000	1.189	NA	246.00		0.65
47	La	*Virola flexuosa*	25.000	1.962	NA	366.00		0.97
					Average 1st appearance: NA	**Total Average:** 375.60		
9	Le	*Calycorectes* sp.	7.700	20.110	25.00	67.00	0.49	0.92
9	Le	*Calyptranthes lucida*	9.400	0.440	28.00	35.00	0.78	0.48
9	Le	*Campomanesia eugenioides*		0.034	118.00	118.00	3.28	1.62
9	Le	*Cecropia hololeuca*	1.500	0.00093	50.00	71.00	1.39	0.97
9	Le	*Cecropia pachystachya*	3.000	0.00085	33.00	94.00	0.92	1.29
9	Le	*Coccoloba* sp.	13.100	0.153	30.00	30.00	0.83	0.41
9	Le	Euphorbiaceae	25.900	NA	23.00	66.00	0.64	0.91
9	Le	*Ficus gomelleira*	NA	0.002	103.00	103.00	2.86	1.41
9	Le	*Guapira opposita*	11.900	0.300	93.00	93.00	2.58	1.28
9	Le	*Helicostylis tomentosa*	27.700	0.250	55.00	96.00	1.53	1.32
9	Le	*Henriettea saldanhaei*	NA	NA	68.00	68.00	1.89	0.93
9	Le	*Hyperbaena domingensis*	22.000	NA	22.00	71.00	0.61	0.97
9	Le	*Inga* sp.	17.500	0.79	56.00	67.00	1.56	0.92
9	Le	*Inga* sp.	14.180	0.79	90.00	90.00	2.50	1.24
9	Le	*Inga edulis*	22.650	0.539	65.00	97.00	1.81	1.33
9	Le	*Inga thibaudiana*	13.000	0.630	45.00	73.00	1.25	1.00

9	Le	*Marlierea* sp.	8.400	0.600	85.00	109.00	2.36	1.50
9	Le	*Marlierea* sp.	10.200	0.600	52.00	58.00	1.44	0.80
9	Le	*Miconia cinnamomifolia*	1.300	0.0003	45.00	49.00	1.25	0.67
9	Le	*Miconia latecrenata*	NA	0.0003	46.00	68.00	1.28	0.93
9	Le	*Miconia* sp.	1.300	0.0003	45.00	67.00	1.25	0.92
9	Le	*Micropholis gardneriana*	14.800	0.467	24.00	30.00	0.67	0.41
9	Le	*Myrcia tenuifolia*	15.500	0.278	50.00	83.00	1.39	1.14
9	Le	Myrtaceae	8.400	NA	21.00	53.00	0.58	0.73
9	Le	Myrtaceae	NA	NA	58.00	58.00	1.61	0.80
9	Le	*Posoqueria latifolia*	32.800	0.027	30.00	30.00	0.83	0.41
9	Le	*Passiflora rhamnifolia*	NA	0.016	36.00	83.00	1.00	1.14
9	Le	*Pourouma guranensis*	17.200	0.500	42.00	64.00	1.17	0.88
9	Le	*Pouteria bangii*	28.900	10.250	27.00	80.00	0.75	1.10
9	Le	*Randia* sp.	34.200	0.055	40.00	74.00	1.11	1.02
9	Le	*Anonna dolabripetala*	31.000	0.234	44.00	68.00	1.22	0.93
9	Le	*Sarcaulus brasiliensis*	19.300	NA	32.00	64.00	0.89	0.88
9	Le	*Tapirira guianensis*	11.300	0.026	62.00	82.00	1.72	1.13
9	Le	*Tocoyena braslliensis*	50.100	0.442	48.00	91.00	1.33	1.25
9	Le	Unknown	9.600	NA	40.00	75.00	1.11	1.03
9	Le	Unknown	13.800	NA	97.00	97.00	2.69	1.33
					Average 1st appearance: 50.78	**Total Average:** 72.83		
13	Sm	*Inga alba*	8.500	0.630	125.00	176.70	0.88	0.95
13	Sm	*Tetragastris altissima*	13.00	0.573	160.00	193.75	1.12	1.05
					Average 1st appearance: 142.50	**Total Average:** 185.23		

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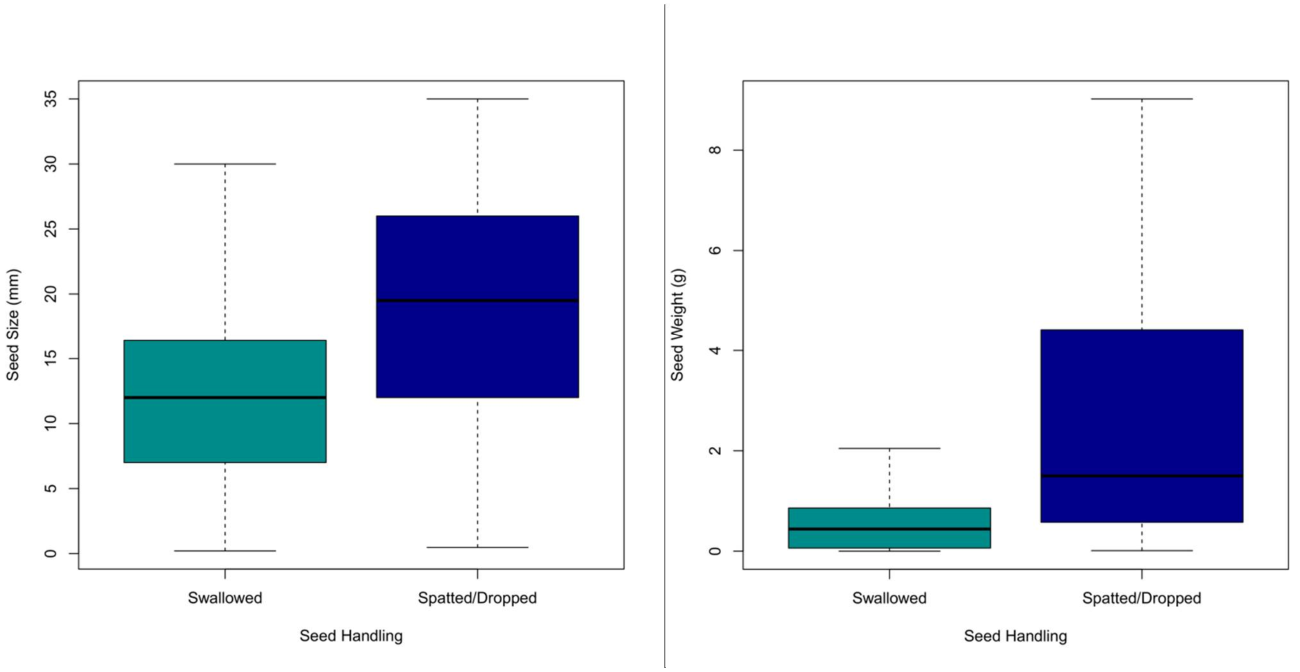
[a] Detailed information on Table S1

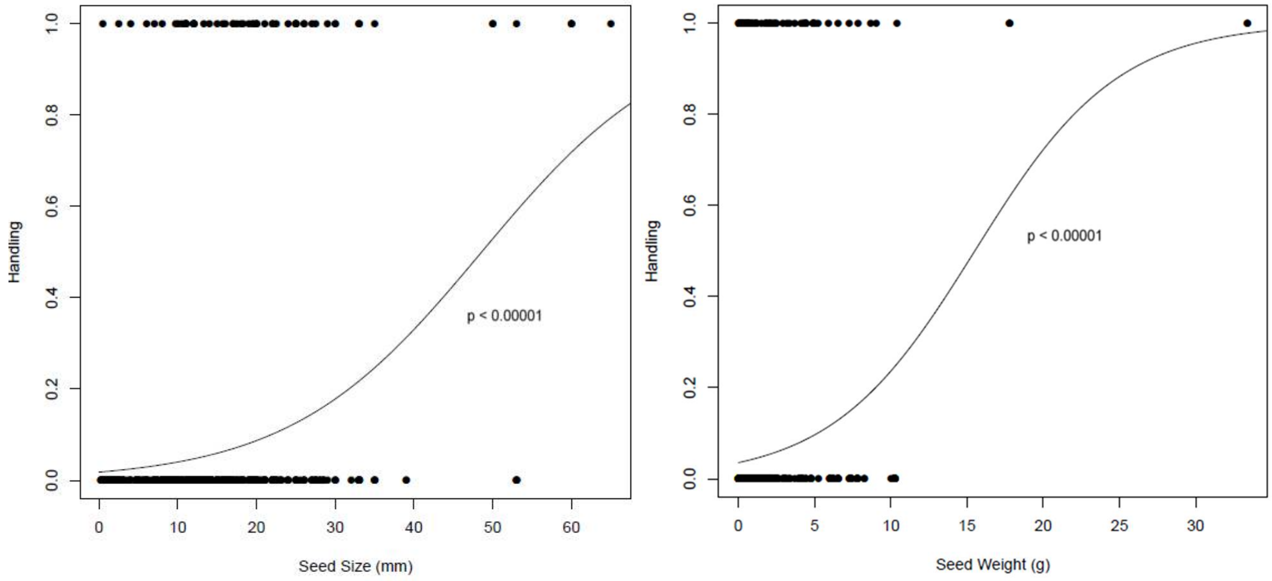
B – Boxplots of the general handling behavior and seed size effects in terms of seed longer length (mm) and seed weight (g)



C – Logistic regressions showing chances of being dropped enhancement according to increasing in longer length (mm) and weight (g)

Hosmer and Lemeshow goodness of fit test:

Seed length (mm): Chi-sqr. = 16.353, df = 8, p-value = 0.038
Seed weight (g): Chi-sqr. = 16.263, df = 8, p-value = 0.039



D – Seed size effects on disperser groups

D.1 - Seed dispersal data sources

DATA FOR SPECIES DISPERSED **BY BATS** CAME FROM:

CHARLES-DOMINIQUE, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: Cecropia, birds and bats in French Guyana, p. 119-135. *In* A. Estrada & T.H. Fleming (Eds). Frugivores and seed dispersal. Dordrecht, Dr. W. Junk Publ., 392p.

GALETTI, M., M. A. PIZO AND L. P. C. MORELLATO, 2011. Diversity of functional traits of fleshy fruits in a species-rich Atlantic rain forest. Biota Neotropica, 11: 181–193.

GARCÍA-ESTRADA, C., A. DAMON, C. SÁNCHEZ-HERNÁNDEZ, L. SOTO-PINTO AND G. IBARRA-NÚÑEZ. 2012. Diets of Frugivorous Bats in Montane Rain Forest and Coffee Plantations in Southeastern Chiapas, Mexico. Biotropica 44:394–401.

LOBOVA, T. A., C. K. GEISELMAN AND S. A. MORI. 2009. Seed dispersal by bats in the Neotropics, New York Botanical Garden Press.

MEDELLIN, R.A. AND O. GAONA. 1999. Seed dispersal by bats and birds in Chiapas, Mexico. Biotropica 31: 478–485.

STEVENSON, P.R., M.J. QUIÑONES & M.C. CASTELLANOS. 2000. Guía de Frutos de los Bosques del Río Duda, Macarena, Colombia. Asociación Para la Defensa de La Macarena - IUCN. Bogotá, Colombia, 467 p.

DATA FOR SPECIES DISPERSED **BY BIRDS** CAME FROM:

WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808-818.

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RIBA-HERNÁNDEZ, P., K. E. STONER AND P. W. LUCAS. 2003. The sugar composition of fruits in the diet of spider monkeys (*Ateles geoffroyi*) in tropical humid forest in Costa Rica. Journal Tropical Ecology 19:709–716.

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PALMERIM, J.M.; D.L. GORCHOV AND S. STOLESON. 1989. Trophic structure of a neotropical frugivore community: is there competition between birds and bats? Oecologia, Berlin, 79: 403-411. Estrada *et al.* (1984) Comparison of frugivory by howling monkeys and bats

Skutch, A. F. 1980. Arils as food of tropical American birds. The Condor, Albuquerque 82: 31-42

MEDELLIN, R.A. AND O. GAONA. 1999. Seed dispersal by bats and birds in Chiapas, Mexico. Biotropica 31: 478–485.

CHARLES-DOMINIQUE, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: Cecropia, birds and bats in French Guyana, p. 119-135. *In* A. Estrada & T.H. Fleming (Eds). Frugivores and seed dispersal. Dordrecht, Dr. W. Junk Publ., 392p.

KELLY, C. K. 1995 Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia 102: 377-388.

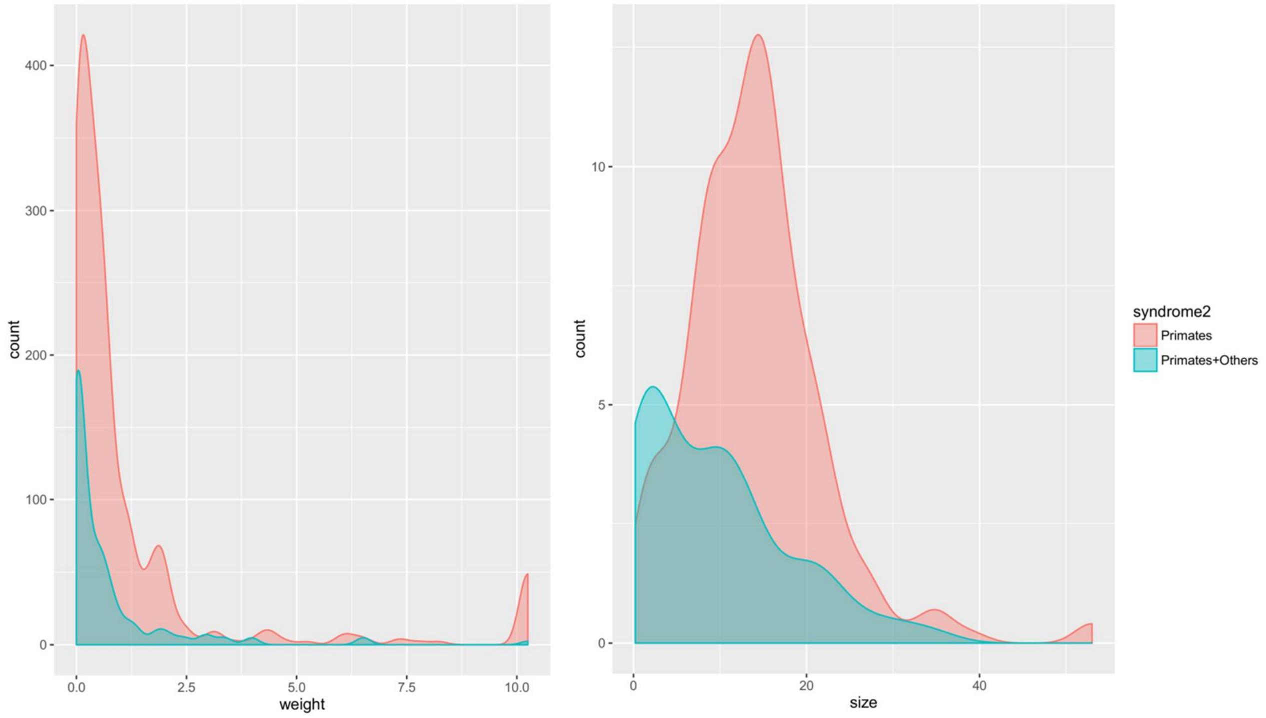
GALETTI, M., M. A. PIZO AND L. P. C. MORELLATO, 2011. Diversity of functional traits of fleshy fruits in a species-rich Atlantic rain forest. Biota Neotropica 11: 181–193.

BURNS, K. C., E. CAZETTA, M. GALETTI, A. VALIDO AND H. M. SCHAEFER . 2009. Geographic patterns in fruit color diversity: do leaves constrain the colour of fleshy fruits? Oecologia 159: 337-343.

MARTINS, V. F., L. P. D. CAZOTTO AND F. A. M. SANTOS. 2014. Dispersal spectrum of four forest types along an altitudinal range of the Brazilian Atlantic forest. Biota Neotrop. 14.

STEVENSON, P.R., M.J. QUIÑONES & M.C. CASTELLANOS. 2000. Guía de Frutos de los Bosques del Río Duda, Macarena, Colombia. Asociación Para la Defensa de La Macarena - IUCN. Bogotá, Colombia, 467pp.

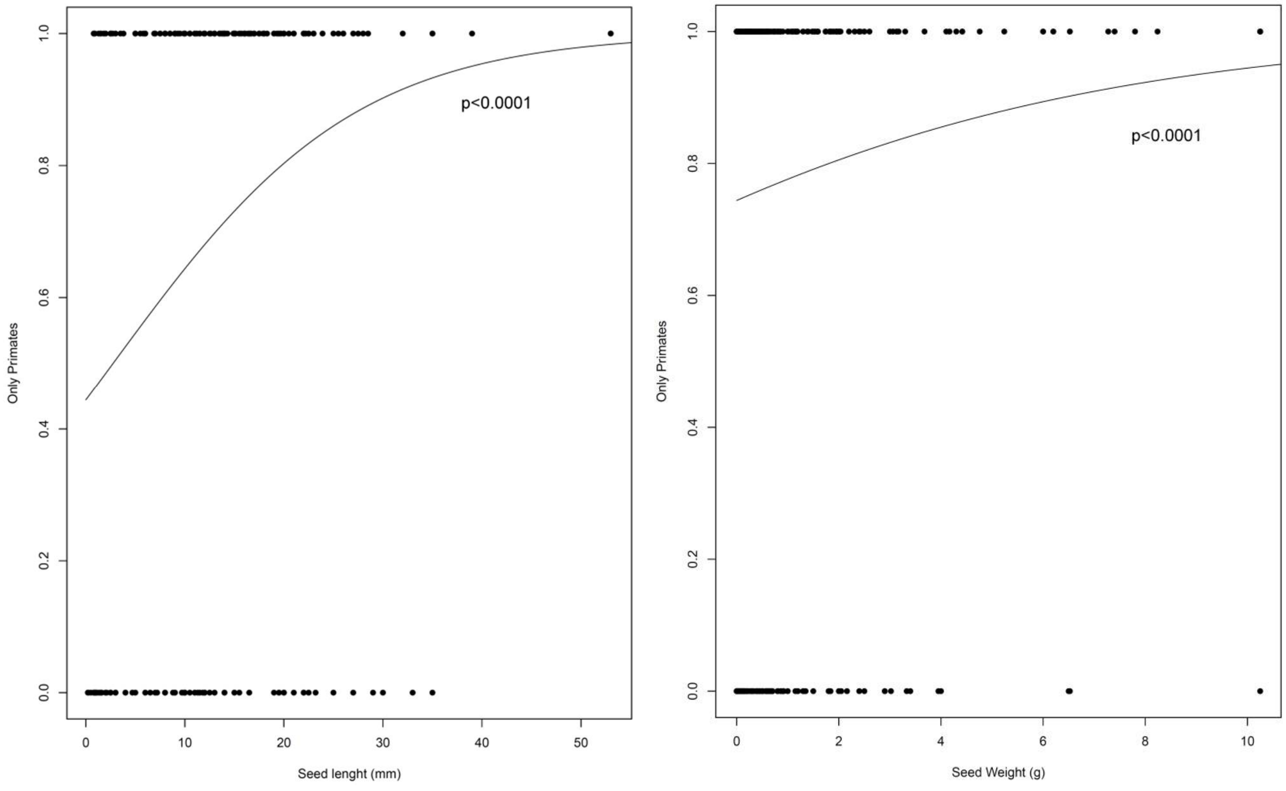
D.2 – Density distribution graphs of seed sizes among disperser groups:

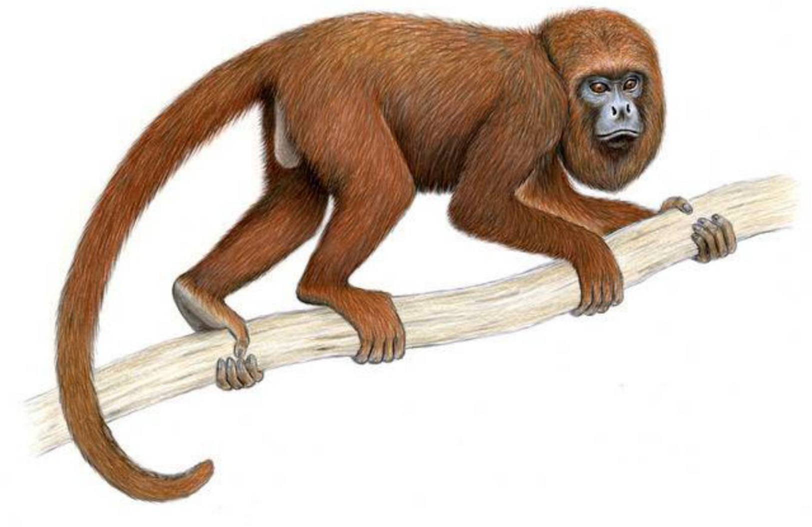


D.3– Logistic regressions showing chances of being dispersed exclusively by Neotropical primates enhancing according to increasing seed sizes

Hosmer and Lemeshow goodness of fit test:

Seed length (mm) - Chi-sqr. = 27.713, df = 8, p-value = 0.0005
Seed weight (g) - Chi-sqr. = 26.416, df = 8, p-value = 0.0009





Aouatta guariba, folivore-frugivore Neotropical primate.
Illustration: Stephen D. Nash

CAPÍTULO 3:

How far do Neotropical primates disperse seeds?

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RESEARCH ARTICLE

How far do Neotropical primates disperse seeds?

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Seed dispersal distance (SDD) is a vital component of vertebrate-mediated seed dispersal process: the average distance at which seeds are deposited away from the parent plant represents the starting template of plant regeneration. We present a simple model to explain and predict observed measures of average dispersal distance and we hypothesize that it is a consequence of how long seeds are retained in the disperser's gut, how rapidly the disperser moves per unit time and how twisted the animal travel path is relative to the straight-line distance moved away from the seed source. We retrieved data on dispersal distances from 26 published studies including nine primate species dispersing up to 112 plant species per study. We used gut transit time (TT) as a proxy for residence time inside the gut, the disperser's travel path per hour as proxy for movement rate, and the daily path length relative to the home range area as a correlate of path twisting (PT). We illustrate this model with comparative data on Neotropical primates. These three variables explained 90% of the variation in the average SDD. Path analysis indicates that additional variables exerted only indirect effects. Our model can be applied to primate populations for which detailed seed dispersal data are missing, and help evaluate conservation priorities for primate species according to the potential service they provide in terms of forest regeneration.

KEYWORDS
dispersal distance, dispersal kernel, ecological modeling, primate seed dispersal, seed dispersal effectiveness

1 | INTRODUCTION

Frugivory and seed dispersal establish a vital eco-evolutionary link between animals and plants (Eriksson, 2016; Jordano et al., 2011). The effectiveness of a disperser depends on its contribution to plant fitness, which is the product of seed dispersal effectiveness (SDE) components. The quantitative component is expressed by the number of seeds dispersed, whereas the qualitative component expresses the probability of a dispersed seed to produce a new adult (Schupp, Jordan, & Gómez, 2010). Seed removal rates are well explained by frugivore body size and nutritional requirements, along with plant traits (Cortês & Uriarte, 2013). In contrast, knowledge of the qualitative component of SDE is less understood because determining its subcomponents—gut passage effects and quality of seed deposition—are extremely challenging (Schupp et al., 2010).

In tropical forests, most trees rely on vertebrates for seed dispersal, and primates play a key role in dispersing great amounts of large seeds for long distances (Fleming & Kress, 2011; Hawes & Peres 2014; Stevenson, Link, Onshuus, Quiroz, & Velasco, 2014). For Neotropical plants, passage through a primate gut increases germination percentage and decreases germination time, suggesting that New World primates provide an important service in terms of treatment inside the gut (Arroyo-Rodríguez, Andresen, Bravo, & Stevenson, 2015; Fuzessy, Cornelissen, Janson, & Silveira, 2016). However, to evaluate the quality of the dispersal service provided by Neotropical primates it is also necessary to understand the factors determining seed dispersal distance (SDD), the shape of seed deposition shadows, and post dispersal seed fate (Culot, Huynen, & Heymann, 2015; Schupp et al., 2010). Because our knowledge on the role of frugivores in the forest regeneration is still scarce the distance a frugivore moves seeds away from the parent plant can be used as a first step in estimating the probability of a dispersed seed to produce a new adult (Comita et al., 2014).

Here, we gathered data from 26 studies on seed dispersal by Neotropical primates to determine patterns and drivers of average SDD. We hypothesize that seed transit time (TT) inside the animal gut and movement patterns are the main drivers of SDD in Neotropical primates.

The distance a frugivore is able to travel may depend on body mass and how rapidly it moves per unit of time within a home range, modulated by forest fragment size (Cortês & Uriarte, 2013; Cousens, Hill, French, & Bishop, 2010). Also, the amount of time a seed remains retained in disperser gut while it moves is expected to positively influence dispersal distance (Fukui, 2003). However, SDD drivers cannot be considered separately.

Large frugivore primates travel longer distances while folivores tend to move shorter (Table 1). A long travel path leads to a tendency to disperse seeds further, despite shorter gut are associated with lower gut differentiation (when compared to a complex gut, such as folivores) (Milton, 1981; Stevenson et al., 2014). On the other hand, folivore TTs can reach 24 hr in Neotropics, and such long TT associated with short travel paths may induce clumped defecation nearby sleeping and parent trees (Russo & Augspurger, 2004).

2 | METHODS

We collected data from published studies on seed dispersal by Neotropical primates. We searched electronically for the following terms within the title, abstract, and keywords of papers incorporated into the Web of Science and Google Scholar databases (1945–2015): "primate seed dispersal distance," "primate dispersal kernel," "primate seed shadow," "primate dispersal distance," and "primate seed fate." The literature list was supplemented with studies cited in the reference lists of the articles surveyed. Studies were included regardless of the duration period. We found only 26 studies on SDD according to our search (see electronic supplementary material S1).

According to preexisting categories reported in original studies we defined four categories of SDD, which were based on potential sibling competition and risk of death due to parent-specific herbivores or pathogens (Augspurger & Kelly, 1984): under/close to parent (0–10 m), density competition (>10–50 m), escape from density competition (>50–100 m), and increased probability of dispersal into other habitats (>100 m). The range of distances in each category was set according the available data reported in the original studies. Our database was built on ecological data, rather than genetic data which are sparely available in the literature. To increase the reliability of our results, we extracted data on the predictor variables from the same study as the dispersal distances. When data were not available in the original paper, we sought studies that used the same population and/or the same study area from where the data on dispersal distances were extracted. We built cumulative distribution curves using the categories of dispersal distance for nine primate species for which ample data are available, and we compared seed shadows among different feeding guilds (see electronic supplementary material S2).

Some of our sources comprise studies based on a single average dispersal distance for different plant species, but a few are based on

TABLE 1 Data available on minimal and maximal seed dispersal distance by Neotropical primates, deposition patterns, number of plant species found on feces, and percentage of feces containing seeds

Primate spp.	Feeding guild	Deposit. pattern	No. species in feces (N)	% feces with seeds (N)	Average dist. (m)	Min dist. (m)	Max dist. (m)
A. belzebuth	FRU	S[1]	41(186)[1]	–	452.5[1]	0[1]	1,281[1]
L. lagothricha	FRU	S[2,3]	14(?)[2] 112(264)[3]	99(1397)[4]	413.5[3,4]	0[4]	1,540[4]
L. rosalia	FRU-INS	S[5]	76(382)[5]	–	100.5[5]	0[5]	858.4[5]
L. chrysomelas	FRU-INS	S[6]	40(282)[6]	80.4(282)[6]	–	22[6]	781[6]
C. apella	FRU-INS	S[7]	–	–	355[7]	–	–
C. capucinus	FRU-INS	S[8, 9], C[10]	23(48)[8] 67(?)[9]	98(48)[8]	212.5[8,9,10]	10[9]	884[9]
A. caraya	FOL-FRU	C[11]	–	–	–	0[11]	1,200[12]
A. guariba	FOL-FRU	C[13]	14(28)[13]	54(28)[13]	–	–	–
A. palliata	FOL-FRU	C[8]	–	–	111.5[14]	10[14]	811.2[14]
A. pigra	FOL-FRU	–	–	–	126[15]	7[15]	439[15]
A. seniculus	FOL-FRU	C[16,2]	9(?)[2]	–	238.5[2,16,20]	0[16]	637[2]
B. arachnoides	FOL-FRU	S[17], I[18]	18(27)[18]	79[18]	–	169[17]	693[17]
Saguinus spp.	INS-FRU	S[20]	155[20]	95(>1000)[20]	239[19]	9.5[19]	656[19]

FRU, Frugivore; FRU-INS, Frugivore-Insectivore; FOL-FRU, Folivore-Frugivore; INS-FRU, Insectivore-Frugivore (classification based upon Norconk, Wright, Conklin-Brittain, & Vinyard, 2009); C, Clumped; S, Scattered; I, Intermediary N, number of fecal depositions sampled; ?, unknown Superscript numbers relate to source (last column).

*S. mystax and S. fuscicollis

Sources: 1, Link and DiFiore (2006); 2, Yumoto et al. (1999); 3, Stevenson (2000); 4, González and Stevenson (2014); 5, Lapenta and Procopio-Oliveira (2008); 6, Cardoso et al. (2011); 7, Wehncke and Dominguez (2007); 8, Wehncke et al. (2004); 9, Wehncke et al. (2003); 10, Valenta et al. (2015); 11, Bravo (2009); 12, Bravo and Zunino (2000); 13, Martins (2006); 14, Estrada and Coates-Estrada (1984); 15, Zárate et al. (2014); 16, Juliot (1996); 17, Bueno et al. (2013); 18, Martins (2006); 19, Heymann et al. (2012); 20, Giraldo et al. (2007); 21, Knogge and Heymann (2003). Complete reference of sources can be found in Electronic supplementary material S1, except for 21, which is not a seed dispersal piece, but complete citation can be found in the references.

distances obtained individually for each species found in feces. In order to compare results among different studies and as a simple measure of the seed shadow, we calculated a single weighted average distance across all plant species used by a primate species in a given site. We used phylogenetically-adjusted regressions from nlme R package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) to evaluate the effects of several independent variables on per-population average SDD. Data was available for 12 primate populations, from nine species. As a proxy of how long the seeds are retained in the disperser's gut we used gut TT, in hours. Average disperser movement rate (MR) was calculated as the daily path length (in meters) divided by 12 hr (the average amount of time an individual remains active during the day for most species). The linearity of the movement, or path twisting (PT), was estimated by the size of the the squared daily path length (in meters) relative to the home range (in m^2). We also included in our model forest fragment size (in hectars), primate body mass (in grams), and feeding guild. Feeding guild was included as indexed using the coefficient of gut differentiation (Chivers & Hladik, 1980). Body mass and home range size have been suggested to be important predictors of SDD in other studies (Culot, Muñoz Lazo, Poncin, Huynen, & Heymann, 2010; Oliveira & Ferrari, 2000). We determined the best-fit model by Akaike model selection using AICcmodavg (Mazerolle, 2016) and additional R packages for data manipulation and inspection: ape (Paradis, Claude, & Strimmer, 2004) and psych (Revelle, 2016). For detailed information, see electronic supplementary material S3.

After understanding how TT and movement patterns, estimated via MR and PT, directly affect SDD, we also explored possible indirect effects by other variables. To disentangle how several primate traits affect average dispersal distance both directly and indirectly, we performed a Partial Least Squares Path Modeling (PLS-PM) using plspm R package. Because the distance traveled by a primate depends on body mass (Stevenson et al., 2014), and that TT of the food in the gut depends on gut complexity (which is also determined by body mass) (Chivers & Hladik, 1980), and because home range area may be limited by the size of the forest fragment, we built a PLS model that included all these variables. Thus, as primate traits we included: home range area (in ha), daily path length (in m), TT (in hr), gut complexity (coefficient of gut differentiation), and body size (mass, in g). We tested each direct and indirect path for its strength and significance. All analyses were performed using R v. 3.2.5 (R Core Team, 2016).

Our research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

3 | RESULTS

In our database of studies, primates dispersed up to 112 plant species, with individual average dispersal distance per plant species ranging from 0 to 1,540 m. From about 50% up to 99% of the fecal samples contained intact seeds, varying among primate species as well as deposition

TABLE 2 Percentage of seeds dispersed by Neotropical primates in each category of distance from parent plant, divided according to distinct seed-survival risk factors. In some studies, data were reported only for the category 0–50 m, as shown

	Feeding guild	0–10 m (%) close to parent		10–50 m (%) density competition	50–100 m (%) escape from DC	>100 m (%) other habitats[a]	Source
A. guariba	FOL-FRU		39.01		14.40	46.16	1
B. arachnoides	FOL-FRU		15.05		29.44	55.73	1
A. belzebuth	FRU		5.90		8.70	85.40	2
L. lagothricha	FRU	1.60		6.3	5.6	86.50	3
C. capucinus (BCI)	FRU-INS		5.50		7.5	87	4
C. apella nigritus	FRU-INS		2.50		5.5	92	4
C. capucinus (PV)	FRU-INS		13.0		12.5	74.5	4
C. capucinus (BCI)	FRU-INS	0.00		2.40	10.50	87.10	5
C. capucinus (PV)	FRU-INS	4.8		8.4	10.5	76.3	6
L. chrysomelas	FRU-INS	24.2		10.8	18.12	46.88	7
L. rosalia	FRU-INS	5.80		26.20	28.00	40.00	8
S. fuscicollis, *S. mystax*	INS-FRU		20.28		11.61	68.11	9

PV, Palo Verde population; BCI, Barro Colorado Island population.

aThe four SDD categories were defined based on data available in the studies used as source. Many attest >100 m as likely to increase in chances to colonize other habitats.

1, Martins (2006); 2, Link and DiFiore (2006); 3, Stevenson, personal communication; 4, Wehncke et al. (2007); 5, Wehncke et al. (2003); 6, Valenta and Fedigan (2010); 7, Cardoso et al. (2011); 8, Lapenta and Procopio-Oliveira (2008); 9, Heymann et al. (2012). Complete reference of sources can be found in See electronic supplementary material S1.

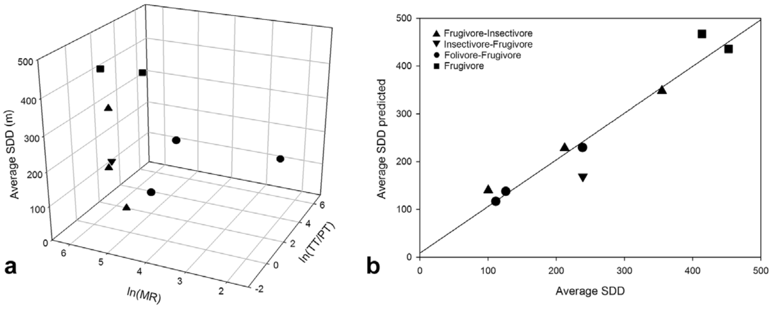

FIGURE 1 (a) 3D plot showing the interaction between those variables that explained most of the variation in per-study average seed dispersal distance. For illustration, we used a composite variable $z = ln(TT/PT)$. TT and PT had similar slopes in the analysis with opposite signs, as shown in Eq. 1. The axes were transformed into natural log, except for the average SDD. (b) Interaction between average seed dispersal distance (SDD) observed in the studies and average seed dispersal distance predicted by the model according to the Eq. 1: $-1183.81 + 93.08[\ln(\mathrm{TT})] + 287.15[\ln(\mathrm{MR})] - 90.05[\ln(\mathrm{PT})]$. Symbols represent each case of study: as a phylogenetically-adjusted analysis, each case of study represents each primate species. MR, movement rate; PT, path twisting; TT, transit time; SDD, seed dispersal distance

patterns, which were classified as clumped or scattered (Table 1). Most primates carried the majority of seeds to distances greater than 100 m away from the parent, but large folivore-frugivores (*Alouatta guariba*) and small frugivore-insectivores (*Leontopithecus* spp.) dispersed seeds to shorter distances relative to the primarily frugivorous species (*Ateles belzebuth* and *Lagothrix lagothricha*) (Table 2).

Our model including TT, MR, and PT explained 90% of the variation in per-population average dispersal distance ($R^2 = 0.895$, $p = 0.002$) (Figure 1, Eq. 1), and it was selected as the best-fit model ($\mathrm{AICc}_{(WT)} = 1.00$) (see electronic supplementary material S4). No other variable (body mass, gut complexity or habitat fragment size) was statistically significant when added to the previous three basic predictors. In addition, body mass and gut complexity were both significantly correlated with TT (Pearson correlation level = 0.80 and 0.86; $p = 0.0001$ and $p < 0.00001$, respectively). Therefore, we obtained the following regression equation to describe the average SDD:

$$\mathrm{SDD} = -1183.81 + 93.08[\ln(\mathrm{TT})] + 287.15[\ln(\mathrm{MR})] - 90.05[\ln(\mathrm{PT})] \tag{1}$$

Consistent with the previous analysis, path modeling indicated strong, direct, and positive effects of TT, daily path, and home range on average dispersal distance. Fragment size affected average dispersal distance only through its effect on the home range, which also had a significant effect on daily path. Body size did not affect SDD directly. It did so by affecting CGD, which, in turn had a strong effect on TT (Figure 2, and see electronic supplementary material S5).

4 | DISCUSSION

Although the noticeable inter-specific variation in SDD, our findings strongly suggest that, in most cases, Neotropical primates disperse seeds away from the parents, which might minimize the negative influence of natural enemies and sibling competition on seed and seedling survival (Comita et al., 2014; Schupp et al., 2010). Addressing the patterns of seed deposition under field conditions is extremely challenging and few data are available to allow cross-species comparisons. Although long-distance seed dispersal alone does not necessarily imply SDE, the information provided here combined with previous knowledge on positive effects on seed germination (Fuzessy et al., 2016) and successful seed survival and seedling establishment after defecation by some primate species (Bravo, 2012) suggest that primates play an important role on regeneration of Neotropical forests.

Our model provides an intuitive and useful method to estimate SDD in Neotropical forests, and supports the idea that temporal and spatial movement patterns combined with TT determine how far primates disperse seeds. Many studies have shown that home range and body size are good predictors of SDD by vertebrates (Bowman, 2003; Santini et al., 2013). Our results reinforce the importance of home range, but suggest that body size (mass) affects seed dispersal only indirectly through its effects on TT by influencing gut complexity. It is a more complex chain process than previously thought, in which body mass itself has no isolated influence on average dispersal distance.

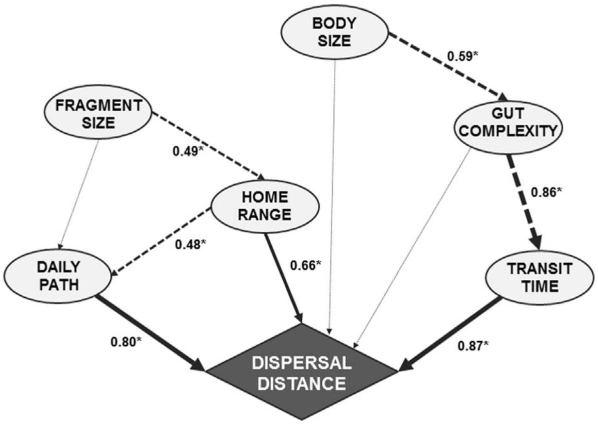

FIGURE 2 Standardized path coefficients among variables determining seed dispersal distance in nine Neotropical primate species. Direct effects are shown in solid lines, indirect effects are depicted in dashed lines and non-significant effects are shown in dotted lines. Line width is proportional to effect strength. *$p < 0.05$

The quality of the seed dispersal service varied among feeding guilds, as average SDD was higher for primarily frugivorous primates (Figure 1a,b). Primarily frugivorous primates, some of the largest in Neotropics, combine moderate gut TTs and long daily path lengths within large home ranges to produce some of the greatest average SDD. They are able to carry most seeds to far from the zone of influence of the parent crown, and maximal distances reach up to 1,540 m, the greatest reported for primates in the Neotropics.

In contrast, folivore-frugivores species of *Alouatta*, also considered large bodied primates, move great amount of the seeds to a region of likely density competition. Despite a long gut TT, howler primates have relatively short daily paths within the home range and tend to move slower than other active frugivores and insectivores primates (Milton, 1981). For instance, *A. seniculus* moves 82 m/hr at Tinigua National Park in Colombia, while *L. lagothricha* moves 137 m/hr at the same fragment (Yumoto, Kimura, & Nishimura, 1999). *A. seniculus* moves 89 m/hr at Nouragues Station in French Guiana (Julliot, 1996) while 167 m/hr was reported for *C. apella* at the same fragment (Zhang & Wang, 1995). Thus not only one isolated variable must be considered to predict average SDD, but the combination of several interacting factors.

Overall, our evidence shows that Neotropical primates, especially primarily frugivorous ones, provide a quality service in terms of SDD in Neotropical forests by moving seeds to sites where competition with parents and pressure from predators and pathogens is expected to be relaxed (Comita et al., 2014). Despite this knowledge, we still lack much detailed information about post-dispersal seed fates (but see Gonzalez-Di et al., 2011 and Bravo, 2012), which is key to fully evaluate SDE. Such combined information might allow us to assess the real role played by primates as ecosystem engineers, and ultimately the outcomes for conservation.

Finally, our model suggests that the distance a primate is able to carry seeds can readily be predicted by variables potentially assessed without intensive field work and can be applied to populations that are hard to habituate or are under threat. Primates are key forest seed dispersers that are globally threatened by human activities (Estrada et al., 2017). The consequences of hunting and habitat fragmentation include truncated dispersal kernels, loss of long-distance dispersal events, and changes in density-dependent mortality and successful plant recruitment, all of which may alter forest dynamics (Jordano et al., 2011). The ability to estimate ecological services provided by primates from simple behavioral and physiological variables provides a useful tool to prioritize tropical conservation efforts.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Ateles hybridus, frugivore Neotropical primate.
Illustration: Stephen D. Nash

CAPÍTULO 4:

How do primates affect seed germination? A meta-analysis of gut passage effects on Neotropical plants

Meta-analyses

Editor's Choice OIKOS

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How do primates affect seed germination? A meta-analysis of gut passage effects on neotropical plants

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Biotic seed dispersal is a key process maintaining biodiversity in tropical forests where most trees produce vertebrate-dispersed seeds. Existing meta-analyses suggest an overall positive effect of vertebrate gut passage on seed germination, but no significant effects for non-flying mammals. However, previous meta-analyses combined rodents (seed predators) and primates (seed dispersers) into the non-flying mammals category, which may confound specific effects of each group on seed germination. However positive effects of monkeys on germination had previously been found in some studies. Here we disentangle the role of Neotropical primates as contributors to seed dispersal in tropical forests by running a meta-analysis to determine the overall magnitude of gut passage effects on seed germination percentage and mean time to germination. We also compare effect sizes as a function of different feeding guilds, gut complexities, and seed size. Our results show a strong, positive effect of primates on seed germination percentage and on the number of days to first germination. Strictly frugivorous monkeys, the group most threatened by extinction, showed the highest dispersal quality, increasing germination percentage by 75%. Primates that include insects in their diets had no average effect on germination percentage or time. Gut passage had different outcomes on seeds with different sizes; both large and small seeds showed similar increases in germination percentages after gut passage, but only large seeds germinated faster than control seeds after gut passage. Our results show a relevant role for primates in providing high seed dispersal quality and as drivers of forest regeneration. The combined effects of defaunation and forest fragmentation may result in decreased regeneration of trees, which has the potential to affect negatively both forest structure and ecosystem processes. Finally, we provide general guidelines for standardizing research on seed dispersal by primates.

Synthesis

Consuming fleshy fruits and dispersing seeds is the main ecological service provided by vertebrates to plants. Vertebrate increases seed germination due to treatment given during digestive system passage. Previous meta-analyses suggest an overall positive effect of vertebrate gut passage on germination, but no insights are available on its variation among different functional groups of mammals. Our analyses indicated that gut passage by Neotropical primates increased seed germination. Strict frugivores, the ones most threatened by extinction, were the most efficient. Our results show a relevant role for primates in providing high seed dispersal quality and as drivers of forest regeneration, which can be meaningful for conservation in a community scale.

The mutualism between fleshy fruits and fruit-eating vertebrates promotes several ecological consequences. Consumption of fleshy fruits and subsequent seed dispersal is a key process in plant ecology. One of the most important outcomes of vertebrate seed dispersal is seed transportation away from parent plants (Primack and Miao 1992, Herrera 2002, Howe and Miriti 2004). This process can reduce competition between related individuals, enhance gene flow, and increase the chances of diaspores reaching and colonizing microsites where conditions are favorable for seedling establishment (Schupp et al. 2010).

In addition to transporting seeds, vertebrates may affect seed germination by the treatment given to the seeds during passage through the digestive system. Given that most trees from tropical forests are dispersed by vertebrates (Howe and Smallwood 1982), understanding the effects of gut passage on germination is a vital step to predict how plant demography and regeneration will respond to increasing forest fragmentation and defaunation (Wang and Smith 2002).

Primates play a major role in forest dynamics and regeneration; they are typically the largest arboreal frugivores in tropical forests and constitute 25–40% of the entire frugivore biomass in tropical forests (Haugaasen and Peres 2005, Fleming and Kress 2011). Primates can spread thousands or even millions of seeds per hectare per year (Martins 2006, Stevenson 2007, Chaves et al. 2011). They possess a wide variety of feeding behaviors, body sizes, feeding guilds, home ranges sizes and ways of handling fruit, thereby creating different seed shadows, dispersal kernels and effects on seed germination (Julliot 1996, Stevenson et al. 2002, Righini et al. 2004, Martins 2006, Bravo 2009).

Depending upon the predominant food in their diet, primates can be classified into three categories of dietary adaptation, here called feeding guilds: insectivore, frugivore and folivore, with appropriate subcategories between them (Hladik 1978, Chivers and Hladik 1980). These categories represent a gradation between a diet based on items relatively difficult to collect but easy to digest (insects), through those for which availability is limited by seasonality (fruits), to those that are widely abundant but hard to digest (leaves). As might be expected, body size and gut morphology are strongly related to those feeding strategies (Kay 1984). The coefficient of gut differentiation (CGD) provides a quantitative index of the relative gut complexity: values are low in insectivores, intermediate in frugivores and high in folivores, suggesting that CGD reflects different degrees of adaptation to distinct dietary challenges (Chivers and Hladik 1980).

Primate body size and gut morphology also affect locomotion, use of space and home ranges, which can contribute to their effectiveness as seed dispersers. In primates, body size is negatively related to consumption/predation of other animals, so smaller bodied primates consume large amount of animals, while larger bodied primates consume relatively few prey and a large amount of fruits (Ford and Davis 1992). Fruit intake can reach up to 86%, in *Ateles* (Norconk et al. 2009), one of the largest frugivores in Neotropical forests and most effective seed dispersers in fragmented areas (Chaves et al. 2011).

Several studies that evaluate how loss of large dispersal agents can change forest dynamics at the community level have shown their importance in maintaining tree recruitment, seedling regeneration and plant diversity (Dirzo and Miranda 1991, 2005, Ganzhorn et al. 1999, Dirzo et al. 2007a, Nunez-Iturri et al. 2008). Large-bodied animals with large home ranges often play key roles in connecting ecosystems and in energy transfer (McCauley et al. 2012). In particular, large mammals and birds can remove larger amounts of seeds, are able to disperse larger seeds, and often move these for longer distances than smaller frugivores (Wotton and Kelly 2012).

Several studies have demonstrated an important role for primate-mediated seed dispersal in plant community ecology. A study performed in Mexico suggests that terrestrial mammals maintain tree diversity through suppression of competitively superior species, which become dominant if hunting eliminates the mammals (Dirzo and Miranda 1991). Likewise, hunting seems to alter dynamics of seedling regeneration by accentuating seed-recruitment limitation among large seeded primate-dispersed trees in Peru (Nunez-Iturri et al. 2008). The presence of the largest lemur species in dry deciduous forests in Madagascar is essential to regenerate trees that depend upon it for seed dispersal (Ganzhorn et al. 1999). How seed passage through primate guts affects seed germination is still not well documented in general. A broad-scale meta-analysis by Traveset and Verdú (2002) showed that the effect of gut treatment by all frugivores is overall positive for both seed germination percentage and speed of germination. These authors compared effect sizes among taxonomic groups and found that birds and bats exhibited positive effects on the percentage of seed germination, whereas non-flying mammals had little effect. However, the category 'non-flying mammals' mixed taxonomically unrelated species such as primates and rodents, and the small overall effect found by Traveset and Verdú (2002) for non-flying mammals could be a result of combining both positive and negative effects from different taxonomic groups. Here, we focus on the role of primates as primary seed dispersers in tropical forests by running a focused meta-analysis for their gut treatment on seed germination of Neotropical trees. Through meta-analysis it is possible to provide insights into the magnitude of these effects and to compare variables that are otherwise impossible to compare in individual studies. Frugivorous primates and fleshy-fruits have a long co-evolutionary history (Fleming and Kress 2011), and it is surprising that no quantitative assessment of primate effects on seed germination has been published to date. Given the increasing disruptions of seed dispersal processes in the Anthropocene (Farwig and Berens 2012), determining how primate gut passage affects germination is urgently needed to implement effective conservation and management strategies.

Our goal in this study was to understand how seed passage through Neotropical primate guts affected germination of forest trees. We focus on Neotropical systems because primates from the Paleotropics and primates from the Neotropics are quite different in terms of body size, diet, ranging patterns, in oral and digestive morphology, and play distinctive roles as seed dispersers (Lambert and Garber 1998). We used meta-analytical methods (Hillebrand and Gurevitch 2014) to first determine the overall magnitude of the effect of primate gut passage on the percentage and speed of germination. We then compared the magnitude of those effects: 1) among the different feeding guilds (frugivores, folivore–frugivores, frugivore–insectivores and insectivore–frugivores); 2) as a function of different complexities of guts (as measured by the coefficient of gut differentiation, CGD); 3) in relationship to different seed sizes; and 4) across different germination test methods (field, greenhouse and laboratory). The predicted patterns for each variable are summarized in Table 1.

Material and methods

Database

This meta-analytical review was based upon published studies on seed dispersal by Neotropical primates. We searched electronically for the following terms within the title, abstract and keywords of papers incorporated into the Web of Science and Google Scholar databases (1945–2014): primate seed dispersal, primate gut passage, primate seed germination, monkey seed dispersal and primate seed fate. The literature list was supplemented with studies cited in the reference lists of the articles surveyed. Studies were included regardless of the language of publication.

To be included in our review, a study must: 1) have been published in peer-reviewed journals, 2) have reported data as germination proportion or percentages, 3) have reported a measure of speed of germination (time to germination,

Table 1. Predicted patterns for variables affecting the magnitude of primate gut passage effects on seed germination percentage and time of forest trees.

Variable	Expected pattern	Explanation
Primate feeding guild	FR > FF > FI > IF*	Frugivores are expected to be more co-evolved with plant and thus provide more favorable treatment of seeds. Their tracts are better suited to this kind of food than folivorous – more complex gut – or insectivorous – simpler gut (Chivers and Hladik 1980, Traveset 1998)
Gut differentiation	Negative slope	The longer the seeds are retained, as a consequence of higher CGD values, the more they are abraded in the gut and thus the lower the germination (Janzen et al. 1985, Murphy et al. 1993).
Seed size	Positive slope	Smaller seeds are more prone to damage in the gut and should show lower germination success (Verdú and Traveset 2004)
Germination methods	Field = greenhouse = laboratory	No a priori effects of treatment were expected (Hillebrand and Gurevitch 2014)

which we converted to days), and 4) have described clearly the context of the experiment (laboratory, greenhouse or in the field). The list of studies that conformed to these criteria is available in Supplementary material Appendix 1.

In some cases we could not determine the actual sample size (the exact number of seeds set to germinate in each replicate), so we used instead the values given for total seed sample size. We excluded studies for which data on germination percentage or germination time was not available for both treatment and control groups. When data were available in figures, we digitized them and extracted the data using the software UTHSCSA Image Tool (University of Texas, USA) after calibrating each picture to the nearest 0.01 mm.

We conducted separate meta-analyses for each of three aspects of germination performance (Traveset et al. 2007): percentage germination for all seeds in a treatment, days until the first seed germinate in each treatment, and average days until germination for all seeds in a treatment. Studies reported slightly different measures of average days to germination: 1) the average of days to germinate for all seeds that germinated in a given treatment; 2) the number of days until 50% of the seeds in a treatment had germinated, and 3) latency of germination, defined as the number of one-week intervals between sowing and emergence of the radicle (in this case we converted weeks to days). Although the term latency usually refers to seed dormancy, we chose to use the former to keep the original terminology by the authors.

We classified the primates according to feeding guilds based upon Norconk et al. (2009). We labeled primate diet specializations using the following criteria: the first label corresponds to the food type constituting 45% or more of the diet, while the second label (if present) relates to the food type comprising 20–45% of the diet (Chivers and Hladik 1980). By these criteria, Neotropical primates were divided into four dietary categories: frugivores, frugivore–folivores, frugivore–insectivores, insectivore–frugivores. To determine how the size (or complexity) of the gut influences germination percentage and time, we made comparisons according to primate CGD (coefficient of gut differentiation). This index is calculated using gastrointestinal sizes (fractional allocation by surface area among the stomach, caecum and colon, relative to the surface area of small intestine) and expressed as gut complexity (Chivers and Hladik 1980). Data were obtained from Chivers and Hladik (1980) and Hartwig et al. (2011). When CGD was not available for a species, we used the genus average assuming conserved trait evolution (Kamilar and Cooper 2013).

To evaluate how seeds of different sizes respond to the effects of primate gut passage we compared germination effects across groups of plant species according to seed size, as assessed by dry mass. Most data on seed mass came from the Royal Botanic Gardens Kew's Seed Information Database (2014, <www.rbgkew.org.uk/data/sid/>) and additional data were collected opportunistically from the published literature (Lorenzi 1998, Galetti et al. 2011). When data on seed size were not available, we used the average of available data for other congeneric species, given that seed size is a conservative trait in plant phylogeny (Moles et al. 2005a). Then we built a frequency distribution of seed sizes in our sample. We log-transformed data to achieve a roughly normal distribution and ascertained that our data were best fit by a mixture of two normal distributions (JMP 11.0, SAS Inst.), so we categorized seed size classes within two groups according to the two curves: seeds weighing less than or equal to 0.031 g were considered small and seeds weighing more than or equal to 0.031 g were considered large (Supplementary material Appendix 2). Finally, to evaluate if studies conducted in the field differed from those conducted in the lab or greenhouse, we made comparisons between these two variables. Plant species classification and nomenclature followed APG III (2009).

Data analyses

We used the response ratio to summarize the effects of passage through primate guts on seed germination. Because most of the data gathered for this meta-analysis lacked information to compute standard errors of individual effect size estimates, an unweighted resampling method was used (Hedges et al. 1999). Ninety-five percent confidence limits around the effect size were calculated and estimates of the effect sizes were considered significant if the bootstrap confidence intervals did not overlap zero (Hedges et al. 1999).

The response ratio is the ratio of some measured quantity in experimental versus control groups and is commonly used as measure of experimental effects because it quantifies the proportionate change that results from experimental manipulation (Hedges et al. 1999). We calculated the natural log of the response ratio for each effect studied (Hedges et al. 1999) as:

$$\mathrm{Lr} = \ln(\bar{X}\mathit{feces}) - \ln(\bar{X}\mathit{control})$$

Effects are reported as the proportional change from control groups (i.e. seeds manually removed from fruits). Negative percentage changes indicate a decrease in seed germination and/or germination times of ingested seeds compared to control groups and positive values indicate an increase in the effect measured due to passage through primate gut (Rosenberg et al. 2000). To estimate the cumulative effect size (E++) for a sample of studies addressing the same effect, effect sizes were combined across studies using an unweighted randomization test (Rosenberg et al. 2000). All analyses were conducted using MetaWin ver. 2.1.3.4 (Rosenberg et al. 2000).

With meta-analysis, one can also partition variance within groups and evaluate whether categorical groups (e.g. feeding guilds) are homogeneous or not with respect to effect sizes using heterogeneity analysis (Q) (Gurevitch and Hedges 1999). We calculated the total heterogeneity (QT), heterogeneity within (QW), and between groups (QB), and we used a χ^2-distribution to evaluate the significance of Q. For each effect tested, we also calculated fail-safe numbers, which indicate how many non-significant, unpublished, or missing studies would need to be added to the sample to change its results from significant to non-significant (Rosenberg et al. 2000). Our analyses were based only on published studies, and studies that show large and significant effects might be more likely to be published than studies that show weak or no effects (the 'file-drawer problem' sensu Rosenthal 1979). As a rule, results are considered robust if the fail-safe number exceeds $5n + 10$, where n is the number of comparisons (Møller and Jennions 2001). In order to assess publication bias we used funnel plots (Supplementary material Appendix 3) as a graphical method, where a symmetrical 'funnel' shape is formed in the absence of bias when the effect size of each study is plotted against sample size.

Results

Qualitative results

Our search revealed 75 studies on seed dispersal by Neotropical primates. Amongst these, only 19 studies addressed the effect of primate gut passage on seed germination and met our criteria for inclusion in our meta-analysis. The frequency of publication of these studies by journal was: Biotropica (5 studies), International Journal of Primatology (4), American Journal of Primatology (2) and the remaining journals with only one study.

These 19 studies generated 460 distinct comparisons: 240 for germination proportion, 180 for germination times and 40 for days until first seed germination. These studies covered a wide variety of Neotropical primate and plant taxa, including 13 of the most important seed dispersers (*Alouatta caraya*, *Alouatta palliata*, *Alouatta pigra*, *Alouatta seniculus*, *Ateles belzebuth*, *Ateles geoffroyi*, *Brachyteles arachnoides*, *Cebus capucinus*, *Lagothrix lagotricha*, *Leontopithecus chrysomelas*, *Leontopithecus rosalia*, *Saguinus fuscicollis* and *Saguinus mystax*) and 156 plant species in 48 families. The most species with germination data was in the family Moraceae (18 spp.), followed by Myrtaceae (14 spp.) and Urticaceae (14 spp.), Fabaceae (11 spp.), Melastomataceae and Rubiaceae (both with 10 spp.) and Sapotaceae (9 spp.). Other families were represented by five or fewer plant species.

Studies conducted in the field or in the lab generated almost the same number of independent comparisons: 43.7% were conducted in the field and 42.1% were conducted in lab. Experiments carried out in the field used pots or plastic bags with natural forest soil as the substrate, placed in forest environment, or used seeds sown directly on the forest floor. Experiments in the lab were placed on petri dishes under controlled conditions. In addition, 11.3% of the comparisons came from studies conducted in a greenhouse (under shading and controlled humidity) and 2.83% (one study) did not specify where samples were placed. Most of the controls were undispersed seeds manually removed from fruits found under the crowns of the parental plants or picked directly from the trees.

Of the 14 studies that reported germination time, the particular measure varied between studies. Of the 180 distinct comparisons for germination time, 30.55% (55 comparisons, in six studies) used "time to reach 50% germination" as the germination time measure; 28.33% (51 comparisons in one study) considered the latency of germination as "number of one-week intervals between sowing and emergence of the radicle"; 21.11% (38 comparisons in four studies) used the average time of germination (or average number of days to germination) as a measure of time and, finally, 20% (36 comparisons in three studies) did not define and/or specify the germination time measure.

Quantitative results

We observed significant and positive effects of passage through a primate's gut on seed germination percentage and on the number of days to first germination. Seeds ingested and defecated by primates germinated 33% more than seeds removed from intact fruits (E++ = 0.33, bootstrap CI = 0.2181 to 0.4542). The first day to germination was 19% earlier for ingested seeds compared to control seeds (E++ = –0.19, CI = –0.3164 to –0.0818). Nevertheless, we found no overall effect of gut passage on germination time (E++ = –0.008, bootstrap CI = –0.1645 to 0.0070) (Fig. 1).

When grouped by feeding guild, strictly frugivorous primates increased germination percentage over two-fold compared to the others guilds ($Q_B = 86.33$, $p \leq 0.001$) (Fig. 2).

Seed germination increased by 75% after gut passage for strict frugivores (E++ = 0.75, bootstrap CI = 0.5291 to 0.9832) versus 34% for folivore–frugivores (E++ = 0.34, bootstrap CI = 0.1200 to 0.5960). In contrast, seed passage through frugivore–insectivores and insectivore–frugivores primates did not affect seed germination percentage (E++ = 0.13, bootstrap CI = –0.0302 to 0.3071; E++ = –0.06, bootstrap CI = –0.3117 to 0.2301, respectively).

Germination time also varied by primate feeding guild. Passage through the gut of folivore–frugivores was associated with a reduction of 27% in germination time (E++ = –0.27, bootstrap CI = –0.3809 to –0.1848), whereas ingestion by frugivores and frugivore-insectivores had no effect on germination time (E++ = –0.11, bootstrap CI = –0.2116 to 0.0059; E++ = –0.13, bootstrap CI = –0.3027 to 0.0161,

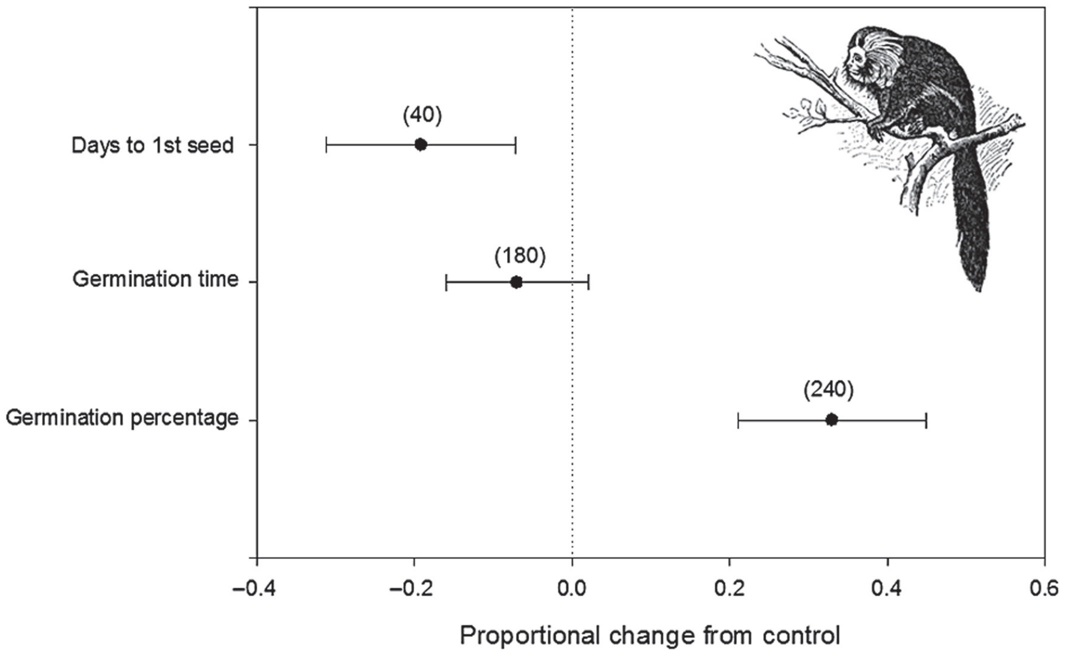

Figure 1. Effect of passage through primate gut on days to first seed germination, average germination time and germination percentage. The cumulative effect size is reported with its 95% confidence interval. Numbers in parentheses indicate the number of independent comparisons for each effect; effects are significant if the confidence intervals do not overlap zero.

respectively). In fact, insectivore–frugivores increased germination time by 18% (E++ = 0.18, bootstrap CI = 0.0095 to 0.3463) and the difference amongst all feeding guilds was statistically significant ($Q_B = 40.06$, $p \leq 0.001$). The number of days to germination of the first seed was 31% lower after ingestion by folivore–frugivores (E++ = –0.31, bootstrap CI = –0.5069 to –0.1606), while passage through the guts of frugivore–insectivores had no effect on this variable (E++ = –0.13, bootstrap CI = –0.2868 to 0.0057). Due to small numbers of available comparisons, we could not evaluate the effects of either frugivore or insective–frugivores ingestion on the number of days to germination of the first seed.

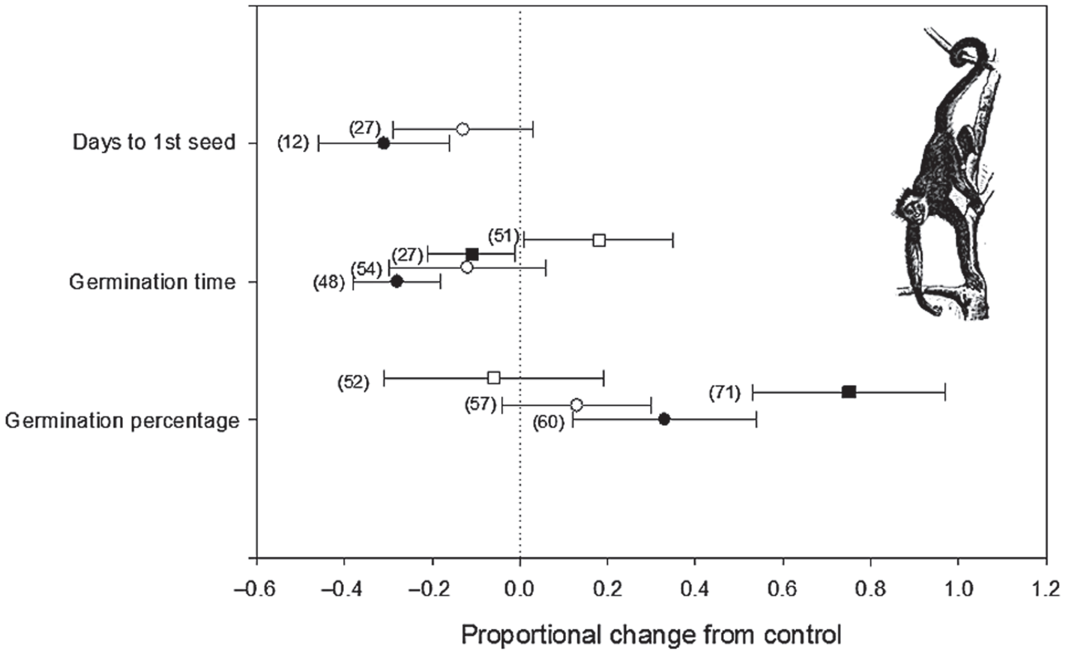

Figure 2. Effect of passage through primate gut on days to first seed germination, average germination time and germination percentage according to primate feeding guild (filled circle: folivore–frugivore; empty circle: frugivore–insectivore; filled square: frugivore; empty square: insectivore–frugivore). The cumulative effect size is reported with its 95% confidence interval. Numbers in parentheses indicate the number of independent comparisons for each effect; effects are significant if the confidence intervals do not overlap zero.

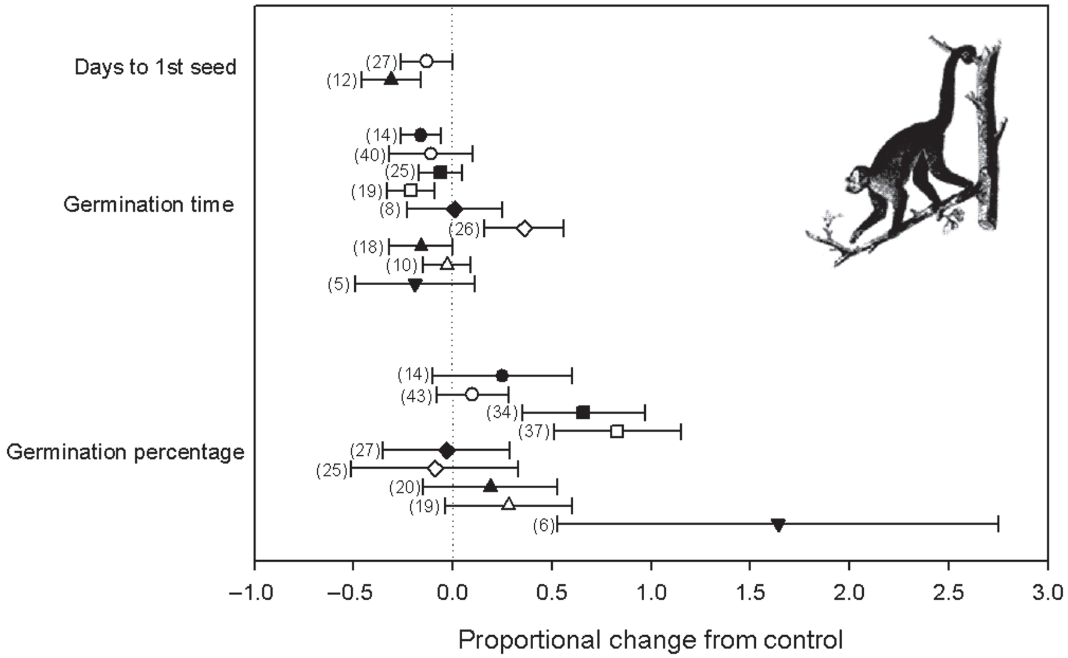

Figure 3. Effect of passage through primate gut on days to first seed germination, average germination time and germination percentage according to primate coefficient of gut differentiation (filled circle: CGD = 0.31; empty circle: CGD = 0.43; filled square: CGD = 0.59; empty square: CGD = 0.60; filled diamond: CGD = 0.89; empty diamond: CGD = 0.99; filled triangle: CGD = 1.39; empty triangle: CGD = 1.495; filled inverted triangle: CGD = 1.6). The cumulative effect size is reported with its 95% confidence interval. Numbers in parentheses indicate the number of independent comparisons for each effect; effects are significant if the confidence intervals do not overlap zero.

Primates with intermediate CGD showed a relative increase in seed germination percentage compared to those with very small and/or very large CGD (excluding CGD = 1.64, which had only 6 independent comparisons) ($Q_{\mathrm{B}} = 134.9$, $p \leq 0.001$): primates with CGD values of 0.59 increase germination percentage by 66% (E++ = 0.66, bootstrap CI = 0.35 a 0.97) and primates with CGD values of 0.60 increase germination percentage by 83% (E++ = 0.83, bootstrap CI = 0.51 a 1.15) (Fig. 3).

Both small and large seeds germinated faster when passed through primate guts (E++ = 0.36, bootstrap CI = 0.0663 to 0.6478 and E++ = 0.33, bootstrap CI = 0.2115 to 0.4570, respectively), but the difference between seed size classes was not statistically significant ($Q_{\mathrm{B}} = 0.1315$, $p = 0.842$). Seed size had no influence on germination time (small seeds: E++ = –0.04, bootstrap CI = –0.2209 to 0.1033; large seeds: E++ = –0.09, bootstrap CI = –0.1819 to 0.0012) and the difference between seed sizes was not significant ($Q_{\mathrm{B}} = 0.65$, $p = 0.60$). However, large seeds had 24% shorter times to first germination when passed through a primate's gut (E++ = –0.2362, bootstrap CI = –0.3901 to –0.1092), whereas small seeds did not differ from control (E++ = –0.1351, bootstrap CI = –0.3283 to 0.0460); the differences between the seed sizes were not significant ($Q_{\mathrm{B}} = 2.83$, $p = 0.41$) (Fig. 4).

We observed statistical differences amongst studies conducted in the field, lab and greenhouse with respect to germination percentage ($Q_{\mathrm{B}} = 21.95$, $p = 0.048$) and germination time ($Q_{\mathrm{B}} = 15.92$, $p = 0.02$). For studies conducted under lab conditions, seeds found in feces germinated 42% more and 20% faster than seeds removed from fruits (E++ = 0.42, bootstrap CI = 0.2514 to 0.6109; E++ = –0.20, bootstrap CI = –0.3252 to –0.0742, respectively). For studies conducted in greenhouses, seeds found in feces germinated 59% more than seeds removed from fruits (E++ = 0.59, bootstrap CI = 0.2670 to 0.9589) but germination time was not affected by gut passage (E++ = 0.05, bootstrap CI = –0.1559 to 0.0583). Finally, experiments conducted in the field showed no significant difference between seeds found in feces or removed from fruits both for germination percentage (E++ = 0.14, bootstrap CI = –0.0477 to 0.3418) and germination time (E++ = 0.04, bootstrap CI = –0.0702 to 0.1689) (Fig. 5).

Assessment of publication bias

Fail-safe numbers for effects of primate gut passage on seed germination percentage (9521 studies) and days to first germination (503 studies) were large relative to the number of independent comparisons included in the meta-analysis (240 studies and 40 studies, respectively), indicating the strength of our results. In contrast, the fail-safe number for effects of primate gut passage on seed germination time (276 studies) was small relative to the number of independent comparisons (180 studies), indicating some weakness on these results. Scatter plots of effects size against sample size of all data exhibited a typical funnel shape (Supplementary material Appendix 3), indicating that studies with small sample sizes show a large dispersion of effect sizes around the true effect, whereas those with large sample sizes have an effect size close to the true value. Our results suggest that there was little publication bias in the studies here included.

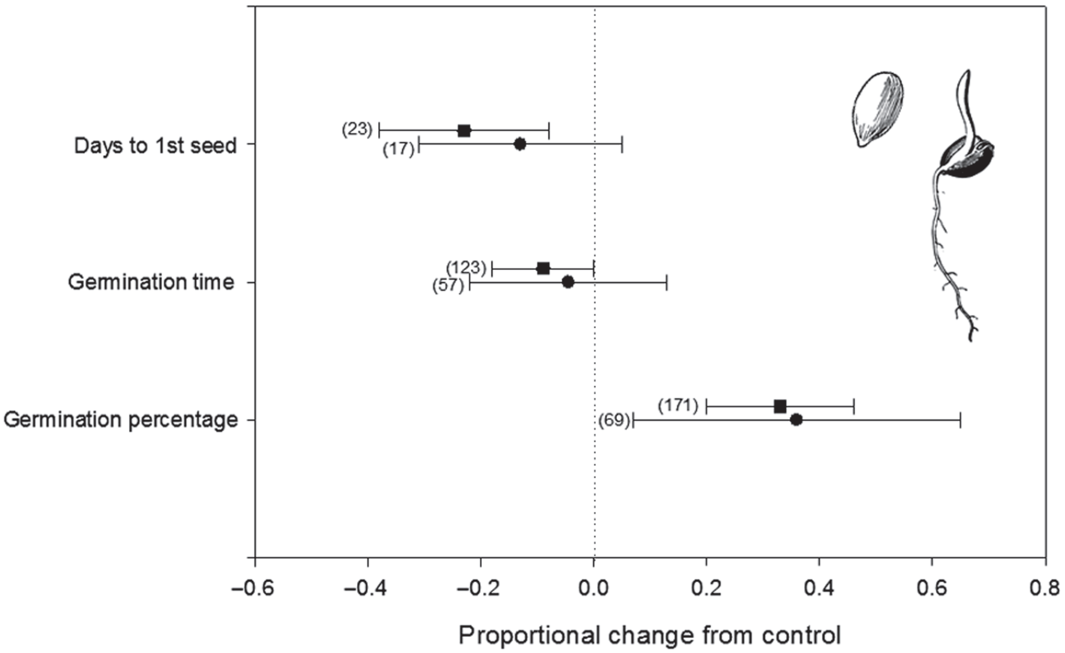

Figure 4. Effect of passage through primate gut on days to first seed germination, average germination time and germination percentage according to seed size (filled circle: small seeds; filled square: large seeds). The cumulative effect size is reported with its 95% confidence interval. Numbers in parentheses indicate the number of independent comparisons for each effect; effects are significant if the confidence intervals do not overlap zero.

Discussion

How do primates affect seed germinability?

This meta-analysis highlights the key role played by Neotropical primates on seed germination of forest trees. We show a previously unrecognized positive effect of gut passage in increasing seed germination by 33% and decreasing germination time by nearly 20%, suggesting they may play a major role in forest structure, dynamics and ecosystem services.

Although positive effects of monkey ingestion on seed germination had previously been shown in individual studies,

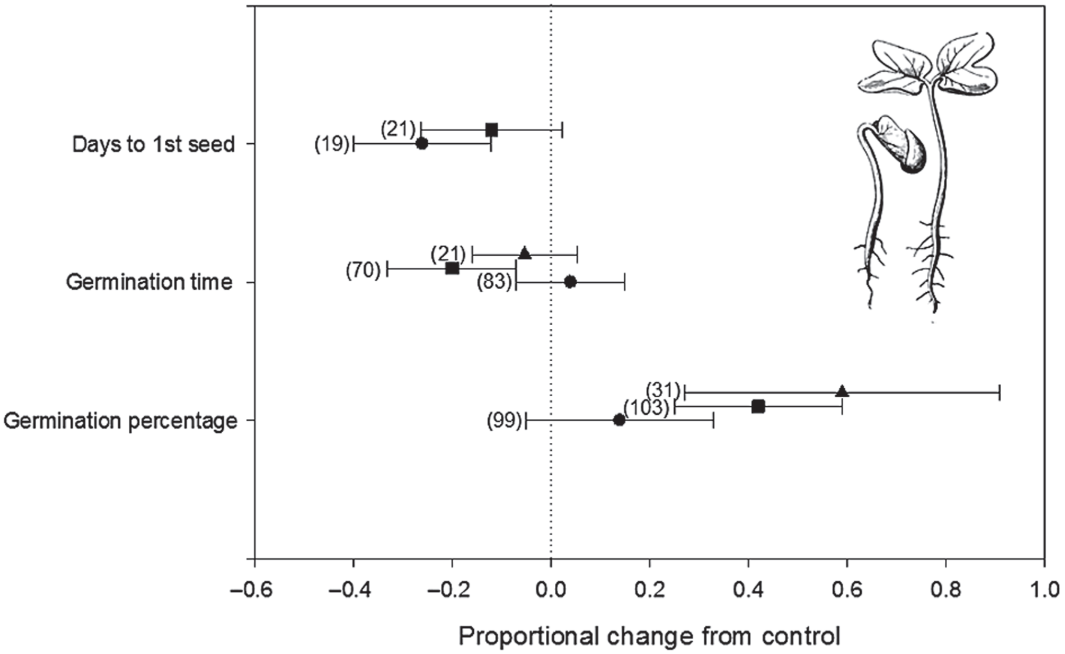

Figure 5. Effect of passage through primate gut on days to first seed germination, average germination time and germination percentage according to experimental conditions (filled circles: field; filled square: lab; filled triangle: greenhouse). The cumulative effect size is reported with its 95% confidence interval. Numbers in parentheses indicate the number of independent comparisons for each effect; effects are significant if the confidence intervals do not overlap zero.

our meta-analysis demonstrates the generality of the effect, estimates its overall magnitude, and compares variables not evaluated before.

How passage through vertebrate gut affects germinability was previously reviewed by Traveset (1998) and Traveset and Verdú (2002), who detected a general enhancement in seed germination in gut-passed seeds compared to the control. Yet, both studies concluded that there was a small or nonsignificant effect after seed passage through non-flying mammal guts: Traveset (1988) found an InOR = + 0.072, n = 113, CI ~ 0.06 to 0.09, while Traveset and Verdú (2002) showed that, in 57% of cases, seed germination rate was not significantly affected by passage through non-flying mammal guts. However, both reviews combined data from experiments performed with unrelated taxa (e.g. bears, primates and rodents) mixed together into a single group. In this case, the combined effects of distinct ecology and morphology can create misinterpretations of the real effects of gut passage on properties of seeds. Despite their recognized role as seed disperses (Jansen et al. 2012), rodents are common seed predators and often act like ecological antagonists to plants (Wenny 2000, Dirzo et al. 2007b), whereas primates are commonly considered mutualists (Chapman 1989, 1995). A meta-analysis assessing the role of rodents in seed germination would help to understand whether possible negative effects of rodents on seeds can cancel out the positive effects of monkeys when these groups are mixed. Also, in the first review, Traveset (1998) showed no effect (or minor germination enhancement) of Old World and Neotropical primates, but they were also placed together as a single group. Primates from the Paleotropics and primates from the Neotropics are influenced by distinct environmental conditions, and they are quite different in terms of ecological and morphological traits, such as food resources, body size, space use, and in oral and digestive morphology resulting in different function in seed dispersal processes (Lambert and Garber 1998). Therefore, mixing Old World and New World species into a single category may limit our ability to draw general conclusions regarding the real role of primates as seed dispersers, the effects they have on plant fitness, and the diverse ways that monkeys and fruits are ecologically and evolutionarily related.

Here we show that Neotropical primates on average accelerate the time to the germination of the first seed by 19% relative to control seeds. By promoting fast-growing seedlings, Neotropical monkeys play an important role as effective dispersers, as germination enhancement is an important component of seed dispersal effectiveness that contributes to seedling recruitment (Schupp et al. 2010). Early seedling emergence has a strong positive effect on plant fitness via both survival and growth (Verdú and Traveset 2005), which are elements negatively impacted by conspecific neighbors (Caughlin et al. 2014). Emerging early also allows seedlings to be the first to capture resources and therefore to grow faster (Arendt 1997). Consistently high temperature and soil moisture of Neotropical rainforests favor the activity of predators and pathogens (Wassie et al. 2009, Gallery et al. 2010, Myster 2015), suggesting that fast germination may have evolved as a strategy to escape predation or parasitism (Augspurger and Kelly 1984, Vazquez-Yanes and Orozco-Segovia 1993).

In our analysis, frugivorous monkeys, those whose diets comprise 80% or more of fruits, showed the highest dispersal quality – they increased seed germination by 75% compared to control seeds. Thus, the feeding guild that depends upon fruits most heavily also provides the best dispersal service in terms of treatment in the gut. This result is not a simple outcome of the intervening effects of seed size. Although strictly frugivorous primates tend to have larger body size and ingest relatively large-seeded fruits, and large seeds tended to benefit more from primate gut passage than did small seeds, frugivorous primates still provided better seed germination outcomes than did frugivore–folivores of comparable body mass. Other feeding guilds of Neotropical primates provided less dependable dispersal service. Folivore–frugivores, those who rely more heavily on leaves in their diet, but who also eat large amount of fruits, were the second-best feeding guild in terms of improving germinability: they enhanced germination percentage by 34%, reduced mean germination time by 27% and the number of days to first seed germinate by 31%. In contrast, primates that include a significant fraction of insects in the diet (frugivore–insectivores and insectivore–frugivores) provided low dispersal quality. They did not significantly affect seed germination percentage and actually delayed germination process: passage through the guts of insectivore–frugivores was associated with an 18% increase in average germination time. These data support the idea that primates with highly flexible diets result in weak selection pressure on fruit traits and thus, are not reliable dispersers (Chapman 1995).

The coefficient of gut differentiation (CGD) is a measure of digestive morphology that may impact directly the dispersal service provided by a given primate species. CGD, the ratio of stomach and large intestine to small intestine by area, weight, and volume, varies between low in insectivorous monkeys and high in folivorous monkeys (Chivers and Hladik 1980). Frugivorous monkeys lie near the middle of this continuum, with intermediate CGD values. We found that the Neotropical primates with intermediate CGDs of 0.59 and 0.60 were both the most frugivorous and most consistently enhanced germination percentage, by 66% and 83%, respectively. These highly effective seed disperses are in the Atelidae, and our results reinforce their functional role as mutualists with Neotropical trees. Neotropical primates with relatively small CGD (0.31–0.43) tended to be more insectivorous and provided little or no benefit to ingested seeds via enhanced germination. Species with relatively high CGD values (1.39–1.50) were folivore–frugivores and tended to provide some benefits via enhanced germination, but not as consistently as did the most frugivorous taxa. The generally tight connection between feeding guilds and CGD suggests that either one can be used to predict how gut passage affects seed germination.

One anomalous result of the CGD analysis deserves further exploration. The species with the largest CGD (1.60) appeared to double germination percentage, the largest average effect for any comparison in this study. However, this CGD value was associated with only six independent comparisons, and five of these came from a single study which was also one of the earliest to measure germination effects of primate gut passage (Estrada and Coates-Estrada 1984). In this study, the germination tests were very unbalanced in sample sizes: the authors used 4800 ingested seeds of *Ficus* sp. and 2334 ingested seeds of *Cecropia obtusifolia* against 200 seeds only in each respective control. In meta-analysis, the observed effect-size estimates can be conceived as having two components of variation, one associated with study-specific sampling errors (quantifying the variation that would be obtained if a given experiment were replicated, in exactly the same way, with a different sample of replicates) and another associated with between-study differences in the underlying study-specific effect-size parameters (variation of true effects) (Gurevitch and Hedges 1999). The sampling error in the first component is the deviation between the effect-size estimate obtained and the study-specific effect-size parameter, the value that would have been obtained if the within-study sample size had been so large that there was essentially no sampling error (Gurevitch and Hedges 1999). In the pioneering study of Estrada and Coates-Estrada (1984), the strongly unbalanced sample sizes between treatment and control groups might have skewed the germination comparison, generating an exaggerated measure of germination benefit from gut passage. It would be worth repeating these germination studies with a more modern experimental design (see guidelines for future research below).

Seed size and germinability after gut passage

Seed mass has substantial ecological significance representing a combined balance between the requirements for dispersal and for seedling establishment (Moles et al. 2005b). Seed size is thought to be a compromise such that wide dispersal would favor evolution of small seeds (Fenner and Thompson 2005) whereas successful establishment would favor the evolution of large seeds (Foster and Janson 1985, Jurado and Westoby 1992, Lloret et al. 1999, Kidson and Westoby 2000). Surprisingly, we found no effect of primate gut passage on different sized seeds. Both small and large seeds showed the same outcome after gut passage. Although larger seeds tend to have a shorter time until the first seed germinates (the first seed tended to germinate 24% faster) they did not differ statistically from small seeds, which showed no effect of gut passage on this measure.

Publication bias and guidelines for future research

Germination methods

Experiments conducted in field, lab and greenhouse settings were quite different concerning germination percentage and time. Studies conducted in the lab or greenhouse showed that seeds passed through primate's gut germinated more often than those removed from fruits, whereas field experiments showed no significant difference between treatments. Furthermore in the lab, seeds found in feces germinated faster than seeds removed from fruits, a result which was not observed either in the greenhouse or in the field. Our data clearly support the idea of germination enhancement following primate gut passage, but also show that increased germinability and reduced germination time do not necessarily translate into higher seedling establishment rates. The differences between controlled versus natural conditions strongly suggest that the activity of secondary seed dispersers, seed predators, seed pathogens, and variable environmental conditions are also key determinants of seedling establishment in primate-dispersed forest trees (Balcomb and Chapman 2003, Andresen and Levey 2004, Thompson et al. 2010, Dalling et al. 2011).

Our results suggest that seed passage through primate guts somehow affects seed physiology (permeability, breaking dormancy and/or hormonal changes), allowing seeds to germinate more and faster (Traveset et al. 2007). However, it was not the goal of the studies we reviewed to find out by what mechanisms primates affect seed physiology. We will need studies that address how guts change chemical and/or mechanical processes of the seeds to better understand what biotic and abiotic factors influence germination and establishment success after dispersal. Such an understanding would help clarify the broad importance of seed ingestion by primates on germination performance, plant fitness and spatial distribution (Albert et al. 2015).

Improving data reporting

It is desirable to increase standardization of experimental design and data reporting in experimental studies of seed germination with primates. An important criterion of a well-written science report is how well it permits repeatability: whether details are described sufficiently to enable duplication of the methods and to attain similar results under the same experimental design (Ruxton and Colegrave 2010) or to enable consistent comparisons between organisms, sites, events or other research topic.

Seventeen of the 19 studies in our database did not provide any measurements of variability around mean values. In other words, 91.3% of independent comparisons in our analyses came from studies with no reported standard deviation and/or standard error. In many reports, it was not possible to identify how many seeds were set to germinate in each replicate, nor if the replicates tested all seeds together at a single germination site. We had to exclude some studies in our meta-analysis due to lack of basic information about the seed germination trials, such as sample size.

We suggest that the following guidelines would result in more accessible, complete and uniform reports on vertebrate gut passage effect on seed germination:

1) extraction of seed from fruit and/or feces: state how fruits and seeds were handled before the experimental trials; what kind of extraction (hand, wash or machine) was used;
2) controls: make clear what was used as treatment and what was used as control during the experiments; use of intact fruits, hand-extracted and gut-passed seeds as reported in Samuels and Levey (2005);
3) experimental design: make clear how many replicates were used for each treatment and the respective number of seeds set to germinate in each replicate; if possible, ensure that experimental (gut-passed) and control seeds are placed randomly across germination plots (especially in greenhouse settings, where local variation in light or watering regime could affect germination rates). Assure independence among replicates, using control replicates from different trees, and from different monkeys on different days;
4) place of testing: state where the experiments were conducted (lab, field or greenhouse);

5) germination conditions: moisture conditions where seeds were placed to germinate (e.g. forest soil, sterilized soil, petri dishes with filter paper, fungicide, watering frequency, etc.), environmental conditions (temperature and humidity) and seed conditions at the beginning of the experiment (i.e. percentage of seed viability before ingestion);
6) length of experiment period: provide the length of the germination trial (after which time, seeds were discarded or not monitored); report the number of days to germination of the first seed per replicate, the mean germination time (as an average of days to germination for all seeds in a replicate, with the respective standard deviation or standard error) and the number of days to the last germination;
7) germination percentage: report the real germination percentage (number of seeds that germinated at the end of test divided by number of seeds that indeed were capable of germinating at beginning, which can be assessed through simple tetrazolium tests (Delouche et al. 1962). Ideally, use more than one replicate for each germination trial (species–treatment combination) and report the average of germination percentage, followed by each respective standard deviation or standard error based on the replicates;
8) standardize terminology. Avoid using terms such as latency and dormancy length with insufficient knowledge of seed dormancy (Baskin and Baskin 2014).

Meaningful treatment design

In the first review evaluating the role of vertebrates on seed germination, Traveset (1998) emphasized that most studies did not test the effect of frugivores in separating the pulp from the seeds due to the lack of a 'intact fruit control' and also that the large majority of studies did not evaluate the viability of the seeds that failed to germinate. Almost two decades later those issues remain the same. Here, more than 99% of the experimental data only tested the possible scarification effect that ingestion by vertebrates has on seed coats (Samuels and Levey 2005). Only one study (Estrada and Coates-Estrada 1984) tested intact fruit against seeds dropped during handling for only one plant species; the same study also was the only one to test seeds in intact feces as one of the treatments, which should be closer to the actual conditions in the field. We highly recommend the use of four treatments whenever possible: 1) seeds passed through a frugivore's gut, aiming to ascertain the effect of frugivory on the seed; 2) hand washed seeds (seeds removed from the fruit pulp and epicarp), aiming to ascertain the possible scarification effect on the seed; 3) intact fruits, aiming to ascertain the cleaning effect; and 4) seeds in feces, aiming to ascertain the possible fertilization effect of the frugivore's feces (Robertson et al. 2006, Traveset et al. 2001, 2007).

In all the studies used here, it was unknown whether seeds that remained at the end of a trial had died after passing through the gut, or were already dead, or could potentially germinate. Future improvements in experimental design will be critical to determine how frugivory affects distinct components of seed dispersal effectiveness, so that these can be used to assess how dispersal-mediated population dynamics of trees will be affected by the combination of ongoing forest fragmentation and thus, ultimately, how dispersal will affect regeneration of Neotropical forests.

Conclusions

Here we show that Neotropical primates are effective mutualists of fleshy-fruited plants and highlight that they vary in their seed dispersing capabilities, depending upon their diets and gut morphology. They promote a significant increase in seed germination and, combined with other studies, our results confirm their significance as dispersers, which can be meaningful for conservation in a community scale. Primates represent one of the largest and dominant vertebrate dispersers in the Neotropics and it is known that the maintenance of frugivorous monkeys can be critical for the regeneration of tropical forests. However, forest loss, fragmentation, hunting and selective logging severely affect primate species and ecological processes involving them. We look forward to future increases in our understanding of the role of diverse animal taxa in supporting the diversity and regeneration of Neotropical forests.

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Supplementary material (available online as Appendix oik-02986 at <www.oikosjournal.org/appendix/oik-02986>). Appendix 1–3.

CONSIDERAÇÕES FINAIS

Primatas vêm sendo cada vez mais reconhecidos pelo impacto positivo na regeneração florestal e na dinâmica da comunidade vegetal. Aqui demonstramos sua eficiência como dispersores de sementes no Neotrópico devido à elevada capacidade de dispersar grande diversidade de espécies, ingerir e dispersar sementes e frutos de variados tamanhos, tipos e cores, além de mover sementes para locais fora da área de influência do parental e favorecer a germinação após a passagem pelo trato digestivo. Porém, aspectos da eficiência qualitativa da dispersão de sementes dependem fortemente da guilda alimentar de primatas Neotropicais. O grau de frugivoria se reflete diretamente no comportamento alimentar, nos padões de locomoção e na morfologia do trato digestivo, influenciando assim a qualidade na manipulação, a distância de dispersão e os efeitos exercidos pelo trato digestivo no sucesso de germinação. Primatas primariamente frugívoros sofrem os maiores graus de ameaça à extinção (Estrada et al. 2017), e tendem a apresentar a maior eficiência qualitativa, enquanto que primatas folívoros, apesar de constituirem o grupo mais bem estudado e serem comprovadamente dispersores legítimos, oferecem um serviço de menor qualidade.

Apesar da grande diversidade de espécies de planta e nos atributos de frutos consumidos e dispersos, identificamos certas especializações que nos permitiram descrever uma síndrome de dispersão primatocórica: frutos médios ou grandes, em sua maioria cobertos por uma casca dura e de cor amarela ou laranja. Porém, devido ao seu hábito alimentar generalista, não foi possível descrever os impactos do mutualismo com primatas na evolução de catacteres morfológicos de frutos. Este hábito alimentar generalista permite que primatas exerçam um papel importante em redes mutualísticas (Nuismer et al. 2012), e seu papel conjunto com outros dispersores na evolução das plantas deve ser explorado em futuras pesquisas.

Por fim, ressaltamos a necessidade de aprimorar a pesquisa para que seja possível cobrir as atuais lacunas. Estudos sobre dispersão de sementes devem uniformizar métodos e buscar direcionar esforços para grupos ainda pouco estudados. Somente assim o conhecimento será útil na tomada de decisões para a conservação (Howe 2016). Atestar primatas como efetivos dispersores de semente permanece uma tarefa desafiadora devido à lacuna no conhecimento acerca do destino das sementes (Chapman et al. 2013 Bufalo et al. 2016). A associação com dispersores secundários, especialmente besouros coprófagos, vem sendo descrita como uma vantagem positiva e adicional (Andresen 2002, Andresen e Feer 2005, Vulinec et al. 2006), mas a informação sobre a sobrevivência e o estabelecimento direto pós-dispersão tem sido fortemente negligenciada (mas veja Valenta et al. 2009, Bravo 2012, Chaves et al. 2015). Sugerimos, assim, que futuros estudos que buscam descrever a eficiência da dispersão de semente por primatas considerem que o processo pode possuir mais de uma fase (Culot et al. 2015), e o destino das sementes pós-dispersão primária deve ser melhor explorado.

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