



**Impacts of hunting on tree  
and vertebrate communities  
in French Guiana**

**Rens W. Vaessen**





# Impacts of hunting on tree and vertebrate communities in French Guiana

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Utrecht University, August 2023

**De invloed van jacht op boom- en vertebrate gemeenschappen in Frans Guyana**

**Impacts de la chasse sur des communautés d'arbres et de vertébrés en Guyane  
française**





**Impacts of hunting on tree and vertebrate communities in  
French Guiana**

**De invloeden van jacht op gemeenschappen van bomen en gewervelden  
in Frans Guyana**

(met een samenvatting in het Nederlands)

**Impacts de la chasse sur communauté des d'arbres et de vertébrés en  
Guyane française**

(avec un résumé en français)

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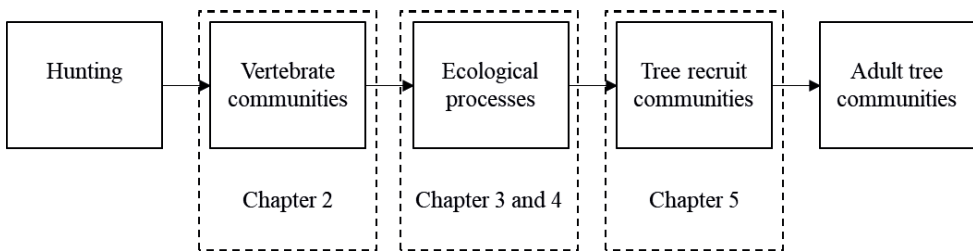
# Chapter I

## General introduction

Rens W. Vaessen

# I. INTRODUCTION

Vertebrates perform key ecological processes that are important for the conservation of tree diversity in tropical forests (Terborgh 1988, Wright 2003). Throughout the tropics, however, vertebrate populations are in decline due to hunting (Brashares 2004, Peres and Palacios 2007, Koerner et al. 2017, Scabin and Peres 2021). Through changes in the vertebrate-mediated ecological processes of seed dispersal, seed predation and browsing, the loss of vertebrates in tropical forest is thought to affect the composition, density and diversity of tree recruit (i.e. seedlings and saplings) communities and eventually adult tree communities (Figure 1) (Dirzo and Miranda 1991, Wright 2003, Terborgh et al. 2008, Galetti and Dirzo 2013, Kurten 2013, Kurten et al. 2015). In the long-term this might even affect forest carbon sequestration and nutrient cycling (Bello et al. 2015, Villar et al. 2020).



**Figure 1.** A conceptual model of how hunting may affect adult tree communities: Through hunting humans can affect vertebrate communities, causing changes in the ecological processes that are mediated by vertebrates, such as seed dispersal, seed predation and browsing. This in turn affects the communities of tree recruits, which in the long-term leads to changes in the adult tree communities. The dashed boxes indicate which subject is covered in each chapter of this thesis.

Although major changes in forest composition have been predicted as a result of hunting, there is a surprisingly poor understanding of how changes in vertebrate communities affect seed dispersal, seed predation and browsing and consequently change the composition of tree recruit communities (Hazelwood et al. 2020, Del-Claro and Dirzo 2021, Williams et al. 2021).

The impacts of hunting on the species composition of vertebrate populations have been reasonably well investigated (e.g. Dirzo et al. 2014, Richard-Hansen et al. 2019, Scabin and Peres 2021). Across the tropics, the decline in large vertebrate species is most severe, while smaller vertebrates are least affected, or even thrive in forests with high hunting pressure (Redford 1992, Wright et al. 2007b, Bugir et al. 2021). These patterns of defaunation can be explained by the preferences of hunters for large vertebrates, which are often easier to target, and provide the most meat. Popular game



species in French Guiana, for example, include the South American tapir (*Tapirus terrestris*), collared peccary (*Pecari tajacu*) and paca (*Cuniculus paca*) (Richard-Hansen et al. 2019). Furthermore, large vertebrates have relatively low rates of reproduction and are therefore unable to quickly restore their population sizes (Robinson and Redford 1986). Small vertebrates, on the other hand, have high reproduction rates, and are thought to benefit from reduced resource competition (Wright 2003).

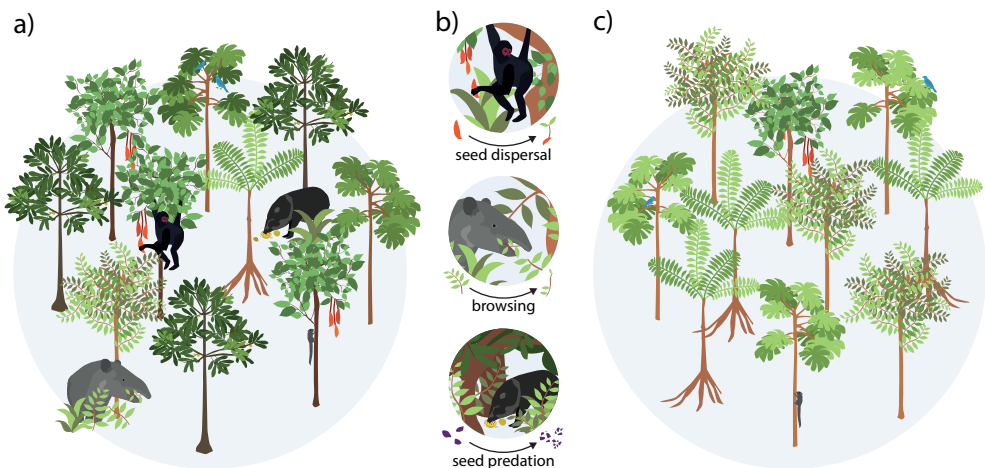
## 2. VERTEBRATE-MEDIATED ECOLOGICAL PROCESSES

Vertebrates perform various ecological processes in the tropics, of which seed predation, seed dispersal and browsing are probably the most important (Wright 2003). These processes can have both positive and negative effects on the survival chances of trees in the early stages of their life-cycle. Hunting-induced defaunation may have a quantitative and qualitative impact on these ecological processes and thus influence the survival chances.

Seed predation by vertebrates, also known as granivory, is the act of an animal feeding on a seed in such a way that the seed loses its viability. Research into the effects of seed predation by vertebrates on tree communities is limited, but studies show that predation can lead to large losses of viable seeds (Beckman and Muller-Landau 2007, Dirzo et al. 2007, Williams et al. 2021), thus limiting the population sizes of plant species preferred by seed predators. Hunting of seed predators would release these plant species from predation, which could hypothetically lead to larger populations of these plant species at the expense of others (Figure 2).

Seed dispersal is the movement of a seed away from the mother tree. Over 80% of tropical woody plant species have seeds that are dispersed by vertebrates (Osuri et al. 2016), including birds, fish, reptiles, bats and other mammals. Seed dispersal, particularly over long distances, is widely considered an important mechanism for maintaining plant diversity in tropical forests (Chave et al. 2002, Wright 2002, Terborgh 2020). As seed predation, species-specific pathogens and intraspecific competition are highest near the mother tree, dispersal away from the tree reduces seed mortality (Comita et al. 2014, Terborgh 2020, Janzen 1970, Connell 1971). Dispersal of seeds thus increases the likelihood of seeds surviving, germinating and developing into a seedling. Furthermore, long-distance seed dispersal may facilitate colonization, climate tracking and increases genetic diversity (Nathan et al. 2008). Therefore, tree species that experience a reduction in seed dispersal due to the loss of vertebrates, would hypothetically decline in population sizes (Figure 2).

Finally, browsing is the act of consuming leaves and twigs. Especially seedlings are vulnerable to browsing, often not surviving an interaction with a browser. There has been very little attention for browsing in hunting research (Del-Claro and Dirzo 2021). Insects are probably responsible for most of the consumption of leaves and twigs (Coley and Barone 1996), which suggests that the loss of vertebrates will result in negligible changes. Nonetheless, Dirzo and Miranda (1991) observed far less browsing marks in the seedling community of a hunted forest compared to a non-hunted forest, implying that the loss of vertebrate browsers may have a major impact on tropical forests. Multiple vertebrate-exclosure studies found an increase in seedling recruitment, but in this type of study it is difficult to distinguish between the effects of reduced browsing and reduced seed predation (Kurten and Carson 2015). One study that focused on the effects of hunting on leaf trait composition in the tropics found no significant differences between a hunted and a non-hunted site (Kurten et al., 2015). Overall, hunting impacts on browsing remain poorly studied.



**Figure 2.** Visualization of the hypotheses: a) Undisturbed forest harbors a high vertebrate and tree diversity. b) Mutualistic and antagonistic vertebrate – plant interactions are important determinants for plant survival, and thus co-shape forests. These interactions differ between species and are driven by both vertebrate traits and plant traits. c) The non-random loss of vertebrates will cause changes in vertebrate-plant interactions, which benefit tree species with certain traits, while it will disadvantage others. This leads to changes in the functional composition of tree communities of tropical forests.

### 3. FUNCTIONAL TRAITS

Tropical forests harbor an enormous species diversity, which impedes the investigation of hunting impacts on vertebrate – plant interactions at a large scale. This problem

can be solved by studying functional traits rather than species. Functional traits are characteristics of vertebrates or plants. For example, functional traits of plants can be the size or shape of a fruit. Functional traits of vertebrates can be gape size or activity patterns. These functional traits determine how plants and vertebrates function in their environment (Nock et al. 2016) and drive the interaction between vertebrates and fruits (including seeds), and between vertebrates and leaves. Functional traits therefore arguably have a high predictive value for vertebrate – plant interactions (McGill et al. 2006). Furthermore, as different species can share traits (i.e. different fruits can have the same color), the diversity of tropical forest can be summarized by a relatively limited set of traits. Functional traits thus make it easier to link hunting-induced changes in vertebrate communities to changes in recruit communities. This thesis therefore focuses strongly on functional traits.

Functional traits are known to be important determinants for vertebrate – fruit interactions that precedes both seed predation and seed dispersal (Valenta and Nevo 2020). As large vertebrates are affected more by hunting than small vertebrates, it is thought that particularly seeds that have interactions with large vertebrates are mostly affected. Large vertebrates are generally able to ingest large seeds, which small vertebrates cannot, and thus it has been hypothesized that large seeded tree species are affected mostly by hunting induced-defaunation (Brodie and Gibbs 2009). However, the body size – seed size relationship has not been convincingly established, and there are multiple examples of relatively small vertebrates dispersing large seeds externally (Jansen et al. 2012, Blanco et al. 2019). Moreover, fruit interactions are not only determined by seed size, but by many traits such as fruit color, fleshiness and scent (Valenta and Nevo 2020), but there has been a lack of attention for these traits in hunting studies.

## 4. STUDY SYSTEM

In this thesis, I focused on the tropical lowland rainforests of French Guiana. French Guiana is an 85,000 km<sup>2</sup> French territory in the eastern part of the Guiana shield. The area has an equatorial climate and receives between 3000 mm and 4000 mm of rainfall annually, with the highest rainfall in the north-east and the lowest in the south-west (Beaufort et al. 2019). Most rain falls between December and July (Beaufort et al. 2019). Soils on the Guiana shield are diverse but mostly consist of nutrient-poor Ferralsols and Acrisols (Hammond 2005). All major rivers, Maroni, Mana, Sinnamary, Approuague and Oyapock, run roughly from south to north (Figure 3).

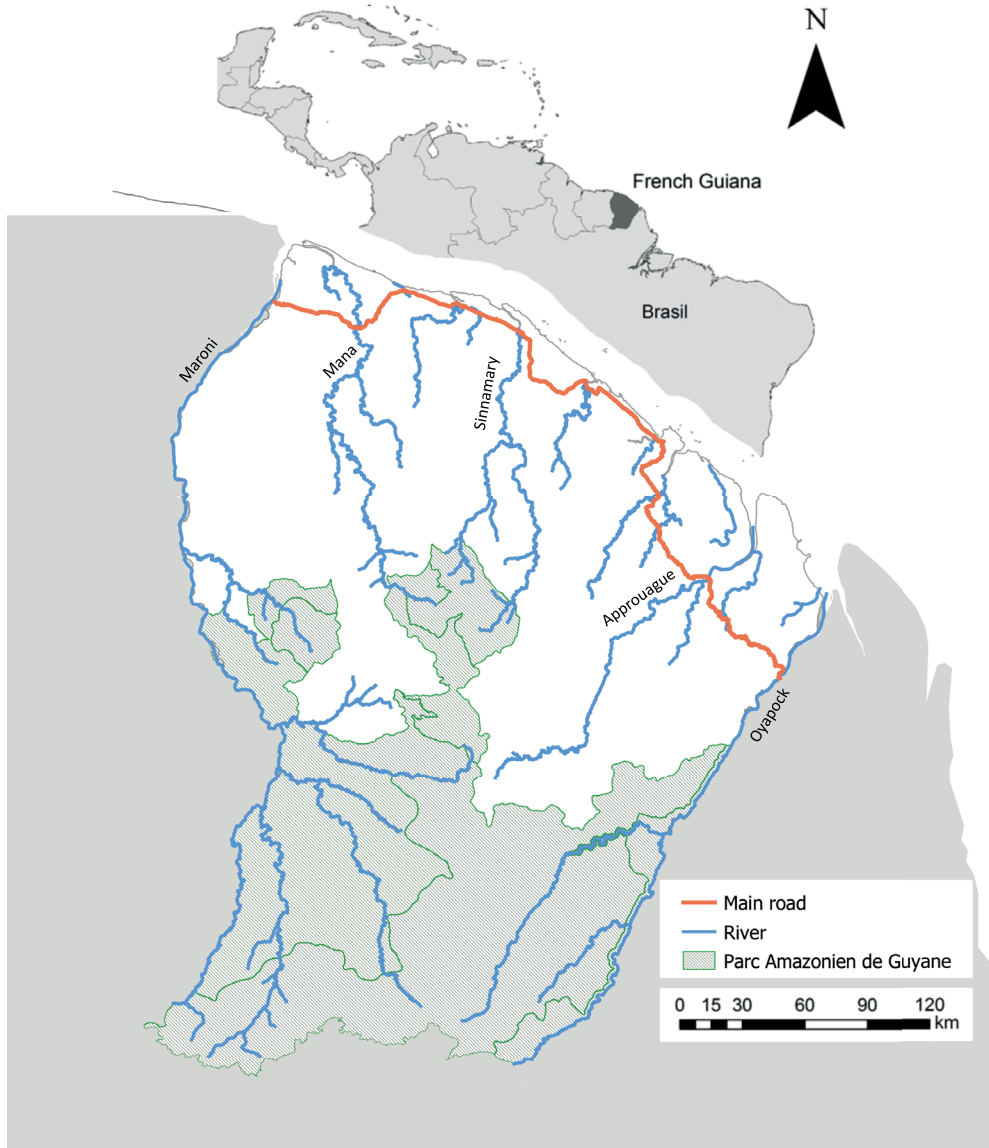
French Guiana has 300,000 inhabitants. Most people live along the coast, where the larger cities are situated. Further concentrations of inhabitants can be found along the river Maroni, which demarks the western border between French Guiana with Suriname, and along the river Oyapock which demarks the eastern border with Brazil. The biodiversity of French Guianan forests is relatively well documented (ter Steege et al. 2016).

### *Hunting in French Guiana*

Unlike most tropical regions, hunting in French Guiana is predominantly recreational. This stems from a hunting tradition that has been passed on through generations. Due to a social safety net provided by the French government, most people in French Guiana are not dependent on hunting for the provision of proteins. Regardless, a relatively small group of indigenous and Maroon communities are upholding their traditional subsistence hunting (Untermaier 2008). People in French Guiana generally have access to cars and motorized boats, which allows them to travel further over roads and rivers. As roads are mostly restricted to the coastal region (Figure 3), hunters use the rivers to travel further inland. Distances travelled by hunters are generally higher in French Guiana compared to traditional hunting patterns elsewhere in the Amazon (Richard-Hansen et al. 2019). There are, however, notable differences in hunting habits between sites within French Guiana: Hunting areas range from 300 km<sup>2</sup> to 2775 km<sup>2</sup>, of which the difference can partly be explained by the proximity of villages competing for hunting areas (Richard-Hansen et al. 2019). Overnight hunts and the use of cars and boats are far more common in the northern parts of French Guiana, and the proportion of mammal biomass in harvests range from 26% to 73% of all harvested vertebrates (Richard-Hansen et al. 2019). Large tracts of tropical forests remain undisturbed, due to law enforcement, strong regulation of forestry practices and especially poor accessibility.

Hunting laws from metropolitan France do not apply in French Guiana, due to the different ecological contexts. Conservation laws limit the areas where hunting is permitted and protect vulnerable species by prohibiting hunting, or limiting the number of individuals that are allowed to be harvested. In 2007, in southern French Guiana a large nature reserve ‘Parc amazonien de Guyane’ was created (Figure 3). Here, as well as in few protected zones elsewhere in French Guiana, hunting is only allowed by indigenous and Maroon communities that have a long history of subsistence hunting (Untermaier 2008). They are allowed to hunt all animals, with the exception of protected species. Nonetheless, illegal hunting practices do occur, for example by illegal gold miners. The impact of illegal hunting has not been quantified, but anecdotes suggest it may be large. The most recent change in hunting regulations is the requirement of a hunting license, although it is freely issued to residents of French Guiana

(Richard-Hansen et al. 2019). The implementation of new hunting regulations is met with strong resistance from large parts of the French Guianan population, due to their strong and wide spread hunting tradition.



**Figure 3.** Map of French Guiana, showing the main road, the major rivers and the Parc amazonien de Guyane. (This map was created from: “geo.data.gouv.fr” n.d. a., “geo.data.gouv.fr” n.d. b., “geo.data.gouv.fr” n.d. c., “HOTOSM.org” n.d.)

## 5. SCOPE OF THE THESIS

How hunting affects tropical forests is largely unclear. There are few empirical studies that have investigated the relationships between hunting and the composition of tree communities in tropical forest (Wright et al. 2007a, Terborgh et al. 2008, Harrison et al. 2013, Kurten et al. 2015, Hazelwood et al. 2020). These studies are limited to comparing a hunted and a non-hunted site, or are limited to a small geographical range. Furthermore, the mechanisms through which hunting can affect forest composition (seed dispersal, seed predation and browsing) are poorly understood. For these reasons little is known about how tree species composition of forests changes due to the loss of vertebrates.

The aim of this research is to better understand how tropical forests are affected by hunting, and thereby provide knowledge that may contribute to the management and conservation of tropical forests. The results may help to identify tree species that are vulnerable to hunting, through which mechanisms, and which vertebrate species play a role. It will therefore help those that manage and conserve the forests of Frans Guyana to take focused measures for protecting forests, for example by implementing new hunting laws that not only focus on the conservation of vertebrate populations, but also tree diversity.

The main research question addressed in this thesis is “How does hunting affect the tree species composition of forests in French Guiana?”. I hypothesize that particularly large mammals will be affected by hunting, which will lead to changes in vertebrate-fruit interactions, and reduce browsing of nutritious and palatable leaves, resulting in a composition with more palatable and more nutritious leaves, with less large-seeded and fleshy fruits and with a lower wood density (Figure 2). To answer the question and test the hypothesis, I first quantify hunting-induced changes in the functional composition of vertebrate assemblages. Then I link vertebrate traits to fruit and seed traits, and quantify how these interactions differ between hunted and non-hunted vertebrate species. Finally, I compare the functional composition between forests that differ in levels of defaunation. This stepwise approach results in four chapters:

In Chapter two “Hunting affects the functional composition of medium- to large game species assemblages in a Neotropical rainforest”, I study the differences in the functional composition of hunted and undisturbed vertebrate assemblages in French Guiana. This study makes use of a novel approach by looking at the effects of hunting on the *functional* composition of vertebrate assemblages, whereas it is common to investigate hunting effects on *species* composition.

Chapter three “Fruit and seed traits and vertebrate-fruit interactions of tree species occurring in Guyana, Suriname and French Guiana” focuses on the collection of data on fruit traits and vertebrate – fruit interactions in the Guianas. This dataset can be used to study interactions between vertebrates and fruits.

In Chapter four “An analysis of trait interactions between vertebrates and fruits in the Guianas and how they are affected by hunting”, I ask how vertebrate traits and fruit traits are linked, and how hunting affects vertebrate - fruit interactions. In answering this question we use the dataset from chapter three. Vertebrate – fruit interactions are the fundament for seed dispersal and seed predation, both ecological mechanisms that are important in shaping forest composition.

In Chapter five “Defaunation changes leaf trait composition of recruit communities in tropical forests in French Guiana” I empirically test differences in the functional composition of tree recruit communities, each with its own level of defaunation. This study uniquely uses regional site replication to investigate the effects of hunting-induced defaunation on forests . Furthermore, defaunation levels are quantified, which is uncommon, greatly improving the predictive value of the study.

In Chapter six “General discussion” I integrate and discuss the results of my research and what the implications of these results are for nature conservation and society. I provide an overview of future research topics that would further increase our understanding of the impacts of hunting on tropical forests.



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# Chapter 2

Hunting affects the functional composition of medium- to large game species assemblages in a Neotropical rainforest

Rens W. Vaessen, Thomas Denis, Marijke van Kuijk, Patrick A. Jansen, Cécile Richard-Hansen

## ABSTRACT

Unsustainable hunting threatens vertebrate communities across the tropics. Assessing hunting impacts on vertebrate communities using trait-based indices rather than species-based indices, is a novel approach that may be more suitable for predicting important ecological processes such as seed dispersal.

We explored how hunting changed the functional composition of vertebrate assemblages in French Guiana, focusing on medium- to large game species. We compared the community-weighted means and -proportions of eight functional traits between 11 hunted and 12 control sites. We also determined if vertebrate density of the assemblages differed between hunted and control sites, and if it correlated to functional traits. Finally, we tested whether hunted sites were functionally less diverse than control sites.

We found significant differences between hunted and control sites for body size, intrinsic rate of natural increase ( $r_{max}$ ), diet and vision type. Vertebrate density was lower at hunted sites, and was correlated with four of eight traits. Hunting affected the relationship between vertebrate density and body size, metabolic rate and diet. Diversity of functional composition was similar for hunted and control sites.

Our results indicate that hunting may severely affect functional composition of vertebrate communities, which may have serious consequences for ecological processes.



## ABSTRACT EN FRANÇAIS

La chasse non durable menace les communautés de vertébrés sous les tropiques. L'évaluation des impacts de la chasse sur les communautés de vertébrés à l'aide d'indices basés sur des traits plutôt que sur des indices basés sur les espèces est une nouvelle approche qui pourrait être plus adaptée pour prédire des processus écologiques importants tels que la dispersion des graines.

Nous avons exploré comment la chasse a modifié la composition fonctionnelle des assemblages de vertébrés en Guyane française, en nous concentrant sur les espèces de gibier de taille moyenne à grande. Nous avons comparé les moyennes et proportions pondérées par la communauté de huit caractères fonctionnels, entre 11 sites chassés et 12 sites témoins. Nous avons également déterminé si la densité de vertébrés des assemblages différait entre les sites chassés et les sites témoins, et si elle était corrélée aux traits fonctionnels. Enfin, nous avons testé si les sites chassés étaient fonctionnellement moins diversifiés que les sites témoins.

Nous avons trouvé des différences significatives entre les sites chassés et les sites témoins en termes de taille corporelle, de taux intrinsèque d'augmentation naturelle ( $r_{\max}$ ), de régime alimentaire et de type de vision. La densité des vertébrés était plus faible sur les sites chassés et était corrélée à quatre des huit caractères. La chasse a affecté la relation entre la densité des vertébrés et la taille corporelle, le taux métabolique et le régime alimentaire. La diversité de la composition fonctionnelle était similaire pour les sites chassés et témoins.

Nos résultats indiquent que la chasse peut gravement affecter la composition fonctionnelle des communautés de vertébrés, ce qui pourrait avoir de graves conséquences sur les processus écologiques.

## I. INTRODUCTION

Unsustainable hunting threatens vertebrate populations across the tropics (Benítez-López et al., 2017; Galetti et al., 2021; Peres and Palacios, 2007) and affects ecosystem processes such as seed dispersal, seed predation and browsing (Galetti et al., 2021; Harrison et al., 2013; Kurten et al., 2015) with long-term consequences for forest carbon sequestration and nutrient cycling (Bello et al., 2015; Villar et al., 2020). Hunting-induced changes in vertebrate communities have commonly been expressed in species-based indices such as density, diversity and richness (Benítez-López et al., 2017; Peres and Palacios, 2007). However, species-based indices are unsuitable to assess the consequences of hunting for vertebrate mediated ecological processes at community level. The biodiversity of tropical forests is vast, which makes it simply not possible to study all vertebrate-mediated ecological processes at a species level. Hence, trait-based approaches may be more appropriate (Luck et al., 2012).

Hunting induced defaunation processes are non-random, as hunters mainly target large-bodied vertebrate species (Benítez-López et al., 2017). Large vertebrates are indispensable for some ecological processes. Firstly, a disproportionate part of browsers are large-bodied species, as their large bodies require constant food intake which can be provided by leaves and twigs (Clauss et al., 2013). Secondly, plants with large seeds rely on large-bodied vertebrates for long-distance dispersal (Pires et al., 2018). It is due to the crucial role that large vertebrates play, that body mass has been used as a predictor for hunting impacts on ecological processes (Bello et al., 2015).

Vertebrate-mediated ecological processes are not determined by body mass only, but by a multitude of functional traits that essentially determine how vertebrates perceive the environment, and how they interact with that environment (Dehling et al., 2016). From seed dispersal syndrome theory, we know that fruit color plays an important role in the relationship with the dispersers (Valenta and Nevo, 2020). Vertebrate color vision (i.e., the number of color pigment types in the eye) may therefore be a good indicator of fruit choice. Second, metabolic rate is a predictor of the consumption volume of a vertebrate (Kleiber, 1947), and thus of the quantitative impact it may have through vertebrate plant interactions. Third, diet preferences (i.e. herbivory, frugivory and carnivory) may be good predictors for the ecological role vertebrates play. Using these traits to characterize the functional composition rather than the species composition of vertebrate communities, would allow for predictions of effects of changes in vertebrate communities on ecological processes.

Several studies have used multi-trait analysis to assess the impacts of anthropological activities on functional diversity indices (Brodie et al., 2021; Laméris et al., 2020)

with hunting being one of the main contributors to a loss in functional diversity (Brodie et al., 2021). The loss of functional diversity suggests that there are changes in functional trait composition. In a study on invertebrate-mediated ecological processes, Gagic et al. (2015) showed that functional diversity indices are far better predictors of ecological processes than species-based indices, however, single-trait indices such as community-weighted means (CWM) performed even better in predicting ecological processes, and thus it makes sense to assess impact of hunting on single trait indices.

Several changes in vertebrate functional composition may occur as a result of hunting. The CWM of vertebrate body mass has been found to decrease with hunting (Peres, 2000). Since several traits are linked to body mass, such as reproductive rate and metabolic rate, these are likely to be affected by hunting as well. Changes in other functional traits, such as diet and vision type, are less evident, but are likely to be similar across hunted sites, as hunters generally target the same vertebrates. This could imply that naturally occurring regional variation in functional composition (Denis et al., 2018) declines as a result of hunting.

Here, we explore the effects of hunting on the functional composition of medium- to large bodied vertebrate assemblages in 11 hunted sites and 12 control sites in the tropical rainforests of French Guiana. In each site, medium- to large-sized vertebrate species were surveyed using line transects with distance sampling (Richard-Hansen et al., 2015). Species density estimates were coupled to eight functional traits to quantify functional composition of the assemblages. We tested four predictions: (1) Community-weighted means of body size, body mass and metabolic rate are lower at hunted sites compared to control sites, intrinsic rate of natural increase ( $r_{\max}$ ) is higher at hunted sites, while other functional traits (i.e. group size, diet, home range and vision type) are not different. (2) Medium- to large-sized vertebrate density is lower at hunted sites compared to control sites. (3) The relationship between vertebrate density, and body mass and metabolic rate is more positive for hunted sites compared control sites and more negative for  $r_{\max}$ , while the relationship between vertebrate density and other traits is unchanged. (4) Similarity in functional composition of the assemblages is greater among hunted sites than among control sites.

## 2. MATERIAL AND METHODS

### Study area

Field data were collected in tropical lowland forests of French Guiana, a 85,000km<sup>2</sup> French territory in the eastern part of the Guiana shield (Figure 1). The territory has an equatorial climate and receives a mean annual rainfall of 3000 mm (Beaufort et al., 2019), with highest rainfall in the coastal areas (Beaufort et al., 2019). Most rain falls between December and July (Beaufort et al., 2019). Although most forests in French Guiana can be considered lowland rainforest, several distinct landscape types are recognized based on biotic and abiotic environmental variables, including vertebrate community composition (Guitet et al., 2013).

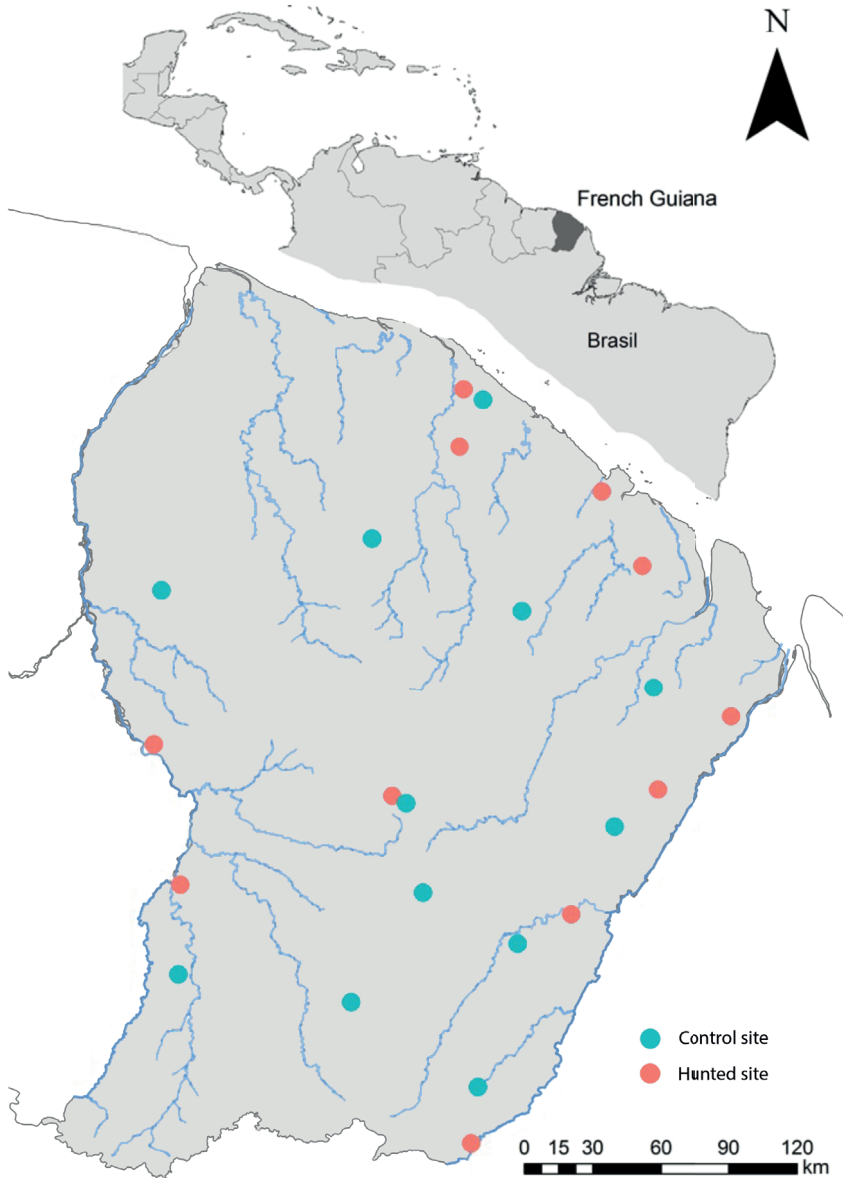
The study included 23 independent sites that were part of long term research on natural variation in vertebrate community composition and on hunting practices in French Guiana (Denis et al., 2016; Richard-Hansen et al., 2019; Richard-Hansen and Hansen, 2004), including 11 sites that were classified as ‘hunted’ and 12 sites as ‘control’ (Figure 1). Hunting pressure was determined through expert opinion (C. Richard-Hansen), based on long term research on hunting practices in French Guiana (Richard-Hansen et al., 2019; Richard-Hansen and Hansen, 2004). Hunted sites were sites where hunting was known to occur on a regular basis, although the intensity varied largely depending on distance from habitation and accessibility. Hunted sites were otherwise undisturbed. Control sites were sites where hunting activity was never observed or only sporadically, and were located within protected areas and/or which are naturally preserved by their remoteness and inaccessibility.

### Data collection

Species densities were estimated by Denis et al. (2018). Vertebrates were censused using line transects with distance sampling, a widely used method for estimating animal densities (Buckland et al., 2005). In accordance with most neotropical studies (Endo et al., 2010), we focused on medium to large-bodied diurnal vertebrates because these species perform ecological processes for which little to no redundancy exists. Furthermore, medium to large-bodied diurnal vertebrate are the preferred game species (Cecile Richard-Hansen et al., 2019) and can be detected visually and/or acoustically. The surveys followed a strict protocol across all sites (Supplementary material).

Density estimates were acquired for 19 medium- to large sized vertebrate species (Table S1), for which the number of detection events was sufficient to run the generalized distance sampling model (Denis et al., 2018). The smallest species included was the marbled wood quail (*Odontophorus gujanensis*) with a body mass of 0.3 kg, which

is generally considered to be within the boundaries of medium- to large vertebrates (Carvalho et al., 2020; Endo et al., 2010), and the largest was the red brocket (*Mazama americana*) with a body mass of 36.0 kg.



**Figure 1.** Study area (French Guiana), with the locations of 23 study sites.

## Functional traits

We selected eight functional traits that are predictors for vulnerability to hunting (body mass, body size, group size,  $r_{\max}$ ) (Denis et al., 2017), and to the vertebrate mediated ecological processes of seed dispersal (diet, vision type, home range, metabolic rate) and browsing (diet, metabolic rate) (Table S1). Trait data were collected from Denis et al. (2019), except for  $r_{\max}$  and vision type, which were collected from literature (Table S2) and metabolic rate, which was proportional to the 0.75 power of body mass in kg (Kleiber, 1947). Vision type was deduced for most species, because species-specific data availability is very limited. Vision type of all birds were assumed tetrachromatic, as birds generally are tetrachromatic (Bowmaker and Hunt, 2006). Mammals are generally dichromatic, except for most South American primates, which can vary between dichromatic and trichromatic, (Bowmaker and Hunt, 2006). The Guianan red howler (*Alouatta macconnelli*) is trichromatic, whereas the vision type of other French Guianan primates varies within species between dichromatic and trichromatic (Bowmaker and Hunt, 2006), however, as they live in groups we considered them functionally trichromatic. We were not able to find  $r_{\max}$  values marbled wood quail, therefore these species were not included in the analyses of  $r_{\max}$ .

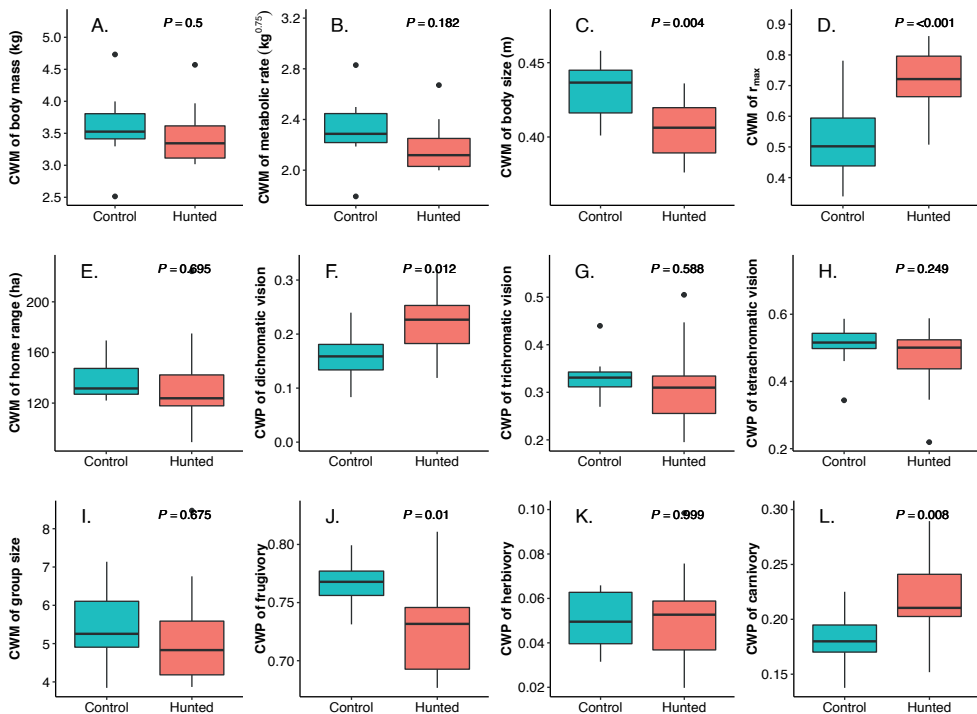
## Data analysis

For body mass, home range,  $r_{\max}$  and group size, we calculated community means weighted by species density (CWM). For diet, we calculated the weighted proportion (CWP) of each category (i.e. Frugivory, Herbivory and Carnivory) and for vision type the proportion of each category (Dichromatic, Trichromatic and Tetrachromatic). Statistical analyses were carried out using the package Vegan V2.5-6 (Oksanen et al., 2019) in R version 3.6.1. To test for differences in trait values between hunted and control sites, we used two-sided students t-tests for which we did not assume equal variance, as the boxplots showed clear differences in variance between the two groups for some traits. To evaluate how hunting affects the relationship between functional traits and vertebrate density (density of all focus species combined), we tested three models per trait or trait category: 1) a model with hunting as an interaction term 2) an ANCOVA with hunting as a confounding factor and 3) a linear regression without controlling for hunting. For each trait we selected the model with the lowest AIC.

To test for hunting induced changes in similarity of functional composition between sites, we compared the Euclidean pair-wise dissimilarities for hunted and control sites using a PERMANOVA with 999 permutations. We used nonmetric multidimensional scaling (NMDS) with body size,  $r_{\max}$ , vision type and diet as input data (other traits were correlated to body size) to visualize the Euclidean dissimilarities and fitted hunting and vertebrate density. We fitted vectors of all traits to check for relationships and latitude and longitude to check for unwanted spatial relationships.

### 3. RESULTS

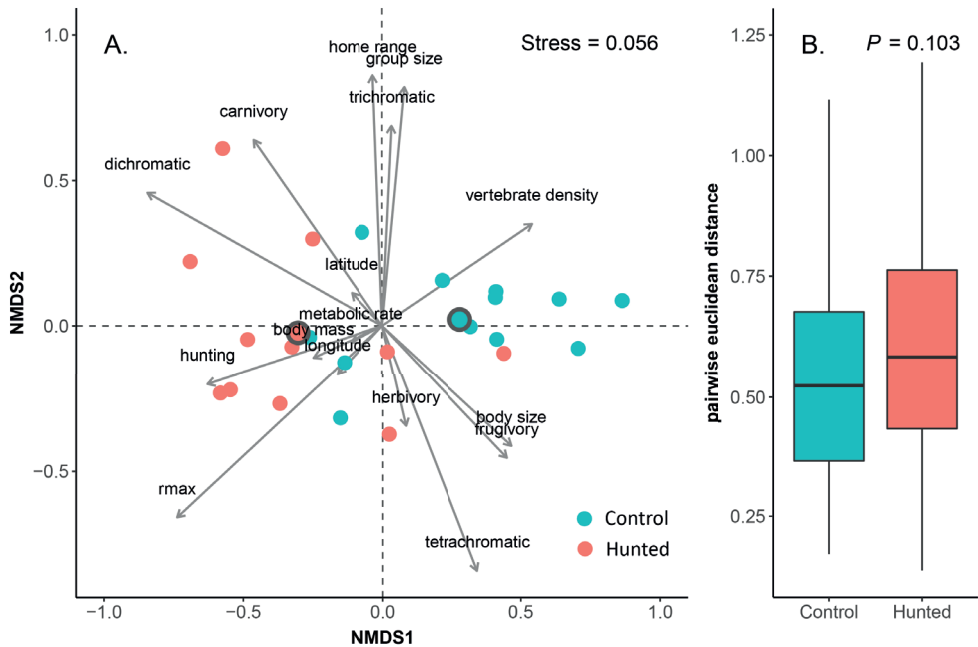
CWM or CWP differed between hunted and control sites for four of the eight traits, without controlling for vertebrate density (Figure 2) which are: body size,  $r_{max}$ , diet for the categories of ‘Frugivory’ and ‘Carnivory’, and vision type for the category ‘Dichromatic’. As a result, the NMDS showed a clear relationship between overall functional composition and hunting, but a considerable overlap between hunted and control sites remained (Figure 3A). The mean pair-wise Euclidean distance was not significantly different between control sites and hunted sites ( $P = 0.103$ , Figure 3A), i.e. there is no difference in similarity.



**Figure 2.** Differences between control sites (blue) and hunted sites (red) in vertebrate CWM or CWP of eight functional traits, of which vision type and diet each have three categories. A. Body mass, B. Metabolic rate, C. Body size, D. intrinsic rate of natural increase ( $r_{max}$ ), E. Home range, F. Dichromatic vision, G. Trichromatic vision, H. Tetrachromatic vision, I. Home range, J. Frugivory, K. Herbivory, L. Carnivory. P-values indicate the significance of difference between the means.

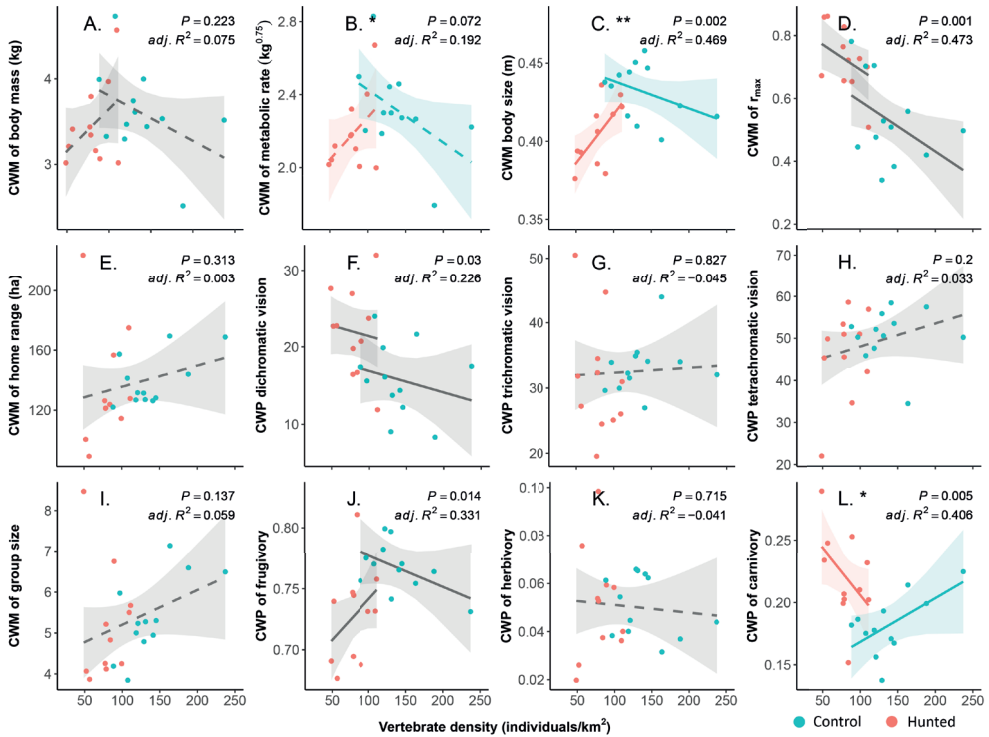
Mean vertebrate density differed significantly between hunted sites (80.5 individuals/ $\text{km}^2$ , range 48.7- 111.1) and control sites (138.9 individuals/ $\text{km}^2$ , range 88.4 - 237.2) (t-test,  $P < 0.001$ ). Vertebrate density had significant negative relationships (based

on control sites) with body size,  $r_{max}$ , dichromatic vision and frugivory, and a positive relationship with carnivory (Figure 4). There was a significant interaction with hunting for metabolic rate, body size and diet for the category “carnivory” (Figure 4). For metabolic rate and body size hunting changed the direction of the relationship with vertebrate density from negative to positive, while for carnivory the relationship with vertebrate density was changed from positive to negative. For both body mass and frugivory the P-value of the interactions was 0.07.



**Figure 3.** A. NMDS of functional composition of vertebrate assemblages, based on Euclidean distances. Blue dots indicate control sites, red dots indicate hunted sites. Encircled dots indicate the centroids of the control and hunted sites. Grey arrows are fitted vectors are for each trait, hunting and vertebrate density. B. Boxplots of pairwise Euclidean distances for control and hunted sites. P indicates the significance of the mean difference between the two groups.





**Figure 4.** Relationships between estimated total vertebrate density and community-weighted means (CWM) or community-weighted proportions (CWP) of eight functional traits, of which vision type and diet each have three categories. A. Body mass, B. Metabolic rate, C. Body size, D. intrinsic rate of natural increase ( $r_{\max}$ ), E. Home range, F. Dichromatic vision, G. Trichromatic vision, H. Tetrachromatic vision, I. Group size, J. Frugivory, K. Herbivory, L. Carnivory. Blue dots indicate control sites and red dots disturbed sites. Lines are least squared linear regressions; where solid lines indicate significant relationships and dashed lines indicate non-significant relationships. Models were selected by AIC. For models including an interaction with hunting, or a main effect of hunting, the regression lines are shown separately for hunted and control sites. Shaded areas indicate 95% confidence intervals. P-values indicate the significance of the models. Lines and 95% confidence intervals are colored, when the interaction with hunting is significant. Adjusted  $R^2$  indicated the model explained variation. Asterisks indicate the significance of the main effect: \* =  $<0.05$ , \*\* =  $<0.01$  and \*\*\* =  $<0.001$ .

## 4. DISCUSSION

Large vertebrates play crucial roles in the functioning of tropical forests, but are widely threatened by unsustainable hunting (Benítez-López et al., 2019; Galetti et al., 2021). We explored how the functional composition of medium- to large vertebrate game species assemblages differed between hunted sites and control sites in the tropical rainforests of French Guiana. Our results indicate that hunting markedly affects the functional composition of the studied assemblages.

Our NMDS analysis showed that there is a clear difference in functional composition between hunted and control sites, but that this difference does not translate into a lower diversity in functional composition for hunted sites, in contrast with our prediction. Although the main spread is across the hunting axis, a large spread remains perpendicular to the hunting vector, suggesting that natural variation still remains an important factor in functional composition. Although we see a clear influence of hunting on functional dissimilarity between sites, the overall variation in functional composition is a largely reflection of the complexity of the regionally occurring natural variation in vertebrate community composition (Richard-Hansen et al., 2015, Denis et al., 2017, Denis et al., 2018).

For the individual traits, we found that CWM of body size was lower at hunted sites compared to control sites, as predicted. Our analysis also confirmed a higher CMW of  $r_{\max}$  at hunted sites. Both the NDMS and the individual trait analysis suggest that  $r_{\max}$  is affected strongest by hunting. As  $r_{\max}$  was not correlated to body size, the large differences between hunted and control sites are likely due to the intrinsic ability of species with high  $r_{\max}$  to recover their populations relatively quickly from hunting induced losses. In contrast with our predictions, body mass and metabolic rate did not differ significantly, despite their correlation to body size. This can, in part, be explained by our third prediction: hunting affected the relationship between vertebrate density and the CWMs of metabolic rate ( $P = 0.04$ ) and body mass ( $P = 0.07$ ). Because the relationship for control sites was negative and the relationship for hunted sites was positive, the means of control sites and hunted sites were similar, even though hunting seemed to reduce the CWMs of metabolic rate and body mass.

Multiple traits correlated with vertebrate density. Particularly for body size and  $r_{\max}$  the models explained a large proportion of the variation. In the context of hunting, vertebrate density of medium- to large vertebrates, might thus be included as predictor for functional composition, particularly when quantification of hunting is difficult.

It is important to notice that our surveys did not capture the entire vertebrate community. Firstly, we did not include nocturnal medium- to large-bodied vertebrates, such as tapir, paca and felids. Secondly, we did not include small vertebrates, which are thought to increase in numbers with increased hunting pressure, due to decreased competition and predation (Dirzo et al., 2014). This density compensation has been shown for primate communities in Amazonian forests (Peres and Dolman, 2000), and rodents' populations in the Atlantic forest (Galetti et al., 2015). Thirdly, we could not include the white-lipped peccary, because the presence of this species is highly variable and unpredictable, due to its very large home ranges and strong temporal variation in population size (Richard-Hansen et al., 2019; Richard-Hansen et al., 2014). However, we did find differences between control and hunted sites and we think that the differences in functional composition would have been even clearer if we would have been able to include the above mentioned species. White-lipped peccary, tapir and paca are severely hunted in French Guiana (Richard-Hansen et al., 2019), and share most trait values with the diurnal large bodied vertebrates that *were* included in our study. Therefore, we can expect that their decrease in hunted sites would reinforce the observed patterns on CWM and CWP traits values. Small vertebrates are highly diverse, but obviously have a small body size. Including small vertebrates could thus strengthen the relationships we found in body size related traits and in diet. This is different for vision type, however, as birds and reptiles, which are tetrachromatic, make up a relatively large part of the small vertebrate group.

Hunting has often been linked to changes in seed dispersal, seed predation and browsing (Harrison et al., 2013; Kurten et al., 2015), which are among the most important vertebrate mediated ecological processes. Here we showed that the functional composition of vertebrate assemblages is affected by hunting. Predicting hunting-induced changes in ecological processes remains a major challenge, however, as our understanding of the precise roles of functional traits in these processes remains poor. The complexity of tropical ecosystems with its enormous biodiversity and a multitude of antagonistic and mutualistic interactions, forces us to gain a more detailed understanding of the relationships between vertebrate functional traits, and vertebrate mediated ecological processes.

The human population of French Guiana has a relatively low density and is mostly not dependent on bushmeat for the provisioning of proteins. Areas with high hunting pressure in this region are often connected to large tracts of undisturbed forest, that likely provide repletion of vertebrates in hunted areas (Novaro et al., 2000). This situation is very different from hunted forests in fragmented landscapes such as the Atlantic forests of Brazil (Galetti et al., 2017). Despite this replenishment, we found strong effects of hunting on functional composition of vertebrate assemblages. Where

previous studies showed hunting-induced changes in species composition (Peres and Palacios, 2007), our study provides insights in the impact on functional composition, which may ultimately lead to changes in ecosystem functioning. We suspect that the many forests across the tropics that experience more substantial hunting, will show even stronger effects on functional composition.

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## SUPPLEMENTARY MATERIAL

### Line transect survey protocol

Line transect surveys followed a strict protocol (Richard-Hansen et al., 2015). At each site 3 or 4 line transects of 3 km in length were cleared from vegetation creating a narrow path to ease the access for the observer and to reduce noise from walking. The paths were cleared at least one week in advance, as to reduce effects on detection probability. Transects were walked between 7:00 - 11:00 and 14:30 - 18:00 at a 1 km/h pace, by a single observer. Observers were randomised across time and transects to minimize observer bias. Distances to observed units were measured with a range finder to the nearest meter. This method was repeated for 7 to 9 days resulting in a sampling effort of at least 140 km, well above the estimated minimum of 100 km (de Thoisy et al., 2008). All surveys were performed during the dry season (August-November), in order to reduce potential seasonal bias in detection or animal behavior.

**Table S1.** Species included in this study and the corresponding traits.  $r_{\max}$  is the intrinsic rate of natural increase; Vision type is based on the number of pigments in the eye.

Species	Common name	Class	$r_{\max}$	Mass (kg)	Metabolic rate (kg <sup>0.75</sup> )	Body size (m)	Home range (ha)	Group size (# ind.)	Diet (%)		Vision type*	
									Frugi-vory	Carni-vory		
<i>Alouatta macconnelli</i>	Guianan red howler	Mammal	0.17	6.8	4.2	0.5	50	4.7	58	40	2	Tri
<i>Ateles paniscus</i>	red-faced spider monkey	Mammal	0.07	8.8	5.1	0.4	250	2	87	11	2	Di/Tri**
<i>Cebus olivaceus</i>	wedge-capped capuchin	Mammal	0.11	2.9	2.2	0.3	100	12	53	7	40	Di/Tri**
<i>Crax allector</i>	black curassow	Bird	0.90	3	2.3	0.7	100	2	91	1	8	Tetra
<i>Dasyprocta leporina</i>	red-rumped agouti	Mammal	1.10	4.4	3.0	0.5	3	1.5	87	2	10	Di
<i>Eira barbara</i>	tayra	Mammal	0.28	4.8	3.2	0.5	2000	1.2	21	0	79	Di
<i>Mazama americana</i>	red brocket	Mammal	0.28	36	14.7	0.8	100	1	56	37	8	Di
<i>Mazama nemorivaga</i>	Amazonian brown brocket	Mammal	0.49	14.3	7.4	0.7	100	1	68	25	7	Di
<i>Myoprocta acouchy</i>	red acouchi	Mammal	1.435	1	1.0	0.3	1	1	99	0	1	Di
<i>Nasua nasua</i>	South American coati	Mammal	0.75	3.1	2.3	0.4	500	7.4	16	28	57	Di
<i>Odontophorus gujanensis</i>	marbled wood quail	Bird	NA	0.3	0.4	0.2	5	5.6	25	25	50	Tetra
<i>Pecari tajacu</i>	collared peccary	Mammal	0.68	18.4	8.9	0.6	500	4.8	64	0	36	Di
<i>Penelope marail</i>	marail guan	Bird	0.40	1	1.0	0.5	30	1.8	97	0	3	Tetra
<i>Pithecia pithecia</i>	white-faced saki	Mammal	0.23	2	1.7	0.3	120	3.7	90	5	5	Di/Tri**
<i>Psoplia crepitans</i>	grey-winged trumpeter	Bird	0.03	1.1	1.1	0.5	100	5.8	83	0	17	Tetra
<i>Saguinus midas</i>	red-handed tamarin	Mammal	0.66	0.5	0.6	0.2	50	5.7	44	0	56	Di/Tri**
<i>Saimiri sciureus</i>	Guianan squirrel monkey	Mammal	0.25	0.9	0.9	0.3	500	20	55	0	45	Di/Tri**
<i>Sapajus apella</i>	tufted capuchin	Mammal	0.16	3.1	2.3	0.3	300	14	81	1	18	Di/Tri**
<i>Tinamidae</i>	tinamou	Bird	1.48	1	1.0	0.4	5	1	89	0	11	Tetra

\* Di = dichromatic, Tri = trichromatic, Tetra = tetrachromatic \*\* Individuals of this species have either dichromatic or trichromatic vision (Bowmaker and Hunt, 2006), but since these species live in groups, we consider them functionally trichromatic.

Bowmaker, J.K., Hunt, D.M., 2006. Evolution of vertebrate visual pigments. *Curr. Biol.* 16, R484–R489.

Species	Source $r_{\max}$	Source vision type
<i>Alouatta macconnelli</i>	Robinson & Redford (1986)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Ateles paniscus</i>	Robinson & Redford (1986)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Cebus olivaceus</i>	Robinson & Redford (1986)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Crax alector</i>	Parry et al. (2009)	Bowmaker & Hunt (2006)
<i>Dasyprocta leporina</i>	Robinson & Redford (1986)	Bowmaker & Hunt (2006)
<i>Eira barbara</i>	Robinson & Redford (1986)	Bowmaker & Hunt (2006)
<i>Mazama americana</i>	Mayor et al. (2016)	Bowmaker & Hunt (2006)
<i>Mazama nemorivaga</i>	unpublished data	Bowmaker & Hunt (2006)
<i>Myoprocta acouchy</i>	unpublished data	Bowmaker & Hunt (2006)
<i>Nasua nasua</i>	Mayor et al. (2016)	Bowmaker & Hunt (2006)
<i>Odontophorus gujanensis</i>	NA	Bowmaker & Hunt (2006)
<i>Pecari tajacu</i>	Mayor et al. (2016)	Bowmaker & Hunt (2006)
<i>Penelope marail</i>	Parry et al. (2009)	Bowmaker & Hunt (2006)
<i>Pithecia pithecia</i>	Ross (1992)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Psophia crepitans</i>	Parry et al. (2009)	Bowmaker & Hunt (2006)
<i>Saguinus midas</i>	Ross (1992)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Saimiri sciureus</i>	Robinson & Redford (1986)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Sapajus apella</i>	Mayor et al. (2016)	Jacobs (1998), Bowmaker & Hunt (2006)
<i>Tinamidae</i>	Parry et al. (2009)	Bowmaker & Hunt (2006)

**Table S2.** Literature used to determine the intrinsic rate of natural increase ( $r_{\max}$ ), and vision type.

Bowmaker, J. K. and Hunt, D. M. 2006. Evolution of vertebrate visual pigments. - *Curr. Biol.* 16: R484–R489.

Jacobs, G. H. 1998. A perspective on color vision in platyrrhine monkeys. - *Vision Res.* 38: 3307–3313.

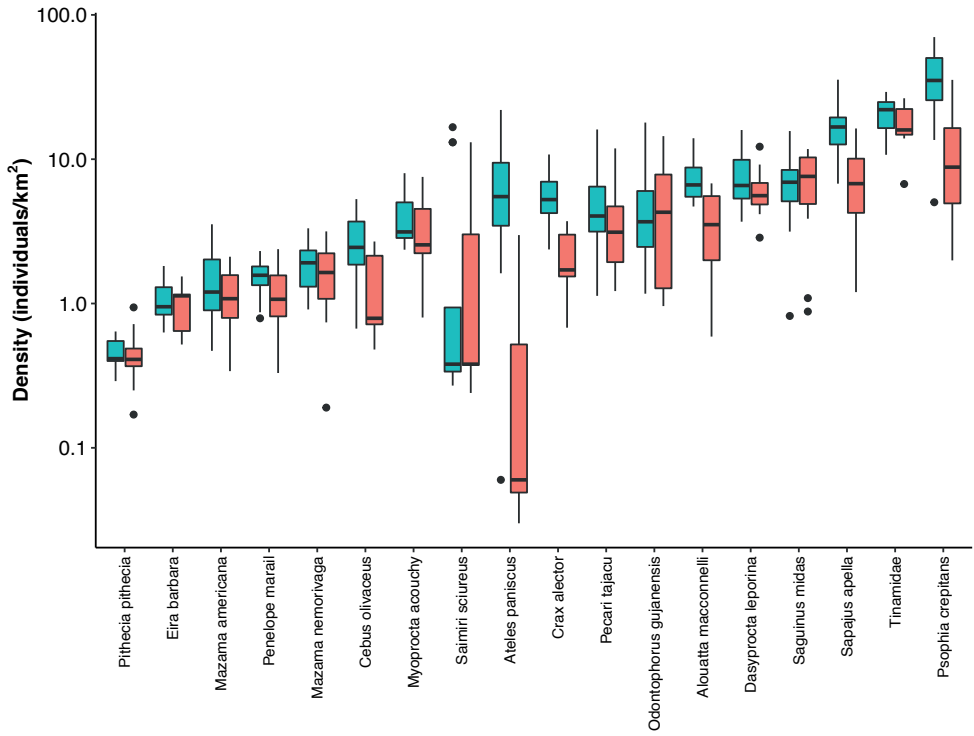
Mayor, P. et al. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. - *Conserv. Biol.* 31: 912–923.

Parry, L., Barlow, J. & Peres, C. A. 2009 Hunting for sustainability in tropical secondary forests. - *Conserv. Biol.* 23: 1270–1280.

Robinson, J. G. & Redford, K. H. 1986 Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. - *Oecologia* 68: 516–520.

Ross, C. 1992. Environmental correlates of the intrinsic rate of natural increase in primates. - *Oecologia* 90: 383–390.w





**Figure S1.** Difference in species densities between control and hunted sites for all species included in this study.



# Chapter 3

## Fruit and seed traits and vertebrate–fruit interactions of tree species occurring in Guyana, Suriname and French Guiana

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## ABSTRACT EN FRANÇAIS

La dispersion des graines est largement considérée comme un mécanisme important pour la conservation de la diversité végétale. Dans les régions tropicales, plus de 80 % des espèces de plantes ligneuses sont dispersées par les vertébrés, souvent via la consommation de fruits. Notre compréhension de ce qui détermine les interactions entre les vertébrés et les fruits est limitée.

Grâce à une recherche documentaire systématique, nous avons compilé une base de données sur les caractéristiques des fruits et des graines et sur les interactions vertébrés-fruits pour les espèces d'arbres et de vertébrés présentes dans les Guyanes, dans le but de faciliter la recherche sur la dispersion des graines et la prédation des graines d'espèces d'arbres dans les Guyanes.

La base de données a été compilée en extrayant des données de 262 sources publiées. Il se compose de 21.082 enregistrements, dont 19.039 enregistrements contiennent des informations sur 19 caractères différents de fruits et de graines appartenant à 1.622 espèces d'arbres différentes. Les 2.043 autres enregistrements contiennent des informations sur les interactions vertébrés-fruits entre 161 espèces de vertébrés et 464 espèces d'arbres.

Nos analyses ont montré un biais taxonomique, en particulier dans les données d'interaction, en faveur des vertébrés de grande taille, la plupart des interactions étant enregistrées pour le saki à dos roux (*Chiropotes chiropotes*), suivi du tapir du Brésil (*Tapirus terrestris*). Pour les plantes, nous avons constaté une surreprésentation des familles des Sapotacées et des Moracées, et une sous-représentation des familles des Rubiacées, des Myrtacées et des Lauracées dans les interactions.

## I. CLASS I. DATA SET DESCRIPTORS

### B. Data set identity:

Fruit and seed traits and vertebrate-fruit interactions of tree species occurring in Guyana, Suriname and French Guiana

### C. Data set identification code:

Guianan\_fruits\_and\_frugivory.csv

### D. Data set description

#### I. Originators:

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#### II. Abstract:

Seed dispersal is widely considered as an important mechanism for the conservation of plant diversity. In tropical regions, over 80% of woody plant species are dispersed by vertebrates, often through the consumption of fruits. Our understanding of what drives interactions between vertebrates and fruits is limited.

Through a systematic literature search, we compiled a database of fruit and seed traits and vertebrate-fruit interactions for tree and vertebrate species occurring in the Guianas, with the aim to facilitate research into seed dispersal and seed predation of tree species in the Guianas.

The database was compiled by extracting data from 262 published sources. It consists of 21.082 records, of which 19.039 records contain information about 19 different fruit and seed traits belonging to 1.622 different tree species. The other 2.043 records contain information on vertebrate-fruit interactions between 161 vertebrate species and 464 tree species.

Our analyses showed a taxonomic bias, particularly in the interaction data, towards large bodied vertebrates, with most interactions recorded for the bearded saki (*Chiropotes chiropotes*), followed by the lowland tapir (*Tapirus terrestris*). For plants we found a overrepresentation of the Sapotaceae and Moraceae families, and an underrepresentation of the Rubiaceae, Myrtaceae and Lauraceae families in the interactions.

### **E. Key words/phrases:**

Guianas, Guyana, Suriname, French Guiana, fruit traits, frugivory, seed dispersal, seed predation, seed traits.

## **2. CLASS II. RESEARCH ORIGIN DESCRIPTORS**

### **A. Overall project description:**

#### **I. Identity:**

Fruit and seed traits and vertebrate-fruit interactions of tree species occurring in Guyana, Suriname and French Guiana

#### **2. Originators:**

Same as above

#### **3. Period of study:**

Dates of the publications from which data were extracted range from 1930 to 2019. The dataset was compiled between 2016 and 2021.

#### **4. Objectives:**

Our objectives were to compile a dataset containing fruit and seed traits of tree species occurring in Guyana, Suriname and French Guiana, and vertebrate-fruit interactions recorded for these tree species.

The dataset can function as a main source for researchers interested in fruit and seed trait data. The vertebrate – fruit interactions data can be used to investigate frugivory, seed dispersal and seed predation in the Guianas, which may also be linked to the fruit characteristics in this dataset. Furthermore, it can be used as an indicator for taxa that are understudied, however, in that case it should also be acknowledged that this dataset is incomplete (see C. Data limitations).

#### **5. Abstract:**

Same as above

#### **6. Sources of funding:**

Foundation Trésor, Padualaan 8, Utrecht, the Netherlands



Prince Bernhard Chair for International Nature Conservation, Utrecht University, Padualaan 8, Utrecht, the Netherlands

Miquel Fund, Utrecht University, Padualaan 8, Utrecht, the Netherlands

## B. Specific subproject description

### I. Site description

The Guianas consist of Guyana, Suriname and French Guiana, covering 463.000 km<sup>2</sup> in the northeastern part of South-America, on the Guiana shield. The Guianas are home to one of the largest tracts of undisturbed tropical forests worldwide, but also contain savannas and montane habitats. The region harbors a large biodiversity including over 1600 non-marine vertebrate species (IUCN, 2021) and over 3700 tree species (Ter Steege et al. 2016). Human population density is low, with most people living in the cities along the coast, and in villages along the multiple large rivers that run through the landscape, generally in south-north direction.

The Guianas have a tropical climate with mean temperatures of up to 30°C, and an East-West precipitation gradient from over 3000mm in North-East French Guiana to 2000mm in West Guyana. The whole region has at least one dry season per year, but more often two.

### 2. Experimental or sampling design

The data were obtained through a systematic literature search following the guidelines of Collaboration for Environmental Evidence (2013). As search terms we used the species names of all known tree species in the Guianas (Ter Steege et al. 2016), species names of all known non-maritime vertebrates occurring in the Guianas (IUCN, 2021), in combination with “fruit”, “seed”, “diet”, “consume\*”, “dispers\*”, “feed”, “feeding”, “eat”. Searches were conducted in Scopus and Web of Science. In addition to the articles obtained through the systematic search, we obtained articles through citations in the articles from the systematic search, and through the dataset from Bello et al. (2017). Furthermore we checked Mori et al. (2002) and the Flora of the Guianas (Görts-Van Rijn et al. n.d.) for fruit traits, and Roosmalen (1985) for fruit traits and vertebrate-fruit interactions. The data acquired belong to species occurring in the Guianas, but were not always originally collected in the Guianas. For vertebrate-fruit interactions we did not discriminate between mutualistic and antagonistic interactions. The data has not been subject to interpretation, and has not been manipulated in any way. As a consequence, traits or interactions may be included multiple times, but from different sources, which in some cases can be contradicting (e.g. different sources may report different fruit colors for the same species).

The dataset was compiled from Adamek 2012; Altrichter et al. 1999; Altrichter et al. 2000; Alvarenga and Talamoni 2006; Alves 2008; Alves 2012; Alves-Costa et al. 2004; Alves-Costa and Eterovick 2007; Alves-Costa 1998; Amaral 2007; Andrade et al. 2011; Andrade et al. 2013; Andresen 1999; Aranguren et al. 2011; Argel-de-Oliveira 1999; Athiè 2009; Bachand et al. 2009; Baldwin and Whitehead 2015; Barcelos et al. 2013; Bardales et al. 2008; Barreto et al. 1997; Batista et al. 2016; Bello et al. 2015; Benítez-Malvido et al. 2014; Bianconi 2009; Bizerril and Raw 1997; Bocanegra-González et al. 2015; Bodmer 1990; Bodmer 1991; Bohlender et al. 2018; Bonaccorso et al. 2007; Borgtoft Pedersen and Balslev 1990; Botero-Delgadillo et al. 2013; Boyle et al. 2012; Branan et al. 1985; Braz et al. 2012; Bredt et al. 2012; Brito et al. 2010; Bueno et al. 2013; Campos et al. 2012; Capece et al. 2013; Cardoso et al. 2011; de Carvalho 1961; De Castro et al. 2012; Castro-Luna and Galindo-González 2012; Cazetta et al. 2008; Chalukian et al. 2013; Cid et al. 2014; Cordero R. and Nicolas B. 1987; Correia 1997; Costa 2006; Cramer et al. 2007; Cruz-Neto et al. 2018; Cruz-Tejada et al. 2018; de Cassia Bianchi et al. 2014; Melo and Varela 2006; De Matos Dias and Bocchiglieri 2016; De Souza-Stevaux et al. 1994; Desbiez et al. 2009; Desbiez et al. 2010; Dirzo and Miranda 1990; Donatti et al. 2011; Enders 1930; Enders 1936; Erard et al. 2007; Espitia Camacho et al. 2018; Esser 1999; Facure et al. 2003; Fadini and De Marco 2004; Fagundes et al. 2013; Faustino and Machado 2006; Henry et al. 2000; Ferreira et al. 2013; Forget 1990; Forget and Milleron 1991; Forget 1996; Forget and Cuijpers 2008; Forget et al. 2001; Forget et al. 2001b; Forgiarini et al. 2013; Fragoso and Huffman 2000; Ragusa-Netto and Fecchio 2006; Fragoso 1997; Fragoso 1999; Franceschinelli and Thomas 2000; Bello et al. 2017; Galetti et al. 2001; Galetti and Pizo 1996; Galetti et al. 2000; Galetti et al. 2013; Galetti and Morellato 1994; Galetti et al. 2010; García-Morales 2012; Gatti et al. 2006b; Gatti et al. 2006a; Gayot et al. 2004; Gervais and Lavigne 2007; Gilardi and Toft 2012; Gondim 2001; Gonçalves et al. 2007; Görts- van Rijn, A.R.A. & Jansen-Jacobs M.J. eds.; 1992; Görts- van Rijn, A.R.A. ed.; 1988; Görts- van Rijn, A.R.A. ed.; 1991; Görts- van Rijn, A.R.A. ed.; 1992; Görts- van Rijn, A.R.A. ed.; 1993; Görts- van Rijn, A.R.A. ed.; 1994; Görts-van Rijn, A.R.A. & Jansen-Jacobs, M.J. Eds.; 1998; Görts-van Rijn, A.R.A. & Jansen-Jacobs, M.J. Eds.; 1998; Granados et al. 2014; de Granville and Gayot 2014; Green 2009; Guillotin et al. 1994; Guimarães 2003; Guimaraes et al. 2006; Guimarães et al. 2008; Gullison et al. 1996; Hallwachs 1986; Hasui and Hofling 1998; Haugaasen et al. 2010; Haugaasen 2008; Heithaus and Fleming 1978; Herbst 1986; Hibert et al. 2011; Beck 2005; Higgins 1979; Horsley et al. 2015; Howe et al. 1985; Ibarra-Manríquez and Cornejo-Tenorio 2010; Izar 2008; Jansen 2003; Jansen et al. 2004; Jansen et al. 2006; Jansen-Jacobs, M.J. ed.; 2009; Jansen-Jacobs, M.J. ed.; 2003; Jansen-Jacobs, M.J. ed.; 2003; Janssen-Jacobs, M.J. ed.; 1997; Janssen-Jacobs, M.J. ed.; 2006; Janssen-Jacobs, M.J. ed.; 1996; Janssen-Jacobs, M.J. ed.; 2007; Janzen 1982; Janzen 1985; Jerzolimski et al. 2009; Hernández-Montero et al. 2015; Jorge

and Howe 2009; Julien-Laferriere 1993; Julien-Laferrière 2001; Julliot 1996; Kabir et al. 2012; Kays 1999; Kelm et al. 2008; Keuroghlian and Eaton 2008; Keuroghlian 2003; Keuroghlian and Eaton 2009; Keuroghlian et al. 2009; Kiltie 1981a; Kiltie 1981b; Kiltie 1981c; Kiltie 1982; Kinzey and Norconk 1993; Kuprewicz 2013; Lapate 2009; Lapenta et al. 2008; Lazure et al. 2010; Lee et al. 2014; Lessa and Geise 2014; Lleellish et al. 2003; Loboiva et al. 2003; Lopez and Vaughan 2007; Lopez-Mata 1987; Mandujano et al. 1994; Manhães 2003; Marinho-Filho 1991; Marques and Fischer 2009; Martini et al. 2008; Martínez-Gallardo and Sánchez-Cordero 1997; Masteguín and Figueiredo 1995; Matta and Scudeller 2012; Maynard et al. 2019; McCoy 1985a, 1985b; McHargue and Hartshorn 1983; Mikich 2002; Minty et al. 2001; Moles et al. 2004; Montoya-Bustamante et al. 2016; Morais 2006; Mori et al. 2002; Mota de Oliveira & Jansen-Jacbs eds.; 2016; Mota de Oliveira, S. ed.; 2012; Mota de Oliveira, S. ed.; 2014; Motta-Junior 1991; Munin et al. 2012; Myers and Erwin 2015; Norconk 1996; Norconk et al. 1997; Notman et al. 1996; Novaes and Nobre 2009; O’Farrill et al. 2013; Oliveira and Ferrari 2000; Oliveira-Silva et al. 2018; Ordano et al. 2011; Oyama and de Souza 2011; Pack et al. 1999; Painter 1998; Palacio et al. 2017; Paracampo et al. 2017; Parrini and Pacheco 2011; Passos et al. 2003; Pereira De Souza and Válio 2001; Peres and Baidier 1997; Peres et al. 1997; Petit 1997; Piccoli et al. 2007; Pinheiro et al. 2013; Pires et al. 2015; Pizo 1997; Pizo et al. 2002; Pizo 2004; Prance, G.T. 1986; Pratt et al. 2005; Pringle et al. 2007; Prone et al. 2012; Ratiarison and Forget 2011; Ratiarison and Forget 2013; Rebein et al. 2017; Reis 1995; Renton 2006; Ribeiro da Silva et al. 2015; Robinson and Eisenberg 1985; Robinson 2015; Rocha et al. 2008; Rocha-Ortega et al. 2017; Rodrigues 2015; Rodrigues et al. 1993; Rodrigues-Junior et al. 2018; Rother 2010; Russo 2003; Russo and Augspurger 2004; Russo et al. 2006; Salas and Fuller 1996; Sánchez et al. 2012; Santos et al. 2012; Santos and Ragusa-Netto 2014; Sartore and Reis 2012; Silva and Tabarelli 2001; da Silva et al. 2013; Silva Matos and Watkinson 1998; Silva 2011; Silvera et al. 2003; Silvius 1999; Silvius 2002; Silvius and Fragoso 2003; Simão et al. 1997; Singha et al. 2018; Simmen and Sabatier 1996; Snook and Negreros-Castillo 2004; Souza and Fagundes 2017; Staggemeier et al. 2017; Stevenson et al. 2000; Stone 2007; Sugiyama and Peterson 2013; Thel et al. 2015; Tobler et al. 2010; Trivedi et al. 2004; Trujillo-Hdz et al. 2016; van Roosmalen 1985; Vaughan et al. 2006; Vélez et al. 2017; Weber et al. 2007; Wenny 1999; Wilkinson and Wenrick Boughman 1998; Williams 2016; Wyatt and Silman 2004; Zaca 2003; Zanon and Dos Reis 2007; Zapata-Mesa et al. 2017; Zhang and Wang 1995.

### 3. Research methods

Statistical analysis focused on bias in focal taxa (either vertebrate or tree) of the original researches. We therefore provide descriptive statistics that provide insights into the representations of taxonomic groups in the dataset. The descriptive statistics are

meant as an indication of biases. Overrepresentation or underrepresentation of taxa were determined visually and were not tested for significance. The statistical analysis was performed in R version 3.6.1 (R Development Core Team 2019).

#### 4. *Project personnel:*

Same as authors

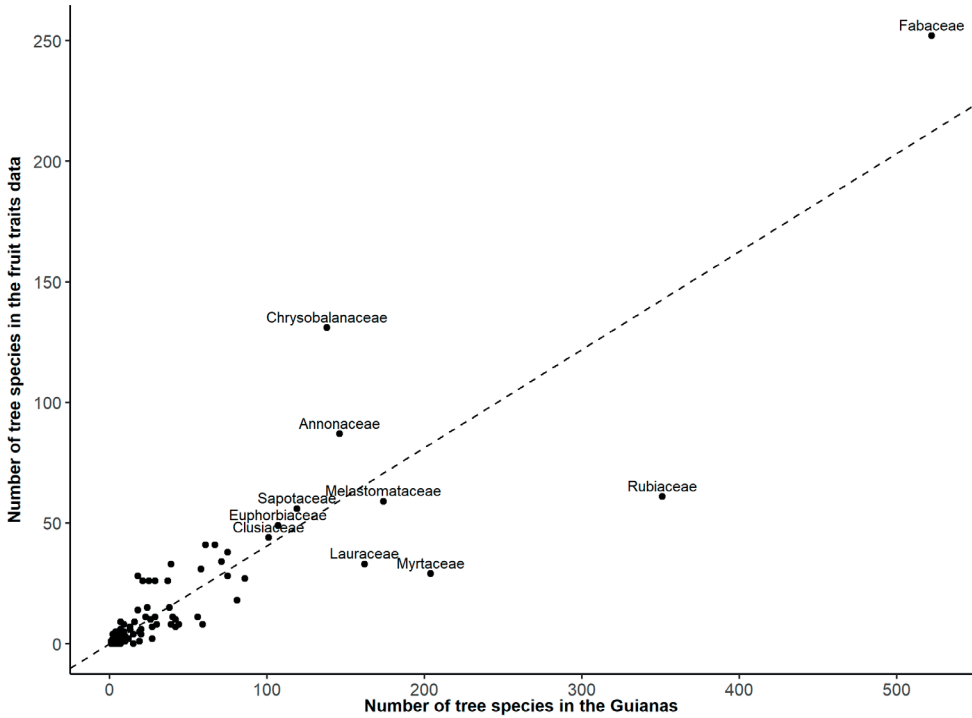
### C. Data limitations

Although we used systematic searches to obtain the data, we recognize that there are many sources of data which we were unable to find, or of which we were unable to obtain the data. The reasons for this include: 1) Sources are not available *digitally*. This is particularly true for older sources, including during times in history in which research interests in plant taxonomy and morphology were high (Ter Steege et al. 2016). 2) Data may be hidden in figures as a result of which the paper does not show up in a digital systematic search. 3) Data may not have been published.

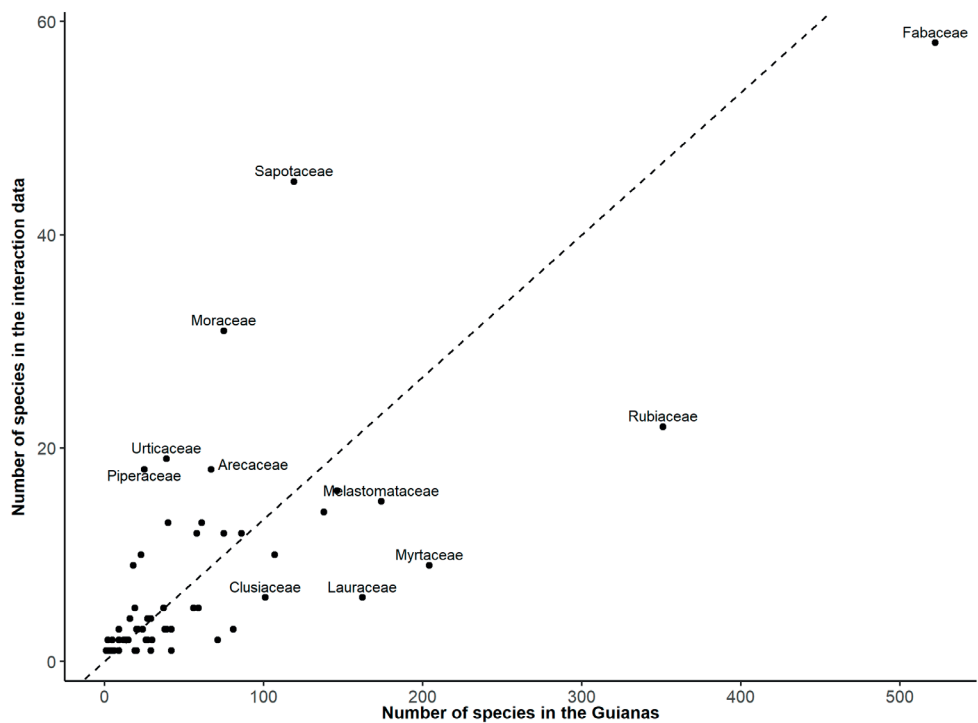
The compilation of the dataset focused on species that occur in the Guianas, but were not always collected within the territorial boundaries of the Guianas. A larger geographical range may, for example, increase intraspecific variation in trait values.

Furthermore it should be recognized by the users of the dataset, that the dataset is subject to major taxonomic biases (Figure 1-3), and that abundances in the dataset does not relate to actual species abundances or interaction abundances.

Figure 1 reveals an overrepresentation of Chrysobalanaceae and an underrepresentation of Rubiaceae in the fruit traits data. In the interaction data multiple plant families are overrepresented of which particularly Sapotaceae and Moraceae stand out, while Lauraceae, Myrtaceae and Rubiaceae are underrepresented (Figure 2). The vertebrate species with the highest representation in the vertebrate-fruit interaction data (Figure 3) appear to be species with a relatively large body mass (body mass data not shown). The three species with the highest representation are: the bearded saki (*Chiropotes chiropotes*), the lowland tapir (*Tapirus terrestris*) and the scarlet macaw (*Ara macao*).



**Figure 1.** The number of tree species per family in the *fruit traits data* as compiled by us, against the number of tree species per family in the Guianas, according to Ter Steege et al. (2016). Each dot represents a plant family. Labeled dots are families with at least 100 species in the Guianas. The dashed line represents the predicted number of tree species in the fruit traits dataset (the ratio of all tree species in the fruit traits data versus all tree species in the Guianas).



**Figure 2.** The number of tree species per family in the *interactions data* against the number of tree species per family in the Guianas, according to Ter Steege et al. (2016). Each dot represents a plant family. The dashed line represents the predicted number of tree species in the fruit traits dataset (the ratio of all tree species in the interaction data versus all tree species in the Guianas). The labeled dots are larger families that have at least 1.5 times more or less species in the interaction data than predicted.





### 3. CLASS III. DATA SET STATUS AND ACCESSIBILITY

#### A. Status

1. Latest update:  
12-16-2021
2. Latest archive date:  
12-29-2021
3. Metadata status:  
12-29-2021, version submitted
4. Data verification:  
Data is all from published and mostly peer reviewed sources.

#### B. Accessibility

1. Storage location and medium:  
Download link: <https://doi.org/10.34894/3X8JWB> (Vaessen et al. 2023) Contact persons: Marijke van Kuijk and Rens Vaessen. Ecology and Biodiversity group, Department of Biology, Utrecht University. Padualaan 8, 3584 CH, Utrecht, the Netherlands. [m.vankuijk@uu.nl](mailto:m.vankuijk@uu.nl), [r.w.vaessen@uu.nl](mailto:r.w.vaessen@uu.nl)
2. Copyright restrictions:  
None
3. Proprietary restrictions:
4. Costs:  
None

### 4. CLASS IV. DATA STRUCTURAL DESCRIPTORS

#### A. Data set file

1. Identity:  
Guianan\_fruits\_and\_frugivory.csv
2. Size:  
21.082 records, 1.95MB
3. Format and storage mode:  
Comma-separated values (.csv)
4. Header information:  
See B. Variable information, Table 1
5. Alphanumeric attributes:  
Mixed

## 6. Special characters/fields:

Data anomalies are indicated as 'NA'

## 7. Authentication procedures:

## B. Variable information

**Table 1.** Description of the fields in the dataset. A. Description of the data retained in under the specified columns. B. Description of each variable as specified under the column "variable"

A	Column	Description	Example
	ID	Unique identification number	223
	Reference	Source of the data	Mori et al. 2002
	Family	Family associated with the species	Nyctaginaceae
	Genus	Genus associated with the Species	Neea
	Species	Species of tree	Neea oppositifolia
	Species_in_source	Species synonym used in the reference	Neea spruceana
	Variable	Variable associated with the species	SEE TABLE B
	Value	Value associated with the variable	SEE TABLE B

B	Variable	Description	Example of value
	Fleshiness	Describes if a fruit is fleshy, fibrous or dry	Dry; Fleshy; Fibrous
	Fleshy_part	Describes which part of a fruit is fleshy	Fleshy_aril; Fleshy_pulp
	Fruit_color	Color of the fruit	Orange; Blue
	Fruit_shape	Shape of the fruit	Pyriform; Globose
	Fruit_type	Type of fruit	Samara; Drupe
	Max_fruit_length	Maximum length of the fruit in cm	10.6
	Max_fruit_width	Maximum width of the fruit in cm	2.5
	Max_seed_length	Maximum length of the seed in cm	1.9
	Max_seed_width	Maximum width of the seed in cm	0.5
	Min_fruit_length	Minimum length of the fruit in cm	1.5
	Min_fruit_width	Minimum width of the fruit in cm	1.8
	Min_seed_length	Minimum length of the seed in cm	0.4
	Min_seed_width	Minimum width of the seed in cm	0.4
	n_seed_cat	Number of seeds in a fruit as a category	numerous
	n_seeds	Number of seeds in a fruit, sometimes mean or range	3; 3.5; 8--14
	Outer_layer	Texture of the outer layer	Hairy; Spiny; Waxy
	Part_eaten	Part of the fruit that is eaten	Fruit; Seed
	Protective_coat	Describes if the outer layer is dehiscent or not	Indehiscent; Dehiscent
	Seed_weight	Weight of the seed in mg	2000
	Vertebrate_interaction	Vertebrate species interacting with the fruit	Thraupis sayaca

C. Data anomalies:

When no information is available, 'NA' is given.

## 5. CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

B. Quality assurance/quality control procedures:

Data has been obtained from primary sources, and have not been subject to interpretation by the authors of this paper.

C. Related materials

D. Computer programs and data-processing algorithms

E. Archiving

Data is available through <https://doi.org/10.34894/3X8JWB> (Vaessen et al. 2023), and alternatively through the corresponding authors.

F. Publications and results

G. History of data set usage

The dataset has not been used in any published studies yet, but is currently part of a study by Vaessen et al. into the relationships between defaunation and tree recruit composition (manuscript in review), and is part of a study by Vaessen et al, that focuses on the role of fruit traits and vertebrate traits in vertebrate-fruit interactions.

## ACKNOWLEDGEMENTS

We would like to thank all biologists who have spent their time collecting fruit and interaction data in the field, allowing us to compile this dataset.

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# Chapter 4

An analysis of trait interactions  
between vertebrates and fruits in the  
Guianas and how they are affected  
by hunting

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## ABSTRACT

Vertebrates help shape tree communities in tropical forests through their interactions with fruits and the concomitant dispersal or predation of seeds. Vertebrate populations in the Guianas are in decline due to hunting, which may have major implications for forest composition. However, our current insights on what drives vertebrate – fruit interactions and how they are affected by hunting are limited.

We studied trait-trait relationships between vertebrates and fruits (including seeds) of tree species in the Guianas by linking large datasets of fruit traits and vertebrate traits, with a dataset of vertebrate fruit interactions. As it is often assumed that defaunation mostly affects the dispersal of large fruits and seeds, which are positively related to wood density, we compared fruit length, seed mass and wood density between tree species that interacted with hunted vertebrates and species that interacted with non-hunted vertebrates.

We found that the relationship between body mass and seed mass was weak. Yet, hunted vertebrates interacted with heavier seeds, longer fruits and fruits from species with higher wood density compared to non-hunted vertebrates. Vision type and activity pattern were important predictors for fruit color.

Our findings indicate that hunting exerts significant effects on both seed dispersal and seed predation, particularly for larger fruits and seeds, consequently influencing forest composition. The diminished dispersal of seeds might result in reduced wood densities within the forests of the Guianas, ultimately leading to decreased biomass. However, due to the uncertain relative influence of seed dispersal and seed predation on forest composition, accurately predicting the impact of hunting remains challenging.

## ABSTRACT EN FRANÇAIS

Les vertébrés contribuent à façonner les communautés d'arbres dans les forêts tropicales grâce à leurs interactions avec les fruits et à la dispersion ou à la prédation des graines concomitante. Les populations de vertébrés des Guyanes sont en déclin à cause de la chasse, ce qui pourrait avoir des implications majeures sur la composition forestière. Cependant, nos connaissances actuelles sur ce qui détermine les interactions vertébrés-fruits et sur la manière dont elles sont affectées par la chasse sont limitées.

Nous avons étudié les relations trait-trait entre les vertébrés et les fruits (y compris les graines) d'espèces d'arbres des Guyanes en reliant de grands ensembles de données de traits de fruits et de traits de vertébrés, avec un ensemble de données d'interactions de fruits vertébrés. Comme il est souvent supposé que la défaunation affecte principalement la dispersion des gros fruits et des graines, qui sont positivement liées à la densité du bois, nous avons comparé la longueur des fruits, la masse des graines et la densité du bois entre les espèces d'arbres qui ont interagi avec des vertébrés chassés et les espèces qui ont interagi avec des vertébrés non chassés.

Nous avons constaté que la relation entre la masse corporelle et la masse des graines était faible. Pourtant, les vertébrés chassés interagissaient avec des graines plus lourdes, des fruits plus longs et des fruits provenant d'espèces ayant une densité de bois plus élevée que les vertébrés non chassés. Le type de vision et le schéma d'activité étaient des prédicteurs importants de la couleur des fruits.

Nos résultats indiquent que la chasse exerce des effets significatifs à la fois sur la dispersion des graines et sur leur prédation, en particulier pour les fruits et les graines plus gros, influençant ainsi la composition de la forêt. La diminution du processus de dispersion des graines pourrait entraîner une réduction des densités de bois dans les forêts de ces Guyanes, conduisant à terme à une diminution de la biomasse. Cependant, en raison de l'influence relative incertaine de la dispersion et de la prédation des graines sur la composition forestière, il reste difficile de prédire avec précision l'impact de la chasse.

## I. INTRODUCTION

In most tropical moist forests over 80% of woody species are dispersed by vertebrates (Osuri et al. 2016). However, many tropical vertebrate populations are in decline, often as a result of hunting (Peres and Palacios 2007, Harrison et al. 2016, Scabin and Peres 2021). For example, in the Guianas, large vertebrates such Peccary (*Dicotyles tajacu*, *Tayassu pecari*), Tapir (*Tapirus terrestris*) and Paca (*Cuniculus paca*) are among the popular game species and have declining population sizes because of it (Peres 2000, Richard-Hansen et al. 2019). In severe cases, hunting leads to empty forests, where medium- and large-sized vertebrates are extirpated, leaving only small vertebrates (Redford 1992, Harrison 2011).

The presence or absence of frugivores can shape the composition of tropical forests (Correa et al. 2015). Hunting-induced defaunation may affect plant diversity of tropical forests, via changes in seed dispersal and seed predation (Bello et al. 2015). Seed dispersal and seed predation are important mechanisms for the conservation of plant diversity in tropical forests (Seidler and Plotkin 2006, Paine and Beck 2007). Seed dispersal is considered to be important for plants to escape species-specific pathogens, intraspecific competition for resources and predation (Janzen 1970, Connell 1971, Comita et al. 2014, Terborgh 2020), and to colonize vacant sites, while frequency-dependent seed predation is considered to be important mechanism preventing local dominance of any species (Janzen 1970, Connell 1971). Furthermore, long-distance seed dispersal facilitates colonization, climate tracking and increases genetic diversity (Nathan et al. 2008). The loss of vertebrates may thus, via changes in seed dispersal and predation, jeopardize the recruitment success of certain species, and have significant consequences for of the composition and diversity of tree communities (Wright 2003, Muller-Landau 2007, Wright et al. 2007a).

To predict such cascading effects on tree diversity, it is crucial to have a good understanding of vertebrate – fruit interactions, as these interactions are the basis of seed dispersal and predation. The large diversity of vertebrates and plants in the tropics, however, makes it practically impossible to identify all interactions between vertebrates and fruits. The Guianas, for example, harbor an estimated 4,581 tree species (Ter Steege et al. 2013), while 1,850 non-aquatic vertebrate species have been recorded for the Guiana shield (Hollowell and Reynolds 2005). Most studies investigating vertebrate - fruit interactions in the tropics have therefore focused on a small geographical region, or on specific taxonomic groups, such as few vertebrate species or few plant species (Henry et al. 2000, Bender et al. 2018). Although these studies provide information on vertebrate-fruit interactions at highly detailed level, they are insufficient to understand the effects of defaunation on interactions at a landscape scale.

Interactions between vertebrates and fruits or seeds are fundamentally driven by preferences of vertebrates for fruits with certain phenotypes, consisting of a combination of traits. Vertebrate sensory traits, such as vision type, make vertebrates sensitive to particular fruit colors and scents. For example, some tetrachromatic birds are able to see ultraviolet, while trichromatic primates, and dichromatic bats cannot (Schaefer et al. 2007). Furthermore, vertebrates may be physically limited to handle, predate, or disperse certain seeds, for example because the fruit containing the seed, is too large to carry or swallow, or the vertebrate is unable to penetrate a protective outer layer. The relationships between vertebrate and fruit traits are thought to be largely the result of co-evolution, in which fruits have adapted to appeal to specific vertebrates. Through convergent evolution several plant species have developed fruits that are similar in traits. Specific combinations of fruit traits which are common across diverse taxonomic groups, are known as dispersal syndromes and can be especially appealing to specific vertebrate species or vertebrate groups. Although the idea of dispersal syndromes is not without contention (Valenta and Nevo 2020), there is mounting evidence that fruit size, color and scent are important traits that determine vertebrate – fruit interactions (Valenta and Nevo 2020, Raffard et al. 2022).

Most assessments of hunting impacts focus on seed size, an important trait for fruit selection by vertebrates. Maximum size of seeds dispersed by vertebrates is limited by gape size, and, through positive correlation, by body mass (e.g. Galetti et al. 2013). As hunting disproportionately affects the population sizes of medium and large vertebrates, large-seeded species in particular may be affected by hunting (Wright 2003, Wright et al. 2007b, Nunez-Iturri et al. 2008). Brodie and Gibbs (2009) hypothesized that this could have major consequences for forest biomass, due to the positive correlations between seed size and wood density (but see Jansen et al. 2010). Based on the premises of this hypothesis, several modelling studies predicted large reductions in biomass of tropical forests, as a result of defaunation (Bello et al. 2015, Peres et al. 2015, Osuri et al. 2016).

However, seed dispersal is complex and multiple factors remain poorly understood. Firstly, the positive relationship between body mass and seed size is based on little empirical evidence, and has not yet been supported by data for large and diverse group of vertebrates. Additionally, there are several examples of relatively small vertebrates dispersing large seeds (e.g. Guimarães et al. 2008, Jansen et al. 2012, Blanco et al. 2019). Secondly, interactions between vertebrates and fruits are not only determined by seed size, but, for example, also by fruit color and scent. Given that mammals are disproportionately affected by hunting, tree species with specific color and scents that are appealing to mammals (Kelber et al. 2003, Lomáscolo and Schaefer 2010, Rodríguez et al. 2013) may be disadvantaged. Human disturbance has also been

shown to affect the activity patterns of vertebrates, in order to avoid interactions with humans (Gaynor et al. 2018). Thirdly, large vertebrates also disperse many small seeds. It is unclear if the loss of dispersal by of these vertebrates can be mitigated by other, smaller, vertebrates. Thus, it is not immediately evident how hunting affects vertebrate-fruit interactions.

Here we aim to investigate the trait-trait relationships between vertebrates and fruits, how hunting may affect the spectrum of vertebrate – fruit interactions, and how that may cascade onto the trait composition of forests. Our approach includes identifying trait–trait relationships between vertebrates and fruits in Guyana, Suriname and French Guiana (Guianas). We used of a dataset of fruit traits collected from hundreds of studies (Vaessen et al. accepted), and we compiled a dataset of vertebrate traits of mammal and bird species in the Guianas. These datasets were linked using a third dataset of vertebrate-fruit interactions (Vaessen et al. accepted). Although we explored trait – trait relationships in general, we made predictions for relationships which we expected to be most relevant in the context of hunting. We tested the predictions that 1) there is a positive relationship between vertebrate body mass and size-related fruit traits; 2) hunted vertebrate species have interactions with larger fruits and seeds than non-hunted species; 3) vertebrate vision type and activity patterns are important predictors for fruit color; and 4) hunted vertebrate species have interactions with fruits of plant species with higher wood density, compared to non-hunted species.

## 2. MATERIALS AND METHODS

### Research area

The study area consisted of Guyana, Suriname and French Guiana (the Guianas), all located on the Guiana shield, in north-eastern South America, with a combined surface area of approximately 463,000 km<sup>2</sup>. The Guianas mostly consist of forested lowlands up to 200 meters elevation, with the notable exception of the mountainous region in the western part of Guyana (up to 3000 m). Soils on the Guiana shield are diverse but mostly consist of nutrient-poor Ferralsols and Acrisols (Hammond 2005). The Guianas have a tropical climate with daily maximum temperatures at sea level over 25°C. Precipitation ranges from 1400 mm to over 3000 mm annually (Bovololo et al. 2012). The Guianas harbor one of the largest remaining tracts of primary tropical forests in the world. The biodiversity in this region is relatively well documented, with approximately 4,581 tree species in the Guianas (Ter Steege et al. 2013) and 1,850 known non-aquatic vertebrate species on the entire Guiana shield (Hollowell and Reynolds 2005).

Several areas in the Guianas are prone to hunting. Hunting mainly takes place in the populated areas along the coast and along rivers. In inland areas hunting is mostly carried out by Amerindians, maroons and gold miners. Here, in general, hunting pressure is lower compared to the coastal areas, but can be very high in close proximity to indigenous villages (Brodie and Fragoso 2021, Van Kuijk et al. 2022). Subsistence is the primary reason for hunting in the Guianas, but recreational hunting is common, especially in French Guiana. Hunted species are similar across the Guianas, but do differ locally due to abundance of game species and cultural preferences (Richard-Hansen et al. 2019).

## Data

For fruit traits and vertebrate – fruit interactions, we used the Guianan fruits and frugivory dataset (Vaessen et al. 2023). This dataset contains 19 fruit traits of 2282 tree species and 1439 unique vertebrate - fruit interactions documented across Guyana, Suriname and French Guiana. Vertebrate trait data were collected from existing databases (“Encyclopedia of Life” n.d., Jones et al. 2009, Bello et al. 2017), and were expanded through literature searches. Wood density data were collected from the global wood density database (Zanne et al. 2009). For species that were not available in the global wood density database we took weighted means of the genus of South American trees, as genus explains most of the species level variation in wood density (Chave et al. 2006).

## Data imputation

The trait dataset was complete for just 20% of the plant species and just 12% of the vertebrate species. Some statistical analyses, however, require datasets without missing data. In some cases, we used our personal botanical knowledge to fill in missing data. Further estimates were done through phylogenetic associations: We calculated genus or family level means of the number of seeds per fruit, fruit length and vertebrate body mass. For fruit fleshiness we took the value of the majority of species within a genus. These imputations resulted in a complete dataset for 43% of the plant species and 12% of the vertebrate species. The low percentage for vertebrates was mainly because home range was available for only a small proportion of the species.

For the remaining missing data we applied a data imputation method proposed by Audigier et al. (2016), which is suitable for datasets containing both continuous and categorical variables. This method outperforms methods that only use the numerical or categorical data (Hunt 2017). To carry out the imputation we used the R-package *missMDA* (Josse and Husson 2016). The imputation was done on the fruit traits data and vertebrate traits data separately so that the imputation did not strengthen any relationships between fruit and vertebrate traits. As the original data only contained



gape widths from birds and bats, we imputed gape widths only for these groups. We kept taxonomic data as predicting variables in the imputation as we assumed this would improve accuracy of the predictions.

## Statistical analysis

To test associations between vertebrate traits and fruit traits (predictions 1 and 2), we used the RLQ (Dolédec et al. 1996) – a three-matrix ordination method – and fourth corner methods (Legendre et al. 1997), which are commonly used. The methods were developed to analyze the relationships between species traits and environmental variables, through the occurrence of species at certain sites. Both methods require the same three matrices: A matrix with environmental variables per site (R), a matrix with species abundance per site (L), and a matrix with species traits (Q). We applied RLQ and fourth corner methods with a slight modification first applied by Dehling et al. (2014): Here we used a matrix with vertebrate traits (R), a matrix with tree species – vertebrate species interactions (L), and a matrix with fruit traits (Q).

The RLQ method is a multivariate method that provides ordination scores that can be visualized with a biplot, whereas the fourth corner method tests bivariate trait – trait associations. For the RLQ we first applied a correspondence analysis on matrix L, and a Hill and Smith analysis (Hill and Smith 1976) on matrix R and Q, as both matrices contained numerical and categorical variables. The RLQ then obtains a linear combination of the vertebrate traits, and a linear combination of the fruit traits, based on the coefficients of the ordinations. The RLQ then maximizes the covariance between the scores of the two linear combinations, mediated by the vertebrate – fruit interactions.

We used the R package *ade4* (Dray and Dufour 2007) to perform the RLQ and fourth corner analysis. For the fourth corner analysis we applied permutation model 6, in which both the plant species and the vertebrate species of the interaction matrix (L) are permuted. We used 49,999 permutations. To adjust P values for multiple testing we used the false discovery rate method (Benjamini and Hochberg 1995).

Given prediction 1, we emphasized the relationship between vertebrate body mass and fruit length, and between vertebrate body mass and seed mass class. These relationships were tested on the original, unimputed data, using a linear regression to estimate how much of the variability in fruit length and seed mass class was explained by body mass. To assess to what degree only large vertebrates interact with large seeds and fruits, we used a quantile regression model to estimate the 90<sup>th</sup> percentile. Both models had an interaction with dispersal group (bat, bird, rodent, primate, terrestrial mammal). To test prediction 3 and 4 we used a t-test to compare the fruit trait means

between fruits that interact with hunted vertebrates and fruits that interact with non-hunted vertebrates. For the group of hunted vertebrates, we selected 22 species based on French Guianan hunting profiles (Richard-Hansen et al. 2019) (Appendix 1: Table S1). These species are also hunted in Suriname and Guyana, however, due to the recreational character of the hunting in French Guiana there are likely some differences in hunting preferences.

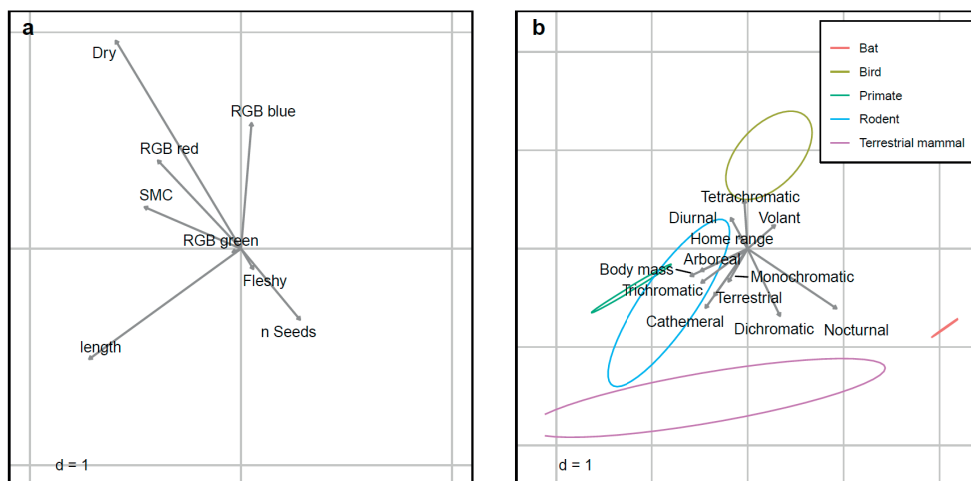
All statistical analyses were carried out in R version 4.1.3 (R Core Team 2022).

### 3. RESULTS

The vertebrate trait dataset contained information of 394 vertebrates species. Of these 155 species had interactions with fruits of 400 species of trees, resulting in a total of 1313 interactions from the Guianan fruits and frugivory dataset (Vaessen et al. accepted). Fruit and vertebrates traits covered a wide range of values. For example, body mass of vertebrates ranged from 6.1 to 207,500 g, seed size ranged by seven orders of magnitude, fruit lengths ranged from 0.15 to 65 cm and the data included nine different color classes.

Overall, interactions between vertebrate species and fruit species were explained by vertebrate traits and fruit traits (Monte-Carlo test;  $p < 0.001$ ). The first two axes of the RLQ had eigenvalues of 0.74 and 0.40 respectively, and explained 57% and 31% of the co-inertia that links the vertebrate traits in matrix R with fruit traits in matrix Q. For fruit traits, the first RLQ axis was associated with fruit length and seed mass class, with lower scores for larger fruits and seeds (Figure 1a), while the second differentiated fruit color and fleshiness, with higher scores for fruit colors containing large proportions of red and blue and for dry fruits. For vertebrate traits, RLQ shows a clear differentiation in dispersal groups, with a slight overlap between primates and rodents (Figure 1b). The first axis mainly differentiates between bats on the right and primates and rodents in the left. The second axis mainly differentiates between birds and terrestrial mammals.

The fourth-corner analysis on all disperser groups combined revealed that multiple vertebrate- and fruit traits were significantly associated with each other (Figure 2). Rodents were the only disperser group showing no significant association with any of the fruit traits.

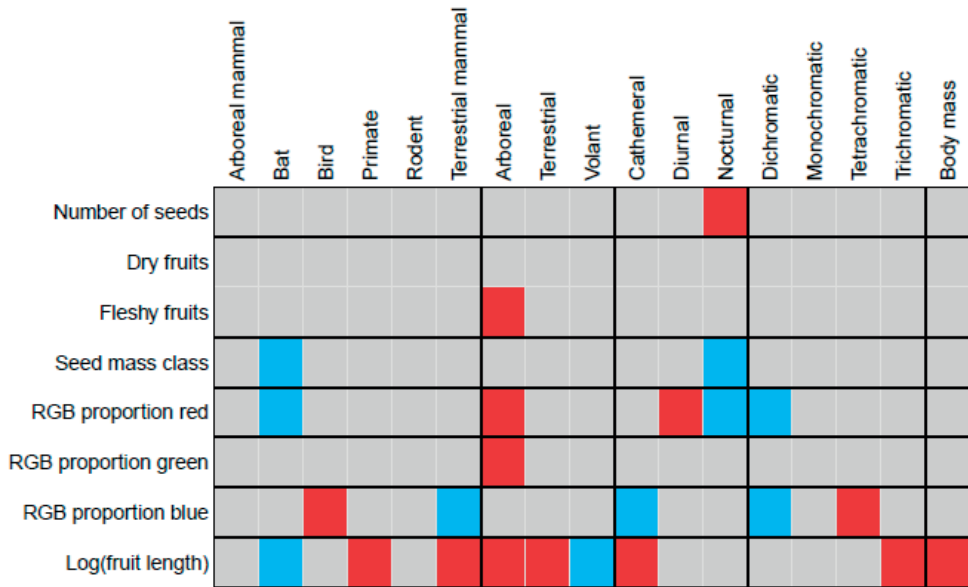


**Figure 1.** Variation in traits of fruit and vertebrate species in Guianan tropical forests. Biplots of RLQ analysis for fruit traits (a) and vertebrate traits (b). In (b) coefficients for ellipses were drawn around the dots of vertebrate species, with each color representing a different disperser group. Value  $d$  indicates the grid size.

Fruit colors containing red were negatively associated with dichromatic vision and nocturnality in vertebrates, and positively associated with diurnality. Fruit colors containing green did not show any significant association with vertebrate vision type or activity type. Fruit colors containing blue showed positive associations with tetrachromatic vision and negative associations with dichromatic vision and cathemerality.

Fruit length had a positive association with vertebrate body mass. Other vertebrate traits with significant associations with fruit length were correlates of body mass, such as the positive associations with primates and terrestrial mammals, and the negative association with bats. Seed mass class only showed a negative association with bats and, likely through correlation, with nocturnal activity pattern. The fourth corner analysis was repeated for each disperser group separately, which resulted in no significant relationships for terrestrial mammals and rodents, while for birds and bats, there was a significant positive association between the logarithm of body mass and the logarithm of fruit length.

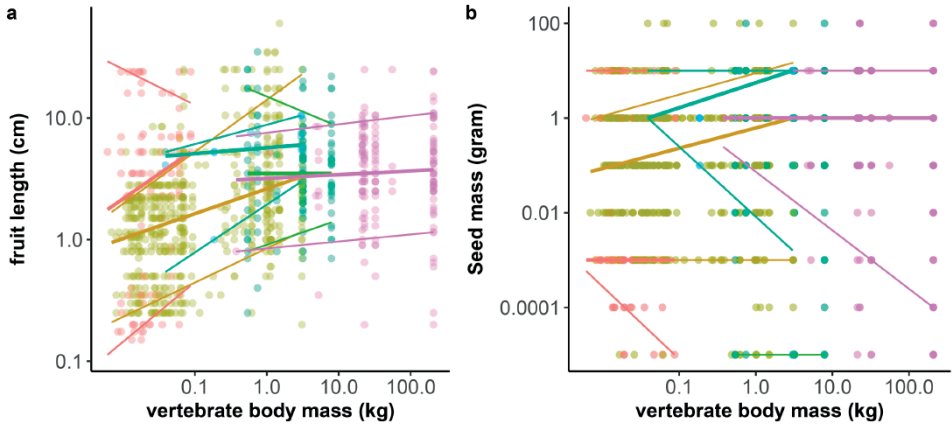
The relationship between the logarithm of body mass and the logarithm of fruit length was significant ( $p < 0.001$ ) (Figure 3a), but with an  $R^2$  of just 0.02, which improved to 0.05 when an interaction with disperser groups was included. Of the separate disperser groups only bats showed a significant positive relationship ( $p < 0.001$ ), while the relationship was only just insignificant for birds ( $p < 0.052$ ). The 90<sup>th</sup> quantiles were significant for all disperser groups, the 50<sup>th</sup> quantiles were significant for all groups except rodents, while the 10<sup>th</sup> quantiles were only significant for bats.



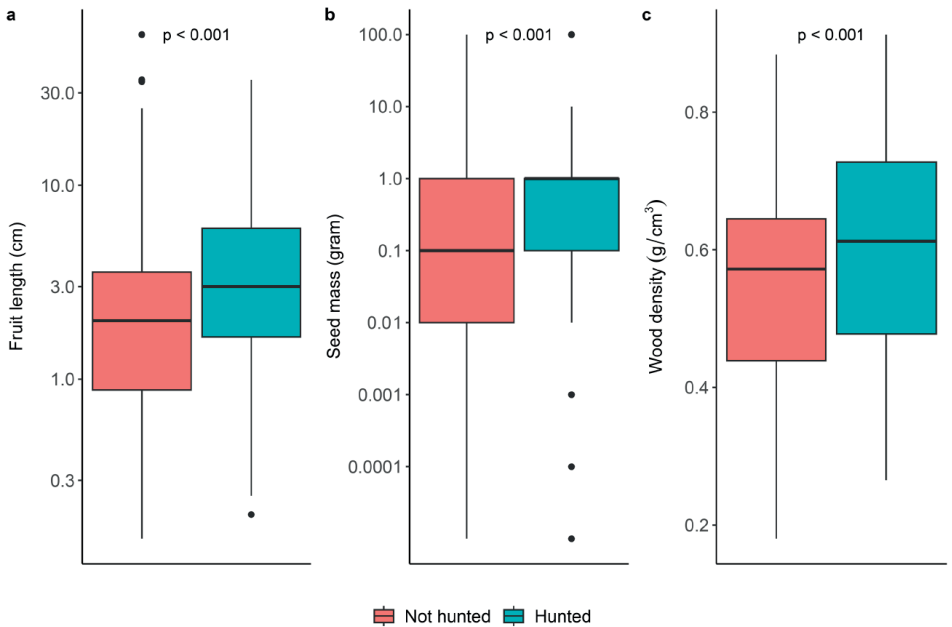
**Figure 2.** Bivariate associations of fruit traits and vertebrate traits for species found in Guianan tropical forests, determined with the fourth corner analysis. Significant negative associations are shown in blue, significant positive associations are shown in red. Black lines separate different variables; white lines separate categories within a variable.

Seed mass class was only significantly related to the logarithm of body mass when the interaction with disperser groups was excluded from the model ( $P < 0.001$ ). However it only explained a fraction of the variation ( $R^2 = 0.01$ ). Separate disperser groups did not show significant relationships. Neither the 90<sup>th</sup> or 10<sup>th</sup> quantiles were significant. The 50<sup>th</sup> quantile was significant for primates and terrestrial mammals.

Plant species that had interactions with hunted vertebrate species had on average a fruit length of 6.6 cm with (range of 0.25 – 52.5). Fruit lengths of plant species that interacted with non-hunted vertebrates averaged 5.4 cm (range 0.23 – 90 cm), which was significantly different ( $p < 0.001$ ,  $R^2 = 0.18$ ), but had large overlap in range (Figure 4a). Seed mass differed significantly ( $p < 0.001$ ,  $R^2 = 0.001$ ) between the non-hunted group with means of 2.4 g (range 0.00001 – 100 g) and for the hunted group with mean 5.5 g (range 0.00001 – 100 g) (Figure 4b). Wood density also differed significantly ( $p < 0.001$ ,  $R^2 = 0.02$ ) with 0.54 g/cm<sup>3</sup> (range 0.18-1.11) for the non-hunted group and 0.59 g/cm<sup>3</sup> (range 0.25-0.93) for the hunted group (Figure 4c).



**Figure 3.** Trait associations of interacting vertebrate and plant species in Guianan tropical forests. a) Relationship between vertebrate body mass and fruit length. b) Relationship between vertebrate body mass and seed mass class. Different colors indicate different dispersal group. Lines are quantile regression lines for the 0.9, 0.5 (thick line) and 0.1 quantiles.



**Figure 4.** Comparison of a) fruit length, b) seed mass and c) wood density of plant species in Guianan tropical forests that interact with hunted (green) and non-hunted vertebrates (red).

## 4. DISCUSSION

It is often assumed that hunting has major implications for the biodiversity and the biomass of tropical forests via altered seed dispersal and seed predation (Dirzo and Miranda 1990, Wright 2003, Dirzo et al. 2014), yet the required insight in vertebrate-fruit interactions and their vulnerability to hunting-induced defaunation remains sparse. We studied the relationships between traits of vertebrates and of fruits of tree species in the Guianas, and determined if they were different for hunted and non-hunted vertebrates. Our findings reveal that the commonly assumed positive relationship between vertebrate body mass and seed size (Bello et al. 2015, Peres et al. 2015, Osuri et al. 2016), is weak. Nonetheless, hunted species in the Guianas interact with significantly larger fruits and seeds compared to non-hunted vertebrates, implying that hunting may affect dispersal and predation of large-seeded plant species more than small seeded plant species.

We observed a positive correlation between body mass and both fruit length and seed mass, which supports our first prediction. However, it is important to note that body mass only accounted for a small portion of the overall variation in fruit length and seed size. The relationship was more prominent for small vertebrates, primarily comprising of bats, birds and rodents. These small vertebrates, however, also interacted with large seeds and fruits (Jansen et al. 2012, Blanco et al. 2019). Conversely, vertebrates weighing over 1 kg demonstrated fewer interactions with small fruits than smaller vertebrates, but still engaged in numerous interactions involving small seeds. This suggests that hunting-induced losses of medium- to large vertebrates may also affect the dispersal and predation of small seeds.

Although the relationship between vertebrate body mass and size-related fruit traits is weak, we found that hunted vertebrates, which generally have a medium- to large body mass, interacted with fruits with heavier seeds than non-hunted vertebrates, in accordance with our second prediction. This aligns with the hypothesis that hunting can affect forest composition, through the reduction of seed dispersal or seed predation of large seeds (Wright 2003, Brodie and Gibbs 2009). Reduced seed dispersal resulting from the absence of large vertebrates may have a negative impact on population size of large seeded species, (Brodie and Gibbs 2009). On the other hand, a decrease in seed predation might be advantageous for large-seeded species, particularly as there is evidence that large seeded species are less vulnerable to density-dependent mortality (Lebrija-Trejos et al. 2016). However, fungi and insects may compensate for reductions in vertebrate seed mortality through seed predation (Wright 2003, Williams et al. 2021). As the fate of seeds after vertebrate – fruit interactions is unknown, the indirect effects of hunting on forest composition currently remain unsure.

Our third prediction focused on the relationship between vertebrate vision type and activity patterns and fruit color. We found that birds, which have tetrachromatic vision, were positively associated with fruit colors that reflect blue light, such as purple, white and blue. The general consensus is that birds prefer contrasting colors, particularly red and black (Wheelwright and Janson 1985). Although our data contained many interactions between birds and red fruits, these interactions were not statistically more prevalent compared to interactions between other dispersal groups and red fruits. Additionally, we found that vertebrates with dichromatic vision, mainly mammals, were negatively associated with colors reflecting blue light. Our findings are in accordance with Lomáscolo and Schaefer (2010) who identified substantial color overlaps between fruits dispersed by birds and primates, but with birds dispersing more blue fruits. Nocturnal vertebrates exhibited a negative association with colors containing red, often dull colors such as green and black, which is in line with the notion that nocturnal vertebrates are sensitive to brightness (Schaefer and Ruxton 2011). Our results affirm that vertebrate vision type and activity patterns are associated to fruit color.

Our findings indicate that hunting may have a strong impact on vertebrate-fruit interactions. We found that hunted vertebrate species interacted with fruits with heavier seeds, compared to non-hunted vertebrates, but also with longer fruits and fruits of species with a higher wood density, in agreement with our fourth prediction. However, we also showed that the vertebrate – fruit interactions are driven by traits of fruits and vertebrates that are not size-related. Fruit color is known as an important predictor for vertebrate – fruit interactions (Korine et al. 2000, Donatti et al. 2007, Lomáscolo and Schaefer 2010), which we confirmed in this study. Fruit color has, however, not yet been taken into account in hunting studies, even though there are multiple scenarios that show how hunting can affect seed dispersal and predation through these relationships. For example, ground-dwelling birds, such as grey-winged trumpeter (*Phophia crepitans*) and black curassow (*Crax allector*) may play an important role in the secondary dispersal of blue and purple fruits on the forest floor but are vulnerable to hunting (Thiollay 2005, Parry et al. 2009). Furthermore, hunted species are known to change activity patterns in response to human disturbance (Gaynor et al. 2018), which may affect their interactions with fruits. In this study we were unable to include scent in our analyses, due to the lack of available data on scent or volatile organic compounds in the literature, but it is likely an important factor in fruit choice. For example, bats and primates have been shown to be attracted to fruit scents (Hodgkison et al. 2013, Nevo et al. 2016), while birds are thought to have less developed olfactory structures (Steiger et al. 2008). Ignoring color and scent in hunting studies will provide an incomplete image of the effects of hunting on vertebrate – fruit interactions.



Although we revealed several trait-trait relationships in vertebrate-fruit interactions based on the data from a large dataset, our understanding of the trait-trait relationships between vertebrates and fruits remains far from complete. It is unlikely that vertebrates always have access to the preferred fruits due to spatial and temporal limitations. For example, most trees produce fruits during wet seasons (Sabatier 1985, Sabatier and Puig 1985, ter Steege and Persaud 1991), when there is plenty of choice for animals, while choices are limited during the dry season and vertebrates may be forced to eat less preferred fruits. The role of such ecological context in vertebrate – fruit interactions may be very important, but has been subject in few studies (Blendinger et al. 2016, Ramos-Robles et al. 2018). It would be useful to further investigate this topic.

This study showed that vertebrate – fruit interactions are driven by multiple vertebrate and fruit traits. In previous studies, there has been a greater emphasis on size-size relationships (Bello et al. 2015, Peres et al. 2016, Osuri et al. 2016), but size – size relationships between vertebrates and fruits are weak and are by itself insufficient to predict the impacts of hunting on forest composition. Nevertheless, our results indicate that larger fruits and seeds are more likely to be affected by hunting than smaller fruits and seeds. As hunting impacts on tropical forests are potentially large and long lasting, we should increase our efforts to understand large scale patterns vertebrate – fruit interactions and seed fate following these interactions.

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# APPENDIX

**Table S1.** Species that were considered hunted in the analyses.

Common species name	Scientific species name	Synonym
Guianan red howler monkey	<i>Alouatta macconnelli</i>	<i>Alouatta seniculus</i>
red-faced spider monkey	<i>Ateles paniscus</i>	
wedge-capped capuchin	<i>Cebus olivaceus</i>	
black curassow	<i>Crax alector</i>	
lowland paca	<i>Cuniculus paca</i>	
red-rumped agouti	<i>Dasyprocta leporina</i>	
tayra	<i>Eira barbara</i>	
red brocket	<i>Mazama americana</i>	
Amazonian brown brocket	<i>Mazama nemorivaga</i>	
red acouchi	<i>Myoprocta acouchy</i>	
South American coati	<i>Nasua nasua</i>	
marbled wood quail	<i>Odontophorus gujanensis</i>	
collared peccary	<i>Pecari tajacu</i>	
marail guan	<i>Penelope marail</i>	
white-faced saki	<i>Pithecia pithecia</i>	
grey-winged trumpeteer	<i>Psophia crepitans</i>	
golden-handed tamarin	<i>Saguinus midas</i>	
Guianan squirrel monkey	<i>Saimiri sciureus</i>	
tufted capuchin	<i>Sapajus apella</i>	<i>Cebus apella</i>
South American tapir	<i>Tapirus terrestris</i>	
white-lipped peccary	<i>Tayassu pecari</i>	
great tinamou	<i>Tinamus major</i>	



**Table S2.** Results of the fourth corner analysis. Pvalue.adj in bold are significant ( $P < 0.05$ ).

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Dispe.arboreal.mammal / Number of seeds	0.039	1.183	0.204	0.397
Dispe.bat.mammal / Number of seeds	0.191	2.743	0.014	0.074
Dispe.bird / Number of seeds	-0.123	-1.762	0.075	0.195
Dispe.primate.mammal / Number of seeds	-0.038	-1.051	0.295	0.485
Dispe.rodent.mammal / Number of seeds	-0.008	-0.275	0.814	0.909
Dispe.terrestrial.mammal / Number of seeds	0.012	0.212	0.834	0.921
Locom.Arboreal / Number of seeds	-0.021	-0.567	0.578	0.708
Locom.Terrestrial / Number of seeds	-0.010	-0.297	0.769	0.877
Locom.Volant / Number of seeds	0.026	0.529	0.612	0.736
Activ.Cathemeral / Number of seeds	-0.011	-0.341	0.739	0.855
Activ.Diurnal / Number of seeds	-0.147	-2.347	0.017	0.074
Activ.Nocturnal / Number of seeds	0.186	2.921	0.008	0.044
Visio.Dichromacy / Number of seeds	0.148	2.353	0.017	0.074
Visio.Monochromacy / Number of seeds	0.046	1.419	0.130	0.284
Visio.Tetrachromacy / Number of seeds	-0.123	-1.762	0.075	0.195
Visio.Trichromacy / Number of seeds	-0.038	-1.051	0.295	0.485
Home range / Number of seeds	-0.027	-0.713	0.474	0.636
log(Body mass) / Number of seeds	-0.039	-0.696	0.512	0.658
Dispe.arboreal.mammal / Flesh.Dry	0.000	-0.669	0.486	0.636
Dispe.bat.mammal / Flesh.Dry	1.000	-1.776	0.065	0.180
Dispe.bird / Flesh.Dry	80.000	-0.048	0.971	0.978
Dispe.primate.mammal / Flesh.Dry	15.000	-1.649	0.112	0.256
Dispe.rodent.mammal / Flesh.Dry	3.000	-0.001	1.000	1.000
Dispe.terrestrial.mammal / Flesh.Dry	18.000	-1.121	0.291	0.485
Locom.Arboreal / Flesh.Dry	15.000	1.067	0.241	0.441
Locom.Terrestrial / Flesh.Dry	21.000	-1.510	0.137	0.286
Locom.Volant / Flesh.Dry	81.000	-0.373	0.722	0.845
Activ.Cathemeral / Flesh.Dry	18.000	-0.911	0.381	0.548
Activ.Diurnal / Flesh.Dry	98.000	-0.140	0.899	0.952
Activ.Nocturnal / Flesh.Dry	1.000	-2.419	0.021	0.080
Visio.Dichromacy / Flesh.Dry	22.000	-1.018	0.336	0.520
Visio.Monochromacy / Flesh.Dry	0.000	-0.384	0.813	0.909
Visio.Tetrachromacy / Flesh.Dry	80.000	-0.048	0.971	0.978
Visio.Trichromacy / Flesh.Dry	15.000	-1.649	0.112	0.256
Home range / Flesh.Dry	0.222	4.747	0.000	<b>0.002</b>
log(Body mass) / Flesh.Dry	0.066	0.908	0.373	0.547
Dispe.arboreal.mammal / Flesh.Fleshy	34.000	0.543	0.544	0.690
Dispe.bat.mammal / Flesh.Fleshy	177.000	-0.840	0.413	0.581
Dispe.bird / Flesh.Fleshy	611.000	0.048	0.971	0.978

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Dispe.primate.mammal / Flesh.Fleshy	170.000	1.649	0.112	0.256
Dispe.rodent.mammal / Flesh.Fleshy	14.000	-0.666	0.501	0.650
Dispe.terrestrial.mammal / Flesh.Fleshy	190.000	1.121	0.291	0.485
Locom.Arboreal / Flesh.Fleshy	252.000	2.971	0.004	<b>0.028</b>
Locom.Terrestrial / Flesh.Fleshy	245.000	1.510	0.137	0.286
Locom.Volant / Flesh.Fleshy	699.000	0.373	0.722	0.845
Activ.Cathemeral / Flesh.Fleshy	175.000	0.911	0.381	0.548
Activ.Diurnal / Flesh.Fleshy	767.000	0.140	0.899	0.952
Activ.Nocturnal / Flesh.Fleshy	254.000	-0.512	0.629	0.749
Visio.Dichromacy / Flesh.Fleshy	391.000	0.803	0.440	0.609
Visio.Monochromacy / Flesh.Fleshy	24.000	1.846	0.093	0.226
Visio.Tetrachromacy / Flesh.Fleshy	611.000	0.048	0.971	0.978
Visio.Trichromacy / Flesh.Fleshy	170.000	1.649	0.112	0.256
Home range / Flesh.Fleshy	-0.222	-4.747	0.000	<b>0.002</b>
log(Body mass) / Flesh.Fleshy	-0.066	-0.908	0.373	0.547
Dispe.arboreal.mammal / Seed mass class	0.003	0.135	0.895	0.952
Dispe.bat.mammal / Seed mass class	-0.280	-3.928	0.000	<b>0.002</b>
Dispe.bird / Seed mass class	0.098	1.389	0.165	0.330
Dispe.primate.mammal / Seed mass class	0.037	0.967	0.336	0.520
Dispe.rodent.mammal / Seed mass class	0.067	1.903	0.061	0.178
Dispe.terrestrial.mammal / Seed mass class	0.071	1.720	0.087	0.219
Locom.Arboreal / Seed mass class	0.048	1.082	0.280	0.485
Locom.Terrestrial / Seed mass class	0.101	2.226	0.025	0.091
Locom.Volant / Seed mass class	-0.122	-1.990	0.046	0.145
Activ.Cathemeral / Seed mass class	0.069	1.721	0.086	0.219
Activ.Diurnal / Seed mass class	0.137	2.133	0.032	0.114
Activ.Nocturnal / Seed mass class	-0.225	-3.452	0.000	<b>0.006</b>
Visio.Dichromacy / Seed mass class	-0.131	-2.036	0.042	0.140
Visio.Monochromacy / Seed mass class	-0.009	-0.222	0.839	0.921
Visio.Tetrachromacy / Seed mass class	0.098	1.389	0.165	0.330
Visio.Trichromacy / Seed mass class	0.037	0.967	0.336	0.520
Home range / Seed mass class	0.011	0.287	0.774	0.877
log(Body mass) / Seed mass class	0.127	1.874	0.060	0.178
Dispe.arboreal.mammal / RGB proportion red	0.024	0.672	0.472	0.636
Dispe.bat.mammal / RGB proportion red	-0.260	-3.634	0.000	<b>0.003</b>
Dispe.bird / RGB proportion red	0.129	1.847	0.065	0.180
Dispe.primate.mammal / RGB proportion red	0.093	2.373	0.018	0.074
Dispe.rodent.mammal / RGB proportion red	0.045	1.220	0.228	0.426
Dispe.terrestrial.mammal / RGB proportion red	-0.047	-1.113	0.265	0.466
Locom.Arboreal / RGB proportion red	0.127	2.788	0.005	<b>0.030</b>

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Locom.Terrestrial / RGB proportion red	-0.057	-1.232	0.217	0.417
Locom.Volant / RGB proportion red	-0.057	-0.927	0.355	0.544
Activ.Cathemeral / RGB proportion red	-0.042	-1.025	0.308	0.493
Activ.Diurnal / RGB proportion red	0.212	3.304	0.001	<b>0.008</b>
Activ.Nocturnal / RGB proportion red	-0.217	-3.317	0.001	<b>0.007</b>
Visio.Dichromacy / RGB proportion red	-0.226	-3.502	0.000	<b>0.006</b>
Visio.Monochromacy / RGB proportion red	0.057	1.631	0.070	0.190
Visio.Tetrachromacy / RGB proportion red	0.129	1.847	0.065	0.180
Visio.Trichromacy / RGB proportion red	0.093	2.373	0.018	0.074
Home range / RGB proportion red	-0.019	-0.506	0.614	0.736
log(Body mass) / RGB proportion red	0.056	0.823	0.414	0.581
Dispe.arboreal.mammal / RGB proportion green	0.031	1.030	0.297	0.485
Dispe.bat.mammal / RGB proportion green	0.003	0.051	0.960	0.978
Dispe.bird / RGB proportion green	-0.040	-0.562	0.577	0.708
Dispe.primate.mammal / RGB proportion green	0.095	2.358	0.018	0.074
Dispe.rodent.mammal / RGB proportion green	0.027	0.832	0.415	0.581
Dispe.terrestrial.mammal / RGB proportion green	-0.060	-1.468	0.144	0.295
Locom.Arboreal / RGB proportion green	0.130	2.788	0.005	<b>0.030</b>
Locom.Terrestrial / RGB proportion green	-0.071	-1.576	0.115	0.258
Locom.Volant / RGB proportion green	-0.048	-0.732	0.468	0.636
Activ.Cathemeral / RGB proportion green	-0.060	-1.524	0.128	0.283
Activ.Diurnal / RGB proportion green	0.035	0.558	0.581	0.708
Activ.Nocturnal / RGB proportion green	0.012	0.190	0.851	0.922
Visio.Dichromacy / RGB proportion green	-0.045	-0.704	0.485	0.636
Visio.Monochromacy / RGB proportion green	0.058	2.060	0.039	0.134
Visio.Tetrachromacy / RGB proportion green	-0.040	-0.562	0.577	0.708
Visio.Trichromacy / RGB proportion green	0.095	2.358	0.018	0.074
Home range / RGB proportion green	-0.083	-2.333	0.019	0.074
log(Body mass) / RGB proportion green	-0.020	-0.332	0.742	0.855
Dispe.arboreal.mammal / RGB proportion blue	-0.027	-0.920	0.372	0.547
Dispe.bat.mammal / RGB proportion blue	-0.092	-1.309	0.170	0.336
Dispe.bird / RGB proportion blue	0.192	2.900	0.002	<b>0.018</b>
Dispe.primate.mammal / RGB proportion blue	-0.043	-1.160	0.248	0.441
Dispe.rodent.mammal / RGB proportion blue	-0.038	-1.226	0.224	0.424
Dispe.terrestrial.mammal / RGB proportion blue	-0.112	-2.744	0.006	<b>0.032</b>
Locom.Arboreal / RGB proportion blue	-0.038	-0.915	0.368	0.547
Locom.Terrestrial / RGB proportion blue	-0.100	-2.247	0.024	0.089
Locom.Volant / RGB proportion blue	0.113	1.923	0.050	0.154
Activ.Cathemeral / RGB proportion blue	-0.111	-2.818	0.005	<b>0.030</b>
Activ.Diurnal / RGB proportion blue	0.143	2.344	0.017	0.074

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Activ.Nocturnal / RGB proportion blue	-0.072	-1.142	0.244	0.441
Visio.Dichromacy / RGB proportion blue	-0.172	-2.772	0.005	<b>0.030</b>
Visio.Monochromacy / RGB proportion blue	-0.008	-0.370	0.844	0.921
Visio.Tetrachromacy / RGB proportion blue	0.192	2.900	0.002	<b>0.018</b>
Visio.Trichromacy / RGB proportion blue	-0.043	-1.160	0.248	0.441
Home range / RGB proportion blue	0.063	1.701	0.090	0.223
log(Body mass) / RGB proportion blue	-0.141	-2.182	0.023	0.087
Dispe.arboreal.mammal / log(Length)	0.026	0.645	0.546	0.690
Dispe.bat.mammal / log(Length)	-0.216	-2.826	0.002	<b>0.018</b>
Dispe.bird / log(Length)	-0.147	-1.981	0.046	0.145
Dispe.primate.mammal / log(Length)	0.193	3.118	0.000	<b>0.006</b>
Dispe.rodent.mammal / log(Length)	0.081	1.465	0.137	0.286
Dispe.terrestrial.mammal / log(Length)	0.182	2.727	0.002	<b>0.018</b>
Locom.Arboreal / log(Length)	0.193	2.812	0.001	<b>0.013</b>
Locom.Terrestrial / log(Length)	0.175	2.523	0.005	<b>0.030</b>
Locom.Volant / log(Length)	-0.301	-4.118	0.000	<b>0.001</b>
Activ.Cathemeral / log(Length)	0.187	3.024	0.001	<b>0.008</b>
Activ.Diurnal / log(Length)	0.009	0.074	0.944	0.978
Activ.Nocturnal / log(Length)	-0.178	-2.322	0.017	0.074
Visio.Dichromacy / log(Length)	0.003	0.066	0.948	0.978
Visio.Monochromacy / log(Length)	0.032	0.919	0.306	0.493
Visio.Tetrachromacy / log(Length)	-0.147	-1.981	0.046	0.145
Visio.Trichromacy / log(Length)	0.193	3.118	0.000	<b>0.006</b>
Home range / log(Length)	0.047	0.738	0.481	0.636
log(Body mass) / log(Length)	0.426	5.788	0.000	<b>0.001</b>

**Table S3.** Results of the fourth corner analysis for the disperser group bats. Pvalue.adj in bold are significant ( $P < 0.05$ ).

Test	Obs	Std.Obs	Alter	Pvalue	Pvalue.adj
Home range / Number of seeds	-0.087	-1.124	two-sided	0.271	0.361
log(Body mass) / Number of seeds	0.060	0.776	two-sided	0.451	0.541
Home range / Seed mass class	-0.158	-2.087	two-sided	0.035	0.083
log(Body mass) / Seed mass class	0.112	1.497	two-sided	0.137	0.273
Home range / RGB proportion red	-0.206	-2.711	two-sided	0.005	<b>0.019</b>
log(Body mass) / RGB proportion red	0.180	2.418	two-sided	0.014	<b>0.041</b>
Home range / RGB proportion green	-0.048	-0.626	two-sided	0.542	0.592
log(Body mass) / RGB proportion green	0.001	0.004	two-sided	0.996	0.996
Home range / RGB proportion blue	-0.110	-1.290	two-sided	0.201	0.345
log(Body mass) / RGB proportion blue	0.097	1.134	two-sided	0.269	0.361
Home range / log(Length)	-0.272	-3.310	two-sided	0.000	<b>0.002</b>
log(Body mass) / log(Length)	0.229	2.785	two-sided	0.003	<b>0.015</b>

**Table S4.** Results of the fourth corner analysis for the disperser group birds. Pvalue.adj in bold are significant ( $P < 0.05$ ).

Test	Obs	Std.Obs	Alter	Pvalue	Pvalue.adj
Locom.Arboreal / Number of seeds	0.076	2.280	less	0.974	1.000
Locom.Terrestrial / Number of seeds	0.019	0.062	less	0.679	1.000
Locom.Volant / Number of seeds	0.903	0.532	less	0.633	1.000
Activ.Diurnal / Number of seeds	0.980	0.776	less	0.777	1.000
Activ.Nocturnal / Number of seeds	0.019	0.062	less	0.679	1.000
Visio.Tetrachromacy / Number of seeds	1.000	<NA>	less	1.000	1.000
log(Body mass) / Number of seeds	0.033	0.157	two-sided	0.889	1.000
Locom.Arboreal / Flesh.Dry	0.000	-0.537	two-sided	0.533	1.000
Locom.Terrestrial / Flesh.Dry	0.000	-0.541	two-sided	0.530	1.000
Locom.Volant / Flesh.Dry	80.000	-0.364	two-sided	0.730	1.000
Activ.Diurnal / Flesh.Dry	80.000	0.541	two-sided	0.530	1.000
Activ.Nocturnal / Flesh.Dry	0.000	-0.541	two-sided	0.530	1.000
Visio.Tetrachromacy / Flesh.Dry	80.000	<NA>	two-sided	1.000	1.000
log(Body mass) / Flesh.Dry	0.110	0.032	less	0.542	1.000
Locom.Arboreal / Flesh.Fleshy	52.000	2.716	two-sided	0.007	0.187
Locom.Terrestrial / Flesh.Fleshy	37.000	2.663	two-sided	0.029	0.405
Locom.Volant / Flesh.Fleshy	522.000	0.364	two-sided	0.730	1.000
Activ.Diurnal / Flesh.Fleshy	574.000	0.669	two-sided	0.522	1.000
Activ.Nocturnal / Flesh.Fleshy	37.000	2.663	two-sided	0.029	0.405
Visio.Tetrachromacy / Flesh.Fleshy	611.000	<NA>	two-sided	1.000	1.000
log(Body mass) / Flesh.Fleshy	0.872	0.761	less	0.769	1.000
Locom.Arboreal / Seed mass class	0.078	2.683	less	0.959	1.000
Locom.Terrestrial / Seed mass class	0.046	1.258	less	0.916	1.000
Locom.Volant / Seed mass class	0.873	0.256	less	0.553	1.000
Activ.Diurnal / Seed mass class	0.952	0.472	less	0.643	1.000
Activ.Nocturnal / Seed mass class	0.046	1.258	less	0.916	1.000
Visio.Tetrachromacy / Seed mass class	1.000	<NA>	less	1.000	1.000
log(Body mass) / Seed mass class	0.014	0.180	two-sided	0.862	1.000
Locom.Arboreal / RGB proportion red	0.063	2.967	less	0.990	1.000
Locom.Terrestrial / RGB proportion red	0.050	2.160	less	0.964	1.000
Locom.Volant / RGB proportion red	0.884	0.846	less	0.808	1.000
Activ.Diurnal / RGB proportion red	0.947	0.217	less	0.556	1.000
Activ.Nocturnal / RGB proportion red	0.050	2.160	less	0.964	1.000
Visio.Tetrachromacy / RGB proportion red	1.000	<NA>	less	1.000	1.000
log(Body mass) / RGB proportion red	-0.032	-0.301	two-sided	0.764	1.000
Locom.Arboreal / RGB proportion green	0.087	4.952	less	1.000	1.000
Locom.Terrestrial / RGB proportion green	0.052	2.475	less	0.970	1.000
Locom.Volant / RGB proportion green	0.857	-0.181	less	0.361	1.000

Test	Obs	Std.Obs	Alter	Pvalue	Pvalue.adj
Activ.Diurnal / RGB proportion green	0.947	0.220	less	0.525	1.000
Activ.Nocturnal / RGB proportion green	0.052	2.475	less	0.970	1.000
Visio.Tetrachromacy / RGB proportion green	1.000	<NA>	less	1.000	1.000
log(Body mass) / RGB proportion green	-0.039	-0.435	two-sided	0.667	1.000
Locom.Arboreal / RGB proportion blue	0.043	1.854	less	0.950	1.000
Locom.Terrestrial / RGB proportion blue	0.043	1.918	less	0.957	1.000
Locom.Volant / RGB proportion blue	0.913	0.696	less	0.722	1.000
Activ.Diurnal / RGB proportion blue	0.956	0.417	less	0.585	1.000
Activ.Nocturnal / RGB proportion blue	0.043	1.918	less	0.957	1.000
Visio.Tetrachromacy / RGB proportion blue	1.000	<NA>	less	1.000	1.000
log(Body mass) / RGB proportion blue	-0.105	-1.164	two-sided	0.265	1.000
Locom.Arboreal / log(Length)	0.046	2.198	less	0.944	1.000
Locom.Terrestrial / log(Length)	0.024	0.717	less	0.856	1.000
Locom.Volant / log(Length)	0.926	1.682	less	0.978	1.000
Activ.Diurnal / log(Length)	0.976	1.811	less	0.991	1.000
Activ.Nocturnal / log(Length)	0.024	0.717	less	0.856	1.000
Visio.Tetrachromacy / log(Length)	1.000	<NA>	less	1.000	1.000
log(Body mass) / log(Length)	0.476	4.681	two-sided	0.000	<b>0.001</b>



**Table S5.** Results of the fourth corner analysis for the disperser group terrestrial mammals. Pvalue.adj in bold are significant ( $P < 0.05$ ).

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Activ.Cathemeral / Number of seeds	0.782	1.367	0.936	1.000
Activ.Nocturnal / Number of seeds	0.187	1.911	0.951	1.000
Visio.Dichromacy / Number of seeds	1.000	<NA>	1.000	1.000
log(Body mass) / Number of seeds	-0.069	-1.047	0.299	1.000
Activ.Cathemeral / Flesh.Dry	18.000	-1.057	0.358	1.000
Activ.Nocturnal / Flesh.Dry	0.000	-1.124	0.378	1.000
Visio.Dichromacy / Flesh.Dry	18.000	<NA>	1.000	1.000
log(Body mass) / Flesh.Dry	0.044	-1.622	0.009	0.300
Activ.Cathemeral / Flesh.Fleshy	175.000	1.057	0.358	1.000
Activ.Nocturnal / Flesh.Fleshy	15.000	1.124	0.378	1.000
Visio.Dichromacy / Flesh.Fleshy	190.000	<NA>	1.000	1.000
log(Body mass) / Flesh.Fleshy	0.956	1.515	0.998	1.000
Activ.Cathemeral / Seed mass class	0.959	1.760	0.983	1.000
Activ.Nocturnal / Seed mass class	0.041	-0.847	0.223	1.000
Visio.Dichromacy / Seed mass class	1.000	<NA>	1.000	1.000
log(Body mass) / Seed mass class	-0.119	-1.251	0.271	1.000
Activ.Cathemeral / RGB proportion red	0.913	1.837	0.991	1.000
Activ.Nocturnal / RGB proportion red	0.086	1.525	0.962	1.000
Visio.Dichromacy / RGB proportion red	1.000	<NA>	1.000	1.000
log(Body mass) / RGB proportion red	0.042	0.618	0.546	1.000
Activ.Cathemeral / RGB proportion green	0.892	1.665	0.975	1.000
Activ.Nocturnal / RGB proportion green	0.107	1.644	0.958	1.000
Visio.Dichromacy / RGB proportion green	1.000	<NA>	1.000	1.000
log(Body mass) / RGB proportion green	-0.032	-0.484	0.637	1.000
Activ.Cathemeral / RGB proportion blue	0.660	0.576	0.725	1.000
Activ.Nocturnal / RGB proportion blue	0.334	3.646	0.986	1.000
Visio.Dichromacy / RGB proportion blue	1.000	<NA>	1.000	1.000
log(Body mass) / RGB proportion blue	-0.159	-2.169	0.023	0.365
Activ.Cathemeral / log(Length)	0.879	1.624	0.983	1.000
Activ.Nocturnal / log(Length)	0.097	1.122	0.858	1.000
Visio.Dichromacy / log(Length)	1.000	<NA>	1.000	1.000
log(Body mass) / log(Length)	0.054	0.790	0.434	1.000

**Table S6.** Results of the fourth corner analysis for the disperser group rodents. Pvalue.adj in bold are significant ( $P < 0.05$ ).

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Locom.Arboreal / Number of seeds	0.862	1.736	0.978	1.000
Locom.Terrestrial / Number of seeds	0.004	-0.994	0.334	1.000
Activ.Diurnal / Number of seeds	1.000	<NA>	1.000	1.000
Visio.Dichromacy / Number of seeds	1.000	<NA>	1.000	1.000
log(Body mass) / Number of seeds	-0.232	-0.727	0.623	1.000
Locom.Arboreal / Flesh.Dry	0.000	-0.860	0.669	1.000
Locom.Terrestrial / Flesh.Dry	3.000	1.564	0.333	1.000
Activ.Diurnal / Flesh.Dry	3.000	<NA>	1.000	1.000
Visio.Dichromacy / Flesh.Dry	3.000	<NA>	1.000	1.000
log(Body mass) / Flesh.Dry	0.041	-0.457	0.550	1.000
Locom.Arboreal / Flesh.Fleshy	5.000	-0.647	0.835	1.000
Locom.Terrestrial / Flesh.Fleshy	9.000	0.647	0.835	1.000
Activ.Diurnal / Flesh.Fleshy	14.000	<NA>	1.000	1.000
Visio.Dichromacy / Flesh.Fleshy	14.000	<NA>	1.000	1.000
log(Body mass) / Flesh.Fleshy	0.922	0.912	0.710	1.000
Locom.Arboreal / Seed mass class	0.024	-1.048	0.169	1.000
Locom.Terrestrial / Seed mass class	0.968	1.070	1.000	1.000
Activ.Diurnal / Seed mass class	1.000	<NA>	1.000	1.000
Visio.Dichromacy / Seed mass class	1.000	<NA>	1.000	1.000
log(Body mass) / Seed mass class	-0.012	-0.012	0.992	1.000
Locom.Arboreal / RGB proportion red	0.000	-1.065	0.169	1.000
Locom.Terrestrial / RGB proportion red	0.797	0.692	0.739	1.000
Activ.Diurnal / RGB proportion red	1.000	<NA>	1.000	1.000
Visio.Dichromacy / RGB proportion red	1.000	<NA>	1.000	1.000
log(Body mass) / RGB proportion red	-0.472	-1.440	0.124	1.000
Locom.Arboreal / RGB proportion green	0.062	-1.465	0.169	1.000
Locom.Terrestrial / RGB proportion green	0.507	0.340	0.669	1.000
Activ.Diurnal / RGB proportion green	1.000	<NA>	1.000	1.000
Visio.Dichromacy / RGB proportion green	1.000	<NA>	1.000	1.000
log(Body mass) / RGB proportion green	-0.556	-1.395	0.251	1.000
Locom.Arboreal / RGB proportion blue	0.000	-1.350	0.331	1.000
Locom.Terrestrial / RGB proportion blue	0.872	1.218	1.000	1.000
Activ.Diurnal / RGB proportion blue	1.000	<NA>	1.000	1.000
Visio.Dichromacy / RGB proportion blue	1.000	<NA>	1.000	1.000
log(Body mass) / RGB proportion blue	0.278	1.000	0.457	1.000
Locom.Arboreal / log(Length)	0.266	0.194	0.559	1.000
Locom.Terrestrial / log(Length)	0.670	0.615	0.835	1.000
Activ.Diurnal / log(Length)	1.000	<NA>	1.000	1.000

Test	Obs	Std.Obs	Pvalue	Pvalue.adj
Visio.Dichromacy / log(Length)	1.000	<NA>	1.000	1.000
log(Body mass) / log(Length)	0.143	0.759	0.665	1.000



# Chapter 5

## Defaunation changes leaf trait composition of recruit communities in tropical forests in French Guiana

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## ABSTRACT

- (1) Hunting impacts tropical vertebrate populations, causing declines of species that function as seed dispersers and predators, or that browse seedlings and saplings. Whether and how the resulting reductions in seed dispersal, seed predation and browsing translate to changes in the tree composition is poorly understood.
- (2) Here, we assess the effect of defaunation on the functional composition of communities of tree recruits in tropical rainforests in French Guiana.
- (3) We selected eight sites along a gradient of defaunation, caused by differences in hunting pressure, in otherwise intact old-growth forests in French Guiana. We measured shifts in functional composition by comparing leaf and fruit traits and wood density between tree recruits (up to 5 cm diameter at breast height) and adults, and tested whether and how these compositional shifts related to defaunation.
- (4) We found a positive relationship with defaunation for shifts in specific leaf area, a negative relationship for shifts of leaf toughness and wood density, and a weak relationship for shifts in fruit traits.
- (5) Our results suggest that the loss of vertebrates affects ecological processes such as seed dispersal and browsing, of which browsing remains understudied. Even though these changes sometimes seem minor, together they result in major shifts in forest composition. These changes have long-term ramifications which may alter forest dynamics for generations.



## ABSTRACT EN FRANÇAIS

- (1) La chasse a un impact sur les populations de vertébrés tropicaux, provoquant le déclin des espèces qui fonctionnent comme disperseurs de graines et prédateurs, ou qui abrutissent les semis et les jeunes arbres. La question de savoir si et comment les réductions résultantes de la dispersion des graines, de la prédation des graines et de l'abrutissement se traduisent par des changements dans la composition des arbres est mal comprise.
- (2) Nous évaluons ici l'effet de la défaunation sur la composition fonctionnelle des communautés de recrues d'arbres dans les forêts tropicales humides de Guyane française.
- (3) Nous avons sélectionné huit sites le long d'un gradient de défaunation, causé par des différences de pression de chasse, dans des forêts anciennes par ailleurs intactes de Guyane française. Nous avons mesuré les changements dans la composition fonctionnelle en comparant les caractéristiques des feuilles et des fruits et la densité du bois entre les recrues d'arbres (jusqu'à 5 cm de diamètre à hauteur de poitrine) et les adultes, et avons testé si et comment ces changements de composition étaient liés à la défaunation.
- (4) Nous avons trouvé une relation positive avec la défaunation pour les changements de surface foliaire spécifique, une relation négative pour les changements de feuilles fibreuses et de densité du bois, et une relation faible pour les changements dans les caractéristiques des fruits.



## I. INTRODUCTION

Hunting is common throughout tropical forests, resulting in the decline of vertebrate populations in many regions (Brashares 2004, Peres and Palacios 2007). Hunting disproportionately affects large-bodied vertebrates, which are preferred game species, leading to compositional changes in the vertebrate community (Peres and Palacios 2007, Bugir et al. 2021). These changes are thought to have cascading effects on forest regeneration, due to the important roles that these vertebrates play in seed dispersal, seed predation and herbivory (Terborgh 1988, Dirzo and Miranda 1991, Wright 2003, Terborgh et al. 2008, Galetti and Dirzo 2013, Kurten 2013, Kurten and Carson 2015).

Interactions between vertebrates and plants are fundamentally driven by the preferences of vertebrates for leaves, seeds, and fruits with certain traits. In leaves, vertebrates generally prefer low toughness, high specific leaf area, high nutrient content and low concentrations of secondary metabolites (Coley and Barone 1996, Kursar and Coley 2003, Poorter et al. 2004, Kitajima and Poorter 2010, Coley and Kursar 2014). Most herbivory occurs at the early stages of leaf development, before leaves toughen. Some plant species have leaves that quickly expand and toughen, supposedly to escape herbivory, but this strategy requires many nitrogen-containing enzymes and thus makes leaves more attractive to herbivores. Other plant species are thought to avoid herbivory by expanding their leaves slowly, requiring much less nitrogen (Kursar and Coley 1991, 2003). For seeds and fruits, preferences of vertebrates are more complex and taxon-specific (Gautier-Hion et al. 1985). Vertebrates that feed on fruits and seeds often prefer specific dispersal syndromes (Pijl 1969, Gautier-Hion et al. 1985), which are mostly defined by the color, fleshiness and size of fruits and seeds. For example, birds typically prefer small, fleshy fruits that have a red or black color (Janson 1983). Because of such preferences, the loss of these vertebrates will likely result in altered patterns of seed dispersal and predation, seedling herbivory and, as a consequence, tree recruitment, which may ultimately change forest composition for many functional traits.

Empirical tests of hunting-induced changes in functional trait composition have been limited mostly to seed size, in particular in relation to vertebrate body mass. Larger vertebrates are assumed to disperse larger seeds (Dirzo et al. 2007, Wright et al. 2007, Nunez-Iturri et al. 2008, Terborgh et al. 2008), hence the loss of large-bodied dispersers has been predicted to reduce the dispersal of large-seeded tree species, increase spatial clustering, and therefore lower the survival odds of these species due to increased density-dependent mortality (Brodie and Gibbs 2009). Because seed mass is positively correlated to wood density and tree height (Bello et al. 2015), hunting could thus

induce a shift towards lower overall forest biomass (Bello et al. 2015, Peres et al. 2016, Osuri et al. 2016). These models, however, oversimplify recruitment, which involves many ecological processes and functional traits. Moreover, recent studies suggest that defaunation-induced changes in forest community composition and structure are not driven by dispersal limitation only (Bagchi et al. 2018, Hazelwood et al. 2020). Browsing may be another mechanism through which defaunation can affect forest composition (Dirzo and Miranda 1991), due to the preference of browsers for leaves with certain traits. However, browsing has received little attention in the context of defaunation (but see: Camargo-Sanabria et al. 2015). Thus the relationship between vertebrate composition and functional trait composition of the plant community remains poorly understood.

A better understanding of the relationship between vertebrate composition and functional trait composition of the plant community could be achieved by comparing the functional composition of trees between forest sites that vary in their level of defaunation, for example as a result of hunting. Such comparison should consider traits that are linked to seed dispersal, seed predation and browsing, which each may change with defaunation. Several studies have applied this approach (Wright et al. 2007, Terborgh et al. 2008, Harrison et al. 2013, Kurten et al. 2015), but only one included traits related to browsing (Kurten et al. 2015). Furthermore, most past studies are, limited to few study sites, or a small geographical area, which limits the predictive value of the results. Regional site replication would therefore be a valuable addition to such studies.

Here, we aimed to assess the effect of defaunation on the functional composition of the community of tree recruits in a tropical forest. We quantified shifts in functional composition between adults and multiple size classes of tree recruits (i.e. seedling, sapling, juvenile and treelet) and compared these shifts across eight sites representing a gradient of defaunation in, otherwise intact, old-growth forests in French Guiana. We hypothesized that the loss of large vertebrates leads to changes in the functional composition of the tree recruit community through their roles in seed dispersal and browsing. We expected that, with increasing defaunation level, 1) tree species with fruit traits related to dispersal by large vertebrates – large fruits and fleshy fruits – decrease in relative abundance, 2) tree species with leaf traits preferred by browsing vertebrates – leaves with low toughness, high SLA, and high nitrogen content – increase in relative abundance, 3) tree species with high wood density decrease in relative abundance.

## 2. MATERIALS AND METHODS

### Study system

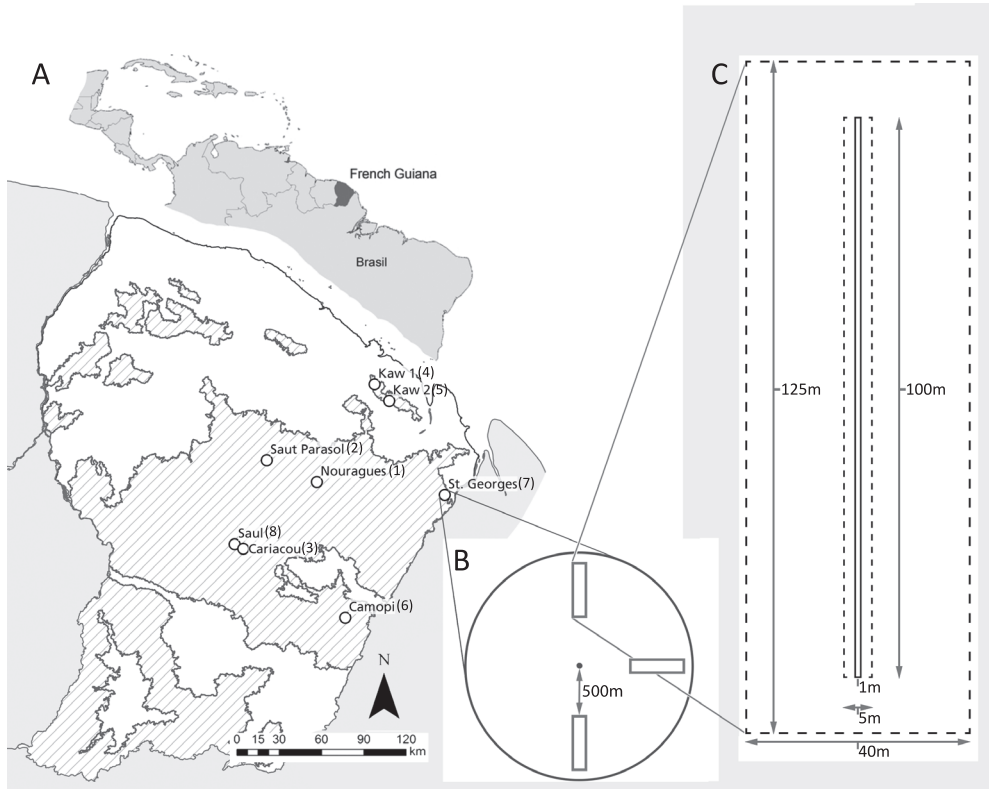
Field data were collected in tropical lowland forests of French Guiana, an 85,000 km<sup>2</sup> French territory in the eastern part of the Guiana shield. The area has an equatorial climate and receives between 3000 mm and 4000 mm of rainfall annually, with the highest rainfall in the north-east and the lowest in the south-west (Beaufort et al. 2019). Most rain falls between December and July (Beaufort et al. 2019). We focused on the habitat type ‘forests of plateaus and high hills’ (Code G and H in table 2 of Guitet et al. (2013)), which covers approximately 41% of French-Guiana (Figure 1). This landscape type is defined by its geomorphological features such as its relatively high elevation and steep slopes (Guitet et al. 2013). Consequently, forests in this landscape type have relatively homogenous plant and vertebrate communities (Guitet et al. 2015a, Richard-Hansen et al. 2015). However, the plant- and vertebrate diversity in these forests is high, and therefore local differences in species- or functional composition within the ‘forests of plateaus and high hills’ are still to be expected. ‘Forests of plateaus and high hills’ are characterized by a high abundance of Fabaceae and Burseraceae trees. Species of the genera *Protium* and *Inga*, and *Dicorynia guianensis* are particularly common (Guitet et al. 2015b). The medium- to large vertebrate communities within ‘forests of plateaus and high hills’ typically include red brocket (*Mazama americana*), collared peccary (*Pecari tajacu*), black curassow (*Crax alector*), black spider monkey (*Ateles paniscus*) and tapir (*Tapirus terrestris*) (Guitet et al. 2015b, Richard-Hansen et al. 2015), which are also hunting sensitive species (Richard-Hansen et al. 2019).

We selected eight sites using three main criteria: 1) the site had been surveyed previously for vertebrates (Richard-Hansen et al. 2015), 2) the site had to be located in a single landscape type (Guitet et al. 2015a) and 3) all sites combined should represent a gradient of defaunation. Hunting was permitted at all but two of the eight sites (Table 1). Hunting pressure varied across sites, mostly as a consequence of accessibility to humans and proximity of human habitations. None of the sites had directly been recently affected by commercial logging, but selective logging has taken place in close proximity (<500 m) to the St. Georges site (7).

### Level of defaunation

At each of the eight sites (Table 1), we quantified the level of defaunation with the defaunation index, D (Giacomini and Galetti 2013) for which we used the existing vertebrate census data (Richard-Hansen et al. 2015) (Appendix S1: Section S1). D may range from 0 (no defaunation) to 1 (complete defaunation) as compared to a

hypothetical undisturbed reference site. Because plants in early life stages are preferentially affected by ground-dwelling browsers, we calculated  $D$  (Appendix S1: Section S1) for ground-dwelling browsers ( $D_{leaf}$ ) (Appendix S2: Table S1), for statistical analysis concerning leaf traits. Because all censused vertebrates are known to interact with fruits, we also calculated  $D$  for all censused vertebrates ( $D_{all}$ ) for statistical analysis concerning fruit and seed traits.



**Figure 1.** (A) Location of the eight study sites in French Guiana. The hatched area is the area with landscape type ‘forests of plateaus and high hills’ (Guitet et al. 2013). (B) Location of plots (rectangles) relative to the site center point. Three of four cardinal directions were chosen for each site based on a set of criteria. (C) Spatial layout of a plot: seedlings were sampled in the central plot of 1\*100m, saplings, juveniles and treelets were sampled in the plot of 5\*100m and adults were sampled in the surrounding plot of 40\*125m.

**Table 1.** Characteristics of the study sites.  $D_{\text{leaf}}$  represents the level of defaunation for all censused ground dwelling browsers and  $D_{\text{all}}$  represents the level of defaunation for all censused browsers.

Site name	Site number	Latitude	Longitude	Hunting permitted	Vertebrate census year	Vegetation census year	$D_{\text{leaf}}$	$D_{\text{all}}$
Nouragues	1	4.0380569	-52.6729167	No	2007	2018	0.37	0.40
Saut Parasol	2	4.1774043	-52.9955918	No	2009	2018	0.20	0.30
Cariacou	3	3.6088132	-53.1472023	Yes	2008	2017	0.49	0.53
Kaw 1	4	4.6653857	-52.3010218	Yes	2012	2017	0.53	0.55
Kaw 2	5	4.5588718	-52.2065257	Yes	2011	2017	0.50	0.53
Camopi	6	3.1824930	-52.5130750	Yes	2002	2018	0.32	0.45
St. Georges	7	3.9551317	-51.8487714	Yes	2018	2019	0.58	0.62
Saül	8	3.6382591	-53.2029712	Yes	2002	2017	0.61	0.60

## Vegetation sampling

Three plots were established at each site, approximately 500 meters away from the central point that had previously been established for the vertebrate censuses, following a cardinal direction (Figure 1). The exact location of each plot was chosen following a set of criteria that were, in order of importance, the absence of gaps in the canopy over the recruits, the absence of steep inclines, and the ease of access for the fieldwork team.

In each plot, seedlings (20 - 100 cm height) were tagged in a strip of 1\*100 m and were identified to lowest possible taxonomic level and measured for height. Saplings (>100 cm height, <1 cm DBH), juveniles (1-2 cm DBH) and treelets (2-5 cm DBH) were tagged in a strip of 5\*100 m, identified and measured for DBH. Adult trees were tagged, identified and measured for DBH in a strip of 40\*125 m. Strips were nested and centered (Figure 1).

## Plant traits

We measured leaf toughness and leaf thickness of tree recruits, and we collected leaf samples to determine SLA and leaf nitrogen content (Appendix S1: Section S1). For each identified species we collected fruit traits from the literature through a systematic review (Vaessen et al. in prep.). Wood density data were collected from the global wood density database (Zanne et al. 2009) (Appendix S1: Section S1). We pooled plot data by site and then calculated the community-weighted mean for continuous traits (CWM), or community-weighted proportion for categorical traits (CWP), of each of the leaf and fruit traits for each size class (i.e. seedlings or saplings, size classes described under “vegetation sampling”). A common issue in studies on defaunation is that size classes are often directly compared between sites, but the inherent natural variation in tree functional composition between sites, would likely overshadow any

short-term (i.e. < 50 years) impacts of defaunation. To overcome this we looked at relative changes in trait composition by calculating the ratio between the CWM or CWP of each of the size classes of tree recruits and the adult size class (see Wright et al. 2007, Terborgh et al. 2008, Hazelwood et al. 2020).

## Analysis

The analysis focused on the relationships between the defaunation index and shifts in functional traits between adult trees and recruits. To test the predictions that defaunation explained differences in abundance of species with specific traits, we performed two types of analysis. First, a linear least squares regression was used to test the relationship between the level of defaunation and CWMs or CWPs of the different functional traits. Second, we created linear mixed effects models to test if significant relationships from the first analysis could be attributed to trait related shifts in species abundances. Statistical analysis were done in R version 3.6.1 (R Development Core Team 2022).

For our first analysis we pooled data by site. We calculated the community weighted mean (CWM) per site and per size class, for leaf toughness, leaf thickness, SLA, leaf nitrogen content, mean fruit length and wood density, and calculated the community weighted proportion (CWP) for the categorical variables of fruit fleshiness and color. As we did not have enough data for mean seed length, it was excluded from analyses.

Natural variation in trait composition makes the comparison of absolute shifts (i.e. directly comparing recruit communities) between sites unsuitable. For example, if the adult community between two sites would differ largely in leaf toughness, it is likely that under similar the circumstances the recruit communities at the same two site would show similar differences in leaf toughness. We therefore controlled for the natural variation in the undisturbed adult communities by calculating the ratio between each of the size classes of tree recruits and the adult size class for the CWM or CWP of each functional trait (recruit:adult ratio). The ratios were tested for relationships with D, using Pearson correlation and least squares regression.

For our second analysis, to test if potential differences in CWM or CWP were due to trait-related changes in relative abundance of species as opposed to natural variation in CWM or CWP, we fitted linear mixed effects models, using the lme4 package (Bates et al. 2015). We calculated the relative abundance of each species by site and the overall species means for each functional trait, and then fitted and compared the following models:

$$\log(\text{ratio}_{i,s}) = \text{trait}_i * D_s + (1|\text{species})$$

$$\log(\text{ratio}_{i,s}) = \text{trait}_i + D_s + (1|\text{species})$$

Here  $\log(\text{ratio}_{i,s})$  represents the logarithm of the ratio of the abundance of the recruits to the abundance of adults for species  $i$  and for site  $s$ ,  $\text{trait}_i$  represents a trait value for species  $i$  for each of the leaf and fruit traits,  $D_s$  represents either  $D_{\text{all}}$  or  $D_{\text{leaf}}$  (depending on the trait) for site  $s$ , and  $(1|\text{species})$  is a random effect where each species is allowed to have its own intercept. If changes to the CWM are related to changes in the relative abundance of tree species because of defaunation, then we expect the interaction term ( $\text{trait}_i * D_s$ ) to result in a better model fit than the model without the interaction term.

We used the package lmerTest and Satterthwaite's approximation to estimate denominator degrees of freedom and thereby p-values from these models (Kuznetsova et al. 2017). To compare the two models, we used Akaike's Information Criterion (AIC). If models differed by more than 2, we considered models to be significantly different. In cases where the AIC's did not differ by more than 2, we compared the AIC to the Bayesian Information Criteria (BIC) and selected the model with the lowest BIC. We present both the AIC and the BIC for all models in Appendix S2: Table S3 and S4.

We used a mixed effects ANOVA to identify whether some species had a larger influence than others on the relationships between D and the CWM or CWP of the tested traits. We performed the ANOVA with Tukey posthoc analysis using the "emmeans" package (Lenth 2021), to check for differences in recruit:adult abundance ratios between species. After identifying species displayed large differences in with we excluded these species from the data and reran the first analysis. If the selected species had a disproportionately large influence on the hunting-induced changes in CWMs and CWPs of the different traits, we expect that the removal of these species from the data will change the significant results from the first analysis to become non-significant.

In addition we performed two PCAs on all sites for all size classes, using the package Vegan V2.5-6 (Oksanen et al. 2019). The first PCA was intended to distinguish



major patterns in functional trait composition. Covariates included were the CWM of leaf toughness, leaf thickness, SLA, leaf nitrogen content, mean fruit length and wood density, and the CWP of fruit fleshiness (using only one of two categories). The second PCA was intended to identify patterns in fruit color composition. Covariates included in the PCA were CWPs of fruit colors.

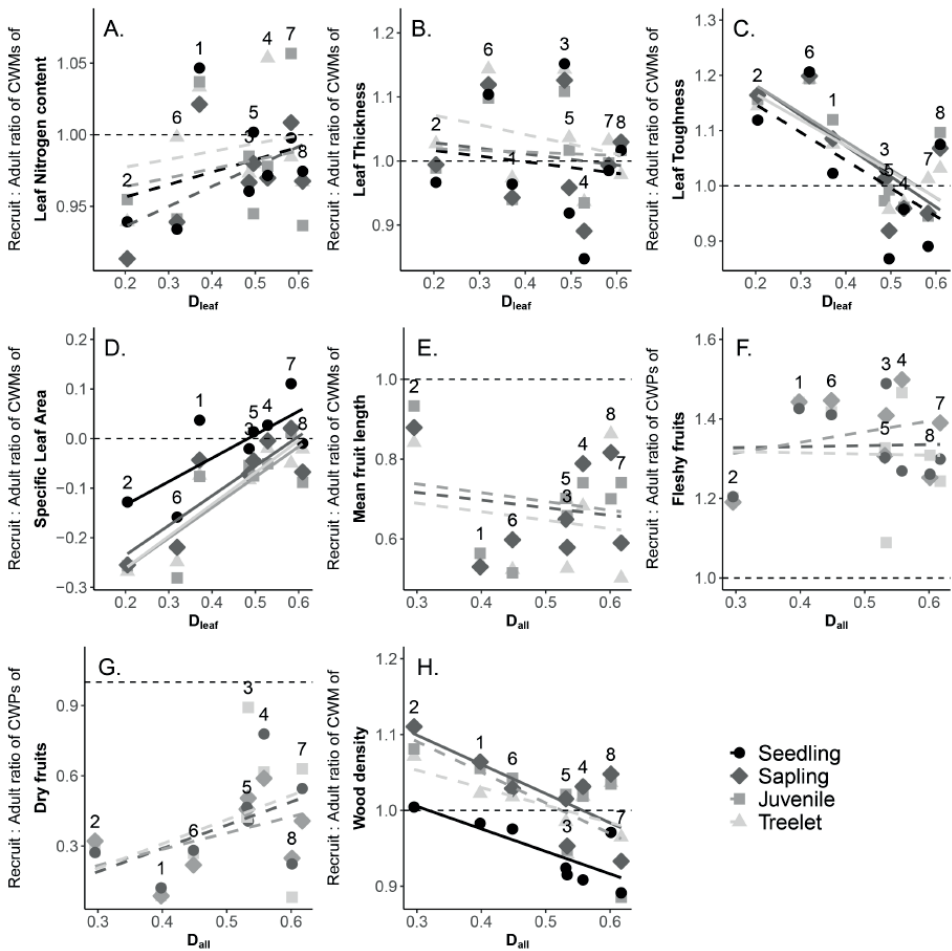
### 3. RESULTS

The surveys yielded a range of 892 - 1562 seedlings (average density 11.88 m<sup>-2</sup>), 230 - 658 saplings (1.33 m<sup>-2</sup>), 134 - 325 juveniles (0.46 m<sup>-2</sup>), 110 - 279 treelets (0.38 m<sup>-2</sup>) and 156 - 334 adults (0.06 m<sup>-2</sup>) per site. For leaf traits, we obtained a value for at least 64% of the individuals, depending on the trait and the size class (Appendix S2: Table S2). For fruit and seed traits, these proportions were generally lower (Appendix S2: Table S2), as these traits could not be imputed for unidentified individuals and we did not have trait data for all species. The proportions were particularly low for the seedling communities, as the proportion identified was lower for seedlings than for any of the other size classes. Therefore the seedling size class was excluded from the least squares regression analysis between D (defaunation index) and the community-weighted means (CWM) and the community-weighted proportions (CWP) of fruit traits, and was entirely excluded from the analysis with linear mixed effects models, which required species means.

Trait composition differed clearly between the size classes within each of the eight sites, which was reflected in the PCA (Appendix S2: Figure S1A). Three more or less distinct clusters were observed, in which saplings, juveniles and treelets formed one cluster, and adults and seedlings each formed a cluster (Appendix S2: Figure S1A). However, there was a large spread of the sites, particularly for the seedling size class, and Euclidean distances between sites were often larger than between seedlings and other size classes. The PCA based on fruit colors showed no distinct patterns (Appendix S2: Figure S2).

The CWMs of leaf toughness of sapling, juvenile and treelet communities significantly decreased, relative to the adult community, as  $D_{\text{leaf}}$  (defaunation index of ground-dwelling browsers) increased (Figure 2C, table 2A). Specific leaf area (SLA) was significantly positively related to  $D_{\text{leaf}}$  for all classes of recruits (Figure 2D, table 2B). Leaf nitrogen content and leaf thickness did not show any significant relationships with  $D_{\text{leaf}}$ , while fruit length, fruit fleshiness did not show significant relationships with  $D_{\text{all}}$  (defaunation index of all censused vertebrates). Wood density of seedling and sapling communities significantly decreased relative to the adult community with

increasing defaunation, whereas relationships were not significant for juvenile and treelet community (Figure 2H, table 2B).



**Figure 2.** Relationship between the recruit:adult ratios of the community-weighted means (CWM) or community-weighted proportions (CWP) of eight functional traits and defaunation index based on all censused vertebrate species ( $D_{all}$ ) or only ground dwelling browsers ( $D_{leaf}$ ). Values greater than one indicate that the CWM or CWP is higher in the recruit community, compared to the adult community. Numbers correspond with site numbers. (A) Leaf nitrogen content, (B) Leaf thickness, (C) Leaf toughness, (D) Specific leaf area, (E) Mean fruit length, (F) Fleshy fruits, (G) Dry fruits, (H) Wood density. Seedlings, saplings, juveniles and treelet communities are represented respectively by circles, diamonds, squares and triangles. Lines indicate least squares regression, with solid lines indicating significant relationships and dashed line indicating non-significant relationships. Color coding represents, from dark to light, seedling, sapling, juvenile and treelet classes. Pearson correlations are shown in table 2.

**Table 2.** Pearson correlations and corresponding P-values between (A)  $D_{\text{leaf}}$  and recruit:adult ratios of the CWMs of four leaf traits, (B)  $D_{\text{all}}$  and recruit:adult ratios of the CWM (Mean fruit length, wood density) or CWP (Dry fruits, Fleshy fruits) of three fruit traits and wood density, Significant correlations ( $p \leq 0.05$ ) are in bold. The header “Figure” refers to the corresponding figures.

A.	Leaf Nitrogen content			Leaf Thickness			Leaf Toughness			Specific Leaf Area		
	<i>r</i>	<i>p-value</i>	Figure	<i>r</i>	<i>p-value</i>	Figure	<i>r</i>	<i>p-value</i>	Figure	<i>r</i>	<i>p-value</i>	Figure
Treeler:Adult	0,40	0,33	2A	-0,25	0,56	2B	-0,82	<b>0,01</b>	2C	0,91	<b>0,00</b>	2D
Juvenile:Adult	0,29	0,48	2A	-0,04	0,93	2B	-0,73	<b>0,04</b>	2C	0,80	<b>0,02</b>	2D
Sapling:Adult	0,59	0,13	2A	-0,17	0,68	2B	-0,79	<b>0,02</b>	2C	0,86	<b>0,01</b>	2D
Seedling:Adult	0,35	0,39	2A	-0,14	0,74	2B	-0,62	0,10	2C	0,74	<b>0,04</b>	2D

B.	Mean fruit length			Fleshy fruits			Dry fruits			Wood density		
	<i>r</i>	<i>p-value</i>	Figure	<i>r</i>	<i>p-value</i>	Figure	<i>r</i>	<i>p-value</i>	Figure	<i>r</i>	<i>p-value</i>	Figure
Treeler:Adult	-0,16	0,71	2E	-0,02	0,96	2F	0,27	0,52	2G	-0,60	0,11	2H
Juvenile:Adult	-0,10	0,82	2E	0,29	0,48	2F	0,45	0,26	2G	-0,68	0,06	2H
Sapling:Adult	-0,12	0,78	2E	0,04	0,92	2F	0,53	0,18	2G	-0,73	<b>0,04</b>	2H
Seedling:Adult										-0,78	<b>0,02</b>	2H

The linear mixed effects models showed significant or marginally significant relationships of the interaction between D and wood density on the species ratio of abundance of recruits and adults, and between D and SLA (Appendix S2, table S3 and S4). Fruit fleshiness, fruit color, wood density, leaf nitrogen content and leaf toughness all showed model improvements when including an interaction of these traits with D compared to the model without an interaction (i.e. AIC or BIC improved by at least 2) (Appendix S2, table S3 and S4). For fruit length and leaf thickness, the model neither improved nor had a significant interaction with D. Our follow-up analysis showed no species to be true outliers in terms of recruit:adult abundance ratios (Appendix S2, Figure 3), but visual inspection revealed that multiple species seemed to have notably higher or lower recruit:adult ratios and trait values, and therefore potentially had a disproportionate effect on the CWMs or CWPs. Based on these criteria, we removed *Quararibea duckei*, *Protium apiculatum* and *Dicorynia guianensis*, after which none of the previously significant relationships between D and the CWMs and CWPs of the functional traits remained significant, indicating that changes in these species drive the observed relationships between hunting and community trait values. We did not observe these changes in significance when only removing two of the three species. Furthermore there are perhaps more species which may have a similar influence on the relationships between D and the CWMs and CWPs of the functional traits, but for which we did not test the effect of removing them from the first analysis.

## 4. DISCUSSION

We studied the functional composition of tree recruit communities at eight sites in French Guiana that ranged widely in their level of defaunation, to test the hypothesis that the loss of large vertebrates leads to changes in functional composition of the tree recruit community due to trait-related changes in species abundance. The CWMs of leaf toughness, SLA and wood density (expressed as a ratio between size classes of tree recruits and the adult size class) showed significant relationships with defaunation. Shifts in CWMs were, however, only partially explained by trait-related shifts in species abundance. Rather, the shifts seemed associated with a combination of factors, including weak trait-related shifts in species abundance and the disproportionate influence of three tree species that were relatively abundant and had trait values towards the further ends of the spectra for multiple traits.

The CWMs of SLA and leaf toughness showed significant relationships with defaunation. These results suggest that recruits with palatable leaves (e.g. high SLA and low leaf toughness) are more abundant with high defaunation, in agreement with our prediction that tree species with traits preferred by browsers benefit from defaunation. Contrary to our prediction, leaf nitrogen content was independent of the level of defaunation, even though nitrogen content is often associated with leaf palatability in recruits (Coley 1983, Coley and Barone 1996). However, the association observed in past studies concerns leaves that have not yet fully matured, which lack the leaf toughening that often provides protection against herbivory. Other studies have found that leaf toughness is a better predictor for herbivory than nitrogen (Coley 1983, Poorter et al. 2004). In this study, we measured leaf nitrogen content on leaves that had seemingly fully developed, at which point nitrogen content may play a limited factor in leaf palatability. Our results in leaf traits differ from Kurten et al. (2015), who found no significant differences in leaf mass per area and leaf toughness between a hunted and control site. However, they directly compared size classes of recruits, without controlling for the functional composition of the adult community.

We found no support for our prediction that species with fruit traits related to dispersal by large vertebrates would decrease in abundance with increased defaunation. Neither the CWMs and CWPs showed significant relationships with defaunation level, nor did the species abundance ratio. Despite these results, we consider it highly unlikely that hunting-induced changes in seed dispersal do not affect recruit functional composition, as Wright et al. (2007) found higher mean seed mass associated to seedling communities at hunted sites, and Kurten et al. (2015) found a significant higher mean seed mass of seedlings in vertebrate exclosures. A plausible explanation is that we were not able to test seed size or mass, two important fruit traits, due to the

relatively low availability of data for the surveyed species. Yet, the tested fruit traits are also known as important determinants of vertebrate dispersal syndromes (Janson 1983), and we therefore expected these traits to be affected by defaunation. The results of our linear mixed effects models suggested that there *is* a relationship between fruit color or fruit fleshiness and defaunation, showed by the great improvement in model fit with the inclusion of the interaction term, but that this relationship was weak, explaining the non-significance of the interaction. This weak effect may be due to the fact that vertebrates rely on these cues in combination with other traits which form a full dispersal syndrome rather than just the fruit fleshiness or color alone (Pijl 1969, Janson 1983, Gautier-Hion et al. 1985). These trait syndromes are not fully captured by analyses of single traits like ours. Therefore, multivariate analyses may be more suitable to investigate defaunation impacts on forest composition, as they probably better capture the complexity of vertebrate-fruit interactions.

Wood density showed a significant negative relationship with defaunation at the seedling and sapling stage, in concurrence with the findings of Kurten et al. (2015), and there were significant wood density-related shifts in species abundance in line with earlier predictions (Jansen et al. 2010, Harrison 2011). It is the only trait that showed clear significant relationships in all analyses. This is striking, because wood density can only be indirectly affected through its correlations with leaf traits (Kitajima and Poorter 2010) and fruit traits (Bello et al. 2015). This result thus illustrates that a combination of - sometimes weak - trait related shifts in species abundance together can result in large changes in forest composition.

We observed changes in the CWM of wood density only in the seedling and sapling size class. This pattern may occur because defaunation induced changes through browsing and seed dispersal are most apparent in the earliest life stages (Wright et al. 2007, Kurten et al. 2015), but can be diluted in later life stages through density dependent mortality, environmental filtering, or a higher proportion of individuals that sprouted pre-hunting. As a result of defaunation-induced lower mean wood density, it is likely that forests will store less biomass in the long-term, as has been modelled by previous studies (Bello et al. 2015, Peres et al. 2015, Osuri et al. 2016). Contrary to these studies, however, we link reduced forest biomass not only to changes in seed dispersal, but also to changes in browsing.

Our results showed that shifts in functional composition are largely driven by a few species. In particular, three species, *Quararibea duckei*, *Protium apiculatum* and *Dicorynia guianensis*, were able to disproportionately influence these relationships. These species were relatively abundant, and had more extreme trait values for several traits. Of these three species, *Quararibea duckei* and *Protium apiculatum* influenced rela-

tionships due to their relative increase in abundance with higher defaunation, while *Dicorynia Guianensis*, a popular timber species, decreased in relative abundance with higher defaunation. Because we did not test all species, it may be that some other tree species have a similar influence on the relationship between defaunation and the functional traits. These results suggest that species whose traits are negatively influenced by defaunation may experience local population reductions. Species with one or few negatively influenced traits, are, in the short-term, perhaps less affected by defaunation at the populations level.

Defaunation has been linked to changes in the composition of recruit communities (Dirzo and Miranda 1991, Wright et al. 2007, Terborgh et al. 2008, Effiom et al. 2013), and is often assumed to be the result of changes in seed dispersal (Bello et al. 2015, Osuri et al. 2016). Indeed, there is evidence that defaunation results in reduced dispersal, and higher clustering of recruits, but the impacts of defaunation on the clustering of recruits seem to be small in the short term (i.e. < 50 years) (Harrison et al. 2013, Bagchi et al. 2018) and it is questionable whether reduced seed dispersal is the only mechanism causing changes in composition of recruit communities (Bagchi et al. 2018, Hazelwood et al. 2020). Our results support the hypothesis that hunting induces changes in forest composition via multiple mechanisms, of which browsing has been underappreciated. Dirzo and Miranda (1991) linked the lower species diversity in a defaunated forest compared to an undisturbed forest to the striking difference in herbivore damage between the two sites. However, since then only few studies have focused on the impact of a reduction in browsing for recruit community composition (Camargo-Sanabria et al. 2015, Kurten et al. 2015).

Our results suggest that minor changes in ecological processes such as browsing and seed dispersal may combine to lead to major changes in forest composition. Hunting thus not only affects the faunal composition of these ecosystems but may have cascading effects on the nature of tree recruitment and thus the composition and dynamics of future forests that may be visible for centuries after.

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## APPENDIX SI

### Supplementary materials and methods

#### Quantifying defaunation

Vertebrates were censused using line transects with distance sampling, following a strict protocol across all sites (Richard-Hansen et al. 2015). At each site three or four line transects of 3 km in length were walked between 7:00 - 11:00 and 14:30 - 18:00 at a 1 km/h pace. Distances to observed vertebrates (solitary or group) were measured with a range finder. This method was repeated for seven to nine days resulting in a sampling effort of at least 140 km, well above the estimated minimum of 100 km (de Thoisy et al. 2008). Vertebrate density estimations were made by Denis et al. (2018), who used a generalized distance sampling model (Chandler et al. 2011). Estimates were acquired for 19 medium to large vertebrate species (Appendix S2, Table S1), including all larger hunting-sensitive species except white-lipped peccary, tapir and paca, which are nocturnal.

We quantified defaunation using the defaunation index (D) (Giacomini and Galetti 2013). The defaunation index is very similar to the more commonly used Bray-Curtis index of dissimilarity (Bray and Curtis 1957). However, contrary to the Bray-Curtis index, in D each species can be assigned a certain weight and secondly, all communities are compared to only a single reference community, which can be a hypothetical community, allowing for a one-dimensional scale. As the defaunation index is a proxy for defaunation, the reference community should represent an undisturbed community. The defaunation index provides values between 0 and 1, with 0 indicating no difference between the focal community and the reference community. We used species metabolic rate as a weight in the D equation, which is roughly equal to species body mass in kg to the power of 0.75 and scales with the caloric intake of a vertebrate (Kleiber 1947). Body mass is the most important factor in game selection by hunters, and metabolic rate is a proxy for the impact a species can have on the ecosystem by consuming either leaves or fruits and seeds. The equation for D is as follows:

$$D(r, f) = \frac{\sum_{k=1}^S m_k^{0.75} (N_{k,r} - N_{k,f})}{\sum_{k=1}^S m_k^{0.75} (N_{k,r} + N_{k,f})}$$

Where  $r$  and  $f$  represent the reference and the focal community.  $S$  is the number of species and  $k$  is a species.  $m_k^{0.75}$  is the metabolic rate of species  $k$ , in which  $m$  is the body

mass in kg.  $N_{k,r}$  represents the abundance of species  $k$  at the reference community  $r$ .  $N_{k,f}$  represents the abundance of species  $k$  at focal community  $f$ .

We chose not to use one undisturbed community as a reference, as this would not take into account the regional variation in vertebrate community composition occurring naturally (Richard-Hansen et al. 2015). Instead we formed a hypothetical reference community by selecting the highest abundance per vertebrate species from 16 censuses at undisturbed sites within the ‘forests of plateaus and high hills’ habitat type. Because our hypothetical reference community contained unrealistically high abundances for all species, it was unlikely that even undisturbed sites approached 0. Yet this approach was effective in separating sites based on the quantitative impact vertebrate communities have on the ecosystem processes such as browsing and seed dispersal, as it includes species abundance and metabolic rate. Based on expert knowledge, we assumed that the major difference in the defaunation index was the result of hunting, however variation in the composition of undisturbed communities has been observed in French Guiana (Richard-Hansen et al. 2015), which in itself may lead to differences in the defaunation index. We calculated  $D$  for ground-dwelling browsers ( $D_{\text{leaf}}$ ) (Appendix S2, Table S1), which we used for statistical analysis concerning leaf traits, as well as for all surveyed vertebrates ( $D_{\text{all}}$ ), which we used for statistical analysis concerning fruit and seed traits.

### **Leaf traits**

For seedlings, leaf traits were measured for every third individual. For each plot, this selection was supplemented with additional measurements, so that each morphospecies had at least five individuals measured, whenever possible. Measurements were linked to species, which was required for data imputation in other size cohorts. Identification rates of seedlings were lower than expected, however, and we therefore also measured leaf traits for other recruit cohorts at sites ‘Nouragues’, ‘Saut parasol’, ‘Saint Georges’ and ‘Camopi’.

Leaf thickness and leaf toughness were measured in the field. We randomly selected one fully grown leaf per selected individual that was not, or only slightly, affected by herbivory or moss cover. We used a thickness gauge (Mitutoyo dial thickness gage, No. 7301) to measure leaf laminar thickness. A dynamometer (Wagner force dial FDN 20) was used to measure leaf toughness; the leaf was clamped between two jointed wooden slats, after which the dynamometer was guided through a hole so that it joined the leaf at a 90° angle. Pressure was applied and slowly increased, until the dynamometer fractured the leaf. During measurements of leaf thickness and leaf toughness, leaf veins were avoided as much as possible.

For leaf nitrogen content per unit dry mass (leaf nitrogen content), leaf samples were collected and oven-dried at 70°C for 24 hours. In the lab the samples were powdered, weighed and analysed with an element analyser (Carlo Erba EA 1110 CHNS-O). For Specific Leaf Area (SLA), we collected per individual one circular disk with a diameter of 8.1 mm. The disks were dried in silica for at least two weeks, after which dry mass was weighed.

Leaf trait data were imputed to adult, treelet and juvenile cohorts, as well as saplings and seedlings which were not directly measured. We chose not to measure leaf traits on adult trees, as we wanted to exclude ontogeny as a factor as much as possible. By imputing recruit level trait values, shifts in functional traits would mostly reflect a shift in species composition. We used species means or weighted genus means when genus was the lowest level of identification. Only for the seedling cohorts we used the plot specific means of the unidentified measured individuals and imputed this value to the unmeasured and unidentified individuals in the plot.

### ***Fruit and seed traits***

To determine fruit and seed traits for the identified species, we systematically searched literature (Vaessen et al. paper in preparation). Traits included mean seed length (Seed length), mean fruit size (Fruit size), fruit fleshiness (Fleshiness; dry or fleshy) and fruit color (Color). The main sources were Van Roosmalen (1985), Mori et al. (2002) and Flora of the Guianas (Görts-Van Rijn, Jansen-Jacobs & Mota de Oliveira (eds.)). For species for which we were not able to find traits through the literature search, and for which the family was not included in Flora of the Guianas, we digitally checked herbarium voucher labels from the Naturalis Biodiversity Center herbarium, for information on fruit and seed traits (<https://bioportal.naturalis.nl/>, May 2020). Fruit type, and therefore fleshiness is taxonomically conservative at the genus level (van Roosmalen 1985) and was therefore linked to the genus, when genus was the lowest taxonomic level of identification.

### ***Wood density***

Wood densities were taken from the global wood density database (Zanne et al. 2009). As genus explains most of the variation in wood density (Chave et al. 2006), we used the weighted mean of the genus of South American trees for individuals with genus level identification.

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## APPENDIX S2

### Supplementary tables and figures

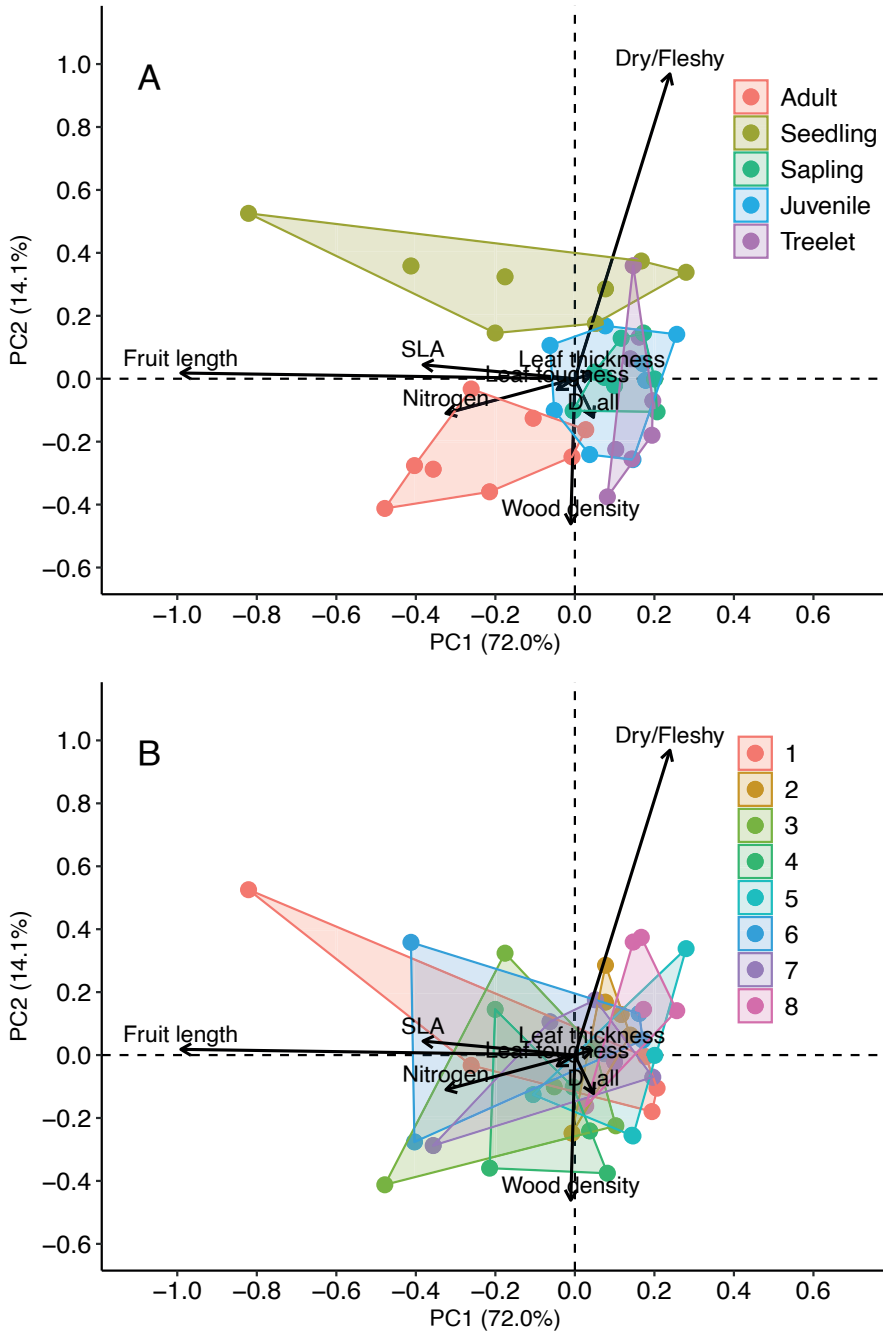
**Table S1.** Vertebrate species included in population density estimations.

Species	Common name	Included in $D_{leaf}$	Class	Mass (kg)
<i>Alouatta macconnelli</i>	Guyan red howler	No	Mammal	6.8
<i>Ateles paniscus</i>	red-faced spider monkey	No	Mammal	8.8
<i>Cebus olivaceus</i>	wedge-capped capuchin	No	Mammal	2.9
<i>Crax alector</i>	black curassow	Yes	Bird	3
<i>Dasyprocta leporina</i>	red-rumped agouti	Yes	Mammal	4.4
<i>Eira barbara</i>	tayra	No	Mammal	4.8
<i>Chelonoidis denticulatus</i>	yellow-footed tortoise	Yes	Reptile	4.4
<i>Mazama americana</i>	red brocket	Yes	Mammal	36
<i>Mazama nemorivaga</i>	Amazonian brown brocket	Yes	Mammal	14.3
<i>Myoprocta acouchy</i>	red acouchi	Yes	Mammal	1
<i>Nasua nasua</i>	South American coati	Yes	Mammal	3.1
<i>Odontophorus gujanensis</i>	marbled wood quail	Yes	Bird	0.3
<i>Pecari tajacu</i>	collared peccary	Yes	Mammal	18.4
<i>Penelope marail</i>	Marail guan	Yes	Bird	1
<i>Pithecia pithecia</i>	white-faced saki	No	Mammal	2
<i>Psophia crepitans</i>	grey-winged trumpeter	Yes	Bird	1.1
<i>Saguinus midas</i>	red-handed tamarin	Yes	Mammal	0.5
<i>Saimiri sciureus</i>	Guianan squirrel monkey	No	Mammal	0.9
<i>Sapajus apella</i>	tufted capuchin	No	Mammal	3.1
<i>Tinamidae</i>	tinamou	Yes	Bird	1

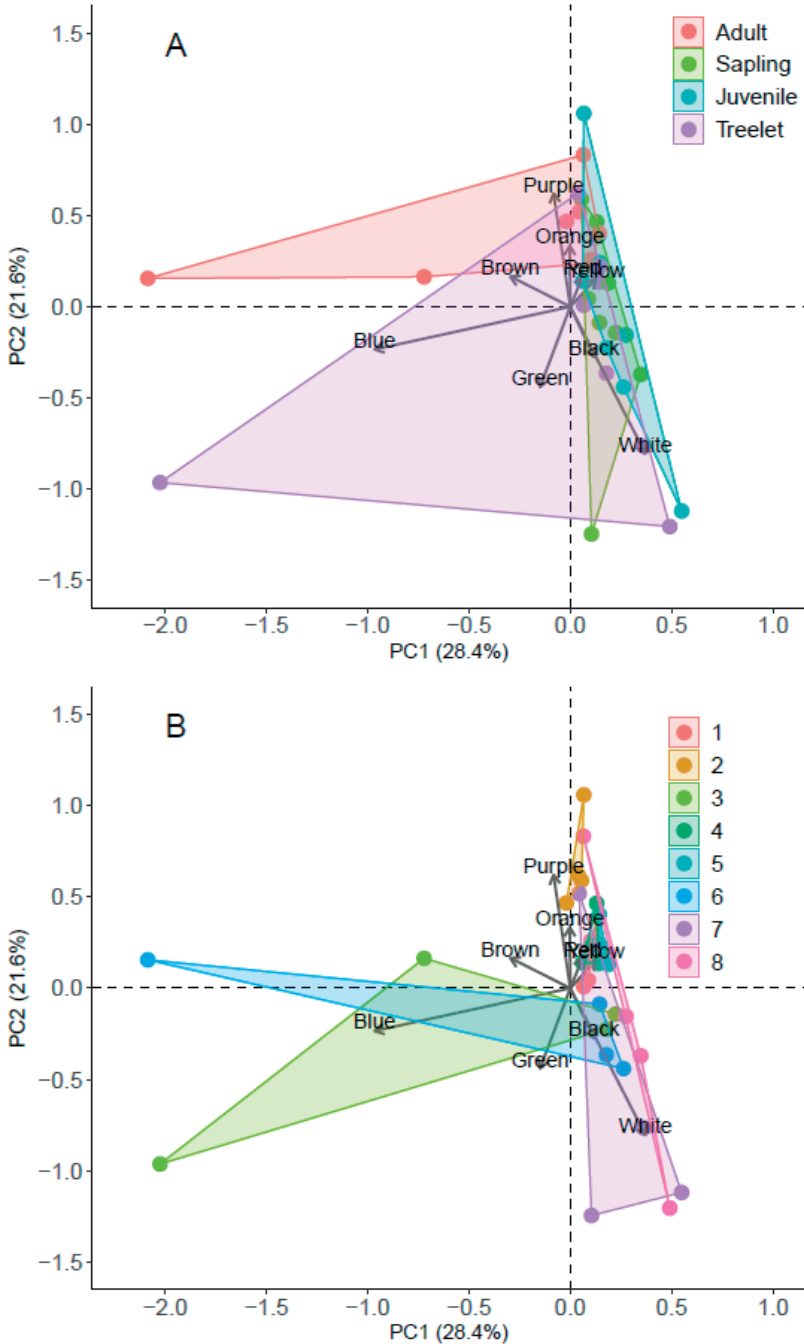
**Table S2.** Proportions of individuals with a value for each of the specified nine functional traits after data imputation, per site and per size cohort. Proportion <0.4 are highlighted in red.

Site	Cohort	Leaf thickness	Leaf toughness	SLA	Leaf N	Dry/fleshy	Mean seed length	Mean fruit length	Fruit color	Wood density
1	Adult	0.67	0.67	0.67	0.66	0.61	0.35	0.44	0.61	0.78
1	Trelet	0.96	0.96	0.96	0.81	0.78	0.40	0.53	0.78	0.84
1	Juvenile	0.95	0.95	0.95	0.76	0.76	0.33	0.51	0.76	0.80
1	Sapling	1.00	1.00	1.00	0.88	0.73	0.28	0.49	0.73	0.79
1	Seedling	1.00	1.00	1.00	1.00	0.32	0.08	0.23	0.32	0.53
2	Adult	0.82	0.81	0.82	0.85	0.69	0.37	0.51	0.69	0.90
2	Trelet	0.88	0.88	0.88	0.86	0.70	0.18	0.43	0.70	0.83
2	Juvenile	0.94	0.93	0.94	0.90	0.69	0.17	0.37	0.69	0.87
2	Sapling	1.00	1.00	1.00	0.96	0.71	0.14	0.48	0.71	0.85
2	Seedling	1.00	1.00	1.00	0.99	0.44	0.10	0.22	0.44	0.60
3	Adult	0.79	0.78	0.79	0.79	0.73	0.43	0.62	0.73	0.90
3	Trelet	0.79	0.75	0.79	0.77	0.56	0.25	0.34	0.56	0.81
3	Juvenile	0.85	0.81	0.85	0.84	0.68	0.20	0.42	0.68	0.83
3	Sapling	0.96	0.86	0.96	0.95	0.59	0.17	0.35	0.59	0.71
3	Seedling	1.00	0.82	0.99	0.97	0.30	0.09	0.14	0.30	0.50
4	Adult	0.66	0.66	0.66	0.64	0.64	0.44	0.54	0.64	0.81
4	Trelet	0.68	0.68	0.68	0.67	0.52	0.20	0.28	0.52	0.72
4	Juvenile	0.68	0.68	0.68	0.67	0.60	0.23	0.35	0.60	0.77
4	Sapling	0.88	0.87	0.88	0.87	0.40	0.15	0.27	0.40	0.59
4	Seedling	1.00	1.00	1.00	1.00	0.21	0.17	0.18	0.21	0.31
5	Adult	0.74	0.72	0.74	0.71	0.71	0.37	0.56	0.71	0.84
5	Trelet	0.80	0.79	0.80	0.78	0.75	0.27	0.49	0.75	0.84
5	Juvenile	0.78	0.78	0.78	0.77	0.72	0.28	0.51	0.72	0.84
5	Sapling	0.88	0.88	0.88	0.86	0.57	0.19	0.40	0.57	0.71
5	Seedling	1.00	1.00	1.00	1.00	0.28	0.05	0.23	0.28	0.44
6	Adult	0.80	0.80	0.80	0.80	0.62	0.47	0.57	0.62	0.88
6	Trelet	0.91	0.90	0.90	0.84	0.60	0.29	0.50	0.60	0.80
6	Juvenile	0.98	0.98	0.98	0.90	0.66	0.20	0.45	0.66	0.88
6	Sapling	1.00	1.00	1.00	0.97	0.62	0.18	0.49	0.62	0.78
6	Seedling	1.00	1.00	1.00	1.00	0.22	0.09	0.19	0.22	0.58
7	Adult	0.78	0.78	0.78	0.77	0.70	0.42	0.62	0.70	0.85
7	Trelet	0.72	0.71	0.72	0.71	0.57	0.26	0.39	0.57	0.71
7	Juvenile	0.73	0.73	0.74	0.73	0.58	0.17	0.33	0.58	0.69
7	Sapling	0.97	0.97	0.97	0.93	0.59	0.17	0.34	0.59	0.70
7	Seedling	0.99	0.99	0.99	0.99	0.38	0.08	0.21	0.38	0.47
8	Adult	0.70	0.69	0.70	0.65	0.69	0.30	0.45	0.69	0.83

8	Treplet	0.69	0.67	0.69	0.67	0.48	0.13	0.30	0.48	0.66
8	Juvenile	0.79	0.79	0.79	0.78	0.67	0.22	0.40	0.67	0.80
8	Sapling	0.87	0.86	0.87	0.84	0.61	0.16	0.36	0.61	0.74
8	Seedling	0.99	0.99	0.99	0.99	0.17	0.06	0.09	0.17	0.44



**Figure S1.** PCA of the functional composition of tree communities at eight sites in French Guiana, including six functional traits: Leaf nitrogen content, leaf thickness, leaf toughness, SLA, fruit length and fruit fleshiness. Functional traits and  $D_{all}$  are represented by vectors. (A) Colored polygons enclose points of specified size cohorts, (B) colored polygons enclose points of specified sites.



**Figure S2.** PCA of the functional composition of tree communities at eight sites in French Guiana, including six functional traits: Leaf nitrogen content, leaf thickness, leaf toughness, SLA, fruit length and fruit fleshiness. Functional traits and  $D_{all}$  are represented by vectors. (A) Colored polygons enclose points of specified size cohorts, (B) colored polygons enclose points of specified sites.



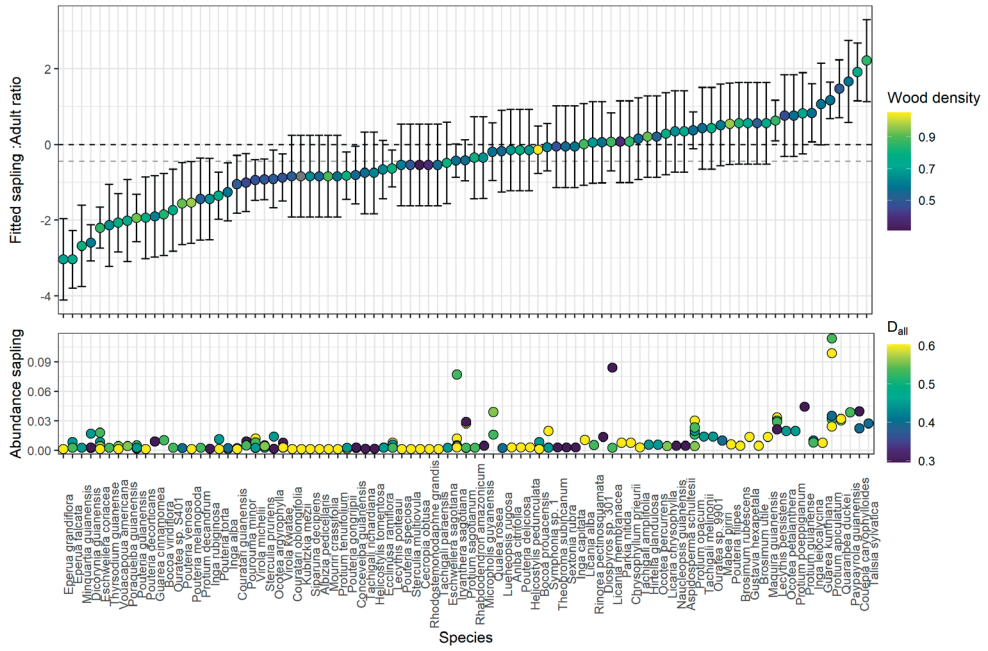
**Table S3.** Summary of the results of the linear mixed effects models for each leaf trait.  $P_{\text{interaction}}$  refers to the P-value of the interaction with  $D_{\text{leaf}}$ ; significant interactions ( $p \leq 0.05$ ) are in bold. Bold AIC and BIC are significantly lower (i.e. 2 points) than the AIC and BIC values of the equivalent models but with opposed interaction.

trait	ratio <sub>abu</sub>	Interaction $D_{\text{leaf}}$	$P_{\text{interaction}}$	AIC	BIC
Leaf Nitrogen content	Sapling:Adult	No		184,0	193,6
	Sapling:Adult	Yes	0,245	<b>179,8</b>	<b>191,4</b>
	Juvenile:Adult	No		173,2	182,7
	Juvenile:Adult	Yes	0,158	<b>168,7</b>	<b>180,0</b>
	Treeler:Adult	No		185,2	194,9
	Treeler:Adult	Yes	0,051	<b>178,9</b>	<b>190,6</b>
Leaf thickness	Sapling:Adult	No		<b>195,8</b>	<b>205,8</b>
	Sapling:Adult	Yes	0,258	197,7	209,6
	Juvenile:Adult	No		<b>187,9</b>	<b>197,7</b>
	Juvenile:Adult	Yes	0,295	190,0	201,7
	Treeler:Adult	No		<b>202,6</b>	<b>212,7</b>
	Treeler:Adult	Yes	0,649	205,8	218,0
Leaf toughness	Sapling:Adult	No		189,2	199,2
	Sapling:Adult	Yes	0,647	<b>184,6</b>	<b>196,5</b>
	Juvenile:Adult	No		180,0	189,8
	Juvenile:Adult	Yes	0,396	<b>175,0</b>	<b>186,7</b>
	Treeler:Adult	No		195,4	205,5
	Treeler:Adult	Yes	0,549	<b>191,0</b>	<b>203,1</b>
Specific Leaf Area	Sapling:Adult	No		197,1	207,0
	Sapling:Adult	Yes	0,067	196,3	208,2
	Juvenile:Adult	No		185,5	195,2
	Juvenile:Adult	Yes	<b>0,040</b>	184,2	195,9
	Treeler:Adult	No		203,3	213,4
	Treeler:Adult	Yes	0,089	203,7	215,8

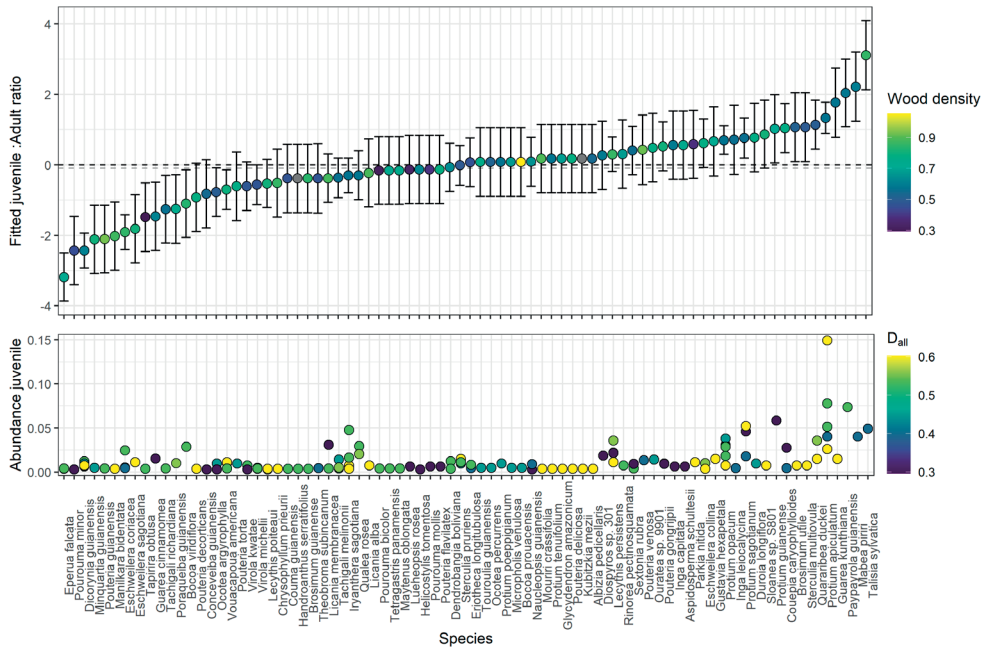
**Table S4.** Summary of the results of the linear mixed effects models for each leaf trait.  $P_{interaction}$  refers to the P-value of the interaction with  $D_{all}$ ; significant interactions ( $p \leq 0.05$ ) are in bold. Bold AIC and BIC are significantly lower (i.e. 2 points) than the AIC and BIC values of the equivalent models but with opposed interaction.

trait	ratio <sub>abu</sub>	Interaction $D_{all}$	$P_{interaction}$	AIC	BIC
Fruit fleshiness	Sapling:Adult	No		125,5	133,3
	Sapling:Adult	Yes	0,738	<b>121,5</b>	<b>130,8</b>
	Juvenile:Adult	No		108,8	116,0
	Juvenile:Adult	Yes	0,631	<b>105,1</b>	<b>113,7</b>
	Trelet:Adult	No		127,9	137,7
	Trelet:Adult	Yes	0,928	<b>124,6</b>	136,1
Fruit color	Sapling:Adult	No		117,9	129,4
	Sapling:Adult	Yes	0,884	<b>103,8</b>	<b>119,6</b>
	Juvenile:Adult	No		91,6	101,4
	Juvenile:Adult	Yes	0,800	<b>76,8</b>	<b>90,2</b>
	Trelet:Adult	No		84,9	94,4
	Trelet:Adult	Yes	0,684	<b>63,5</b>	<b>77,6</b>
Fruit length	Sapling:Adult	No		139,5	<b>147,4</b>
	Sapling:Adult	Yes	0,402	140,8	150,3
	Juvenile:Adult	No		106,7	113,4
	Juvenile:Adult	Yes	0,410	107,0	115,0
	Trelet:Adult	No		120,2	127,7
	Trelet:Adult	Yes	0,251	120,4	129,3
Wood density	Sapling:Adult	No		195,2	205,2
	Sapling:Adult	Yes	<b>0,037</b>	<b>185,7</b>	<b>197,8</b>
	Juvenile:Adult	No		182,9	192,8
	Juvenile:Adult	Yes	<b>0,010</b>	<b>171,6</b>	<b>183,4</b>
	Trelet:Adult	No		204,4	214,8
	Trelet:Adult	Yes	0,350	<b>198,9</b>	<b>211,4</b>

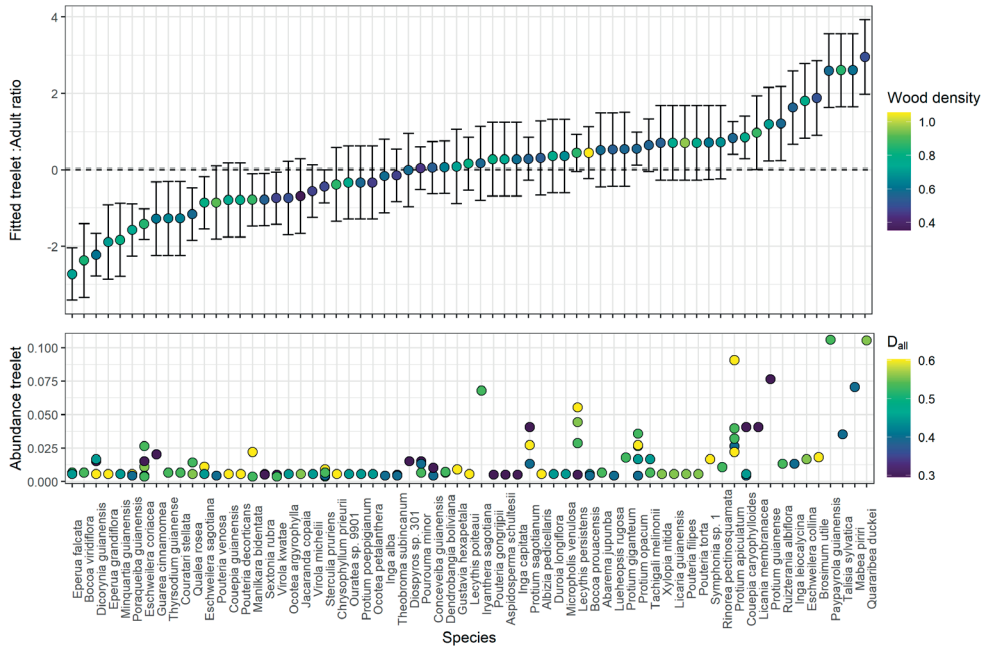
A.



B.



C.



**Figure S3.** The fitted recruit:Adult ratios for each species, and the recruit abundance for each species at each site where it was found. A. Saplings, B. Juveniles, C. Treelets.

**Table S5.** Pearson correlations for site specific CWMs or CWPs for each recruit cohort. Significant correlations ( $p \leq 0.05$ ) are in bold.

Trait 1	Trait 2	Seedling		Sapling		Juvenile		Treelet	
		<i>r</i>	<i>p-value</i>	<i>r</i>	<i>p-value</i>	<i>r</i>	<i>p-value</i>	<i>r</i>	<i>p-value</i>
Fruit length	Dry/Fleshy	-0.18	0.67	-0.31	0.45	-0.25	0.56	-0.20	0.63
Fruit length	SLA	0.20	0.64	-0.02	0.96	-0.19	0.66	0.35	0.39
Fruit length	Leaf thickness	0.11	0.79	0.32	0.43	0.38	0.35	0.30	0.47
Fruit length	Leaf toughness	0.70	0.05	-0.05	0.91	-0.13	0.76	-0.65	0.08
Fruit length	Wood density	0.37	0.37	0.18	0.67	0.12	0.78	-0.26	0.53
Fruit length	Leaf nitrogen content	<b>0.72</b>	<b>0.04</b>	0.34	0.41	0.54	0.17	0.38	0.35
Dry/Fleshy	SLA	0.30	0.47	-0.15	0.73	-0.26	0.53	0.23	0.59
Dry/Fleshy	Leaf thickness	0.20	0.64	0.47	0.24	0.12	0.78	0.02	0.96
Dry/Fleshy	Leaf toughness	-0.32	0.44	-0.22	0.61	0.40	0.33	-0.15	0.72
Dry/Fleshy	Wood density	-0.10	0.82	-0.21	0.61	-0.15	0.71	-0.18	0.68
Dry/Fleshy	Leaf nitrogen content	0.26	0.53	-0.20	0.63	0.32	0.43	-0.09	0.83
SLA	Leaf thickness	-0.24	0.56	-0.16	0.71	0.09	0.84	-0.49	0.21
SLA	Leaf toughness	-0.01	0.98	-0.35	0.40	-0.32	0.44	<b>-0.72</b>	<b>0.04</b>
SLA	Wood density	-0.62	0.10	-0.67	0.07	-0.44	0.27	<b>-0.77</b>	<b>0.03</b>
SLA	Leaf nitrogen content	0.69	0.06	0.66	0.08	0.01	0.97	0.36	0.39
Leaf thickness	Leaf toughness	0.63	0.09	0.12	0.77	-0.59	0.13	0.12	0.78
Leaf thickness	Wood density	0.62	0.10	-0.01	0.98	-0.10	0.82	0.26	0.54
Leaf thickness	Leaf nitrogen content	0.17	0.68	0.18	0.67	0.20	0.63	-0.06	0.89
Leaf toughness	Wood density	0.64	0.09	0.67	0.07	0.35	0.40	0.82	<b>0.01</b>
Leaf toughness	Leaf nitrogen content	0.51	0.20	0.31	0.46	0.42	0.30	-0.01	0.97
Wood density	Leaf nitrogen content	-0.03	0.94	-0.03	0.94	0.26	0.53	-0.07	0.87

**Table S6.** Pearson correlations between Wood density, SLA, Leaf toughness and the defaunation index ( $D_{all}$  or  $D_{leaf}$ ) for each size cohort. Significant correlations ( $p \leq 0.05$ ) are in bold.

Trait	Defaunation index	Cohort	<i>r</i>	<i>p-value</i>
Wood density	$D_{all}$	Adult	<b>0.14</b>	<b>0.000</b>
Wood density	$D_{all}$	Treelet	0.03	0.265
Wood density	$D_{all}$	Juvenile	-0.05	0.056
Wood density	$D_{all}$	Sapling	<b>-0.08</b>	<b>0.000</b>
Wood density	$D_{all}$	Seedling	-0.02	0.099
SLA	$D_{leaf}$	Adult	<b>-0.18</b>	<b>0.000</b>
SLA	$D_{leaf}$	Treelet	<b>0.07</b>	<b>0.007</b>
SLA	$D_{leaf}$	Juvenile	<b>0.10</b>	<b>0.000</b>
SLA	$D_{leaf}$	Sapling	<b>0.13</b>	<b>0.000</b>
SLA	$D_{leaf}$	Seedling	<b>0.04</b>	<b>0.000</b>
Leaf toughness	$D_{leaf}$	Adult	<b>0.19</b>	<b>0.000</b>
Leaf toughness	$D_{leaf}$	Treelet	0.00	0.865
Leaf toughness	$D_{leaf}$	Juvenile	-0.02	0.438
Leaf toughness	$D_{leaf}$	Sapling	<b>-0.04</b>	<b>0.017</b>
Leaf toughness	$D_{leaf}$	Seedling	<b>-0.03</b>	<b>0.003</b>





# Chapter 6

## General discussion

Rens W. Vaessen

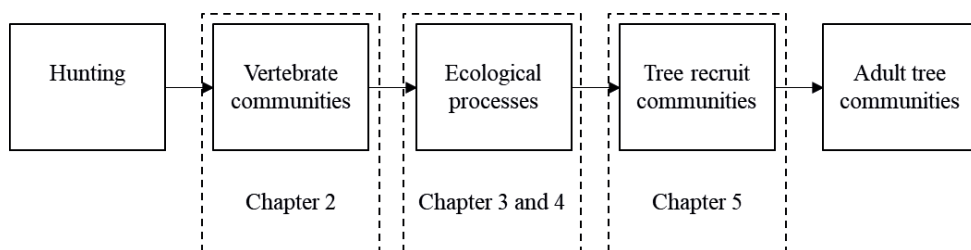




## I. SYNTHESIS

Tropical rainforests contain the world's highest plant diversity (Pimm and Joppa 2015). The conservation of this plant diversity is highly dependent on vertebrates, through their roles in seed dispersal, seed predation and browsing (Wright 2003, Seidler and Plotkin 2006, Paine and Beck 2007, Terborgh 2020). Emmons (1989) first explicitly hypothesized that the loss of vertebrates could lead to a loss of plant diversity. Since then, a large body of research has investigated the effects of hunting, or defaunation, on forest regeneration, through observational research by comparing a hunted forest with a non-hunted forest (e.g. Dirzo and Miranda 1991, Wright et al. 2007, Terborgh et al. 2008), through experimental research by using vertebrate exclosures that mimic defaunation (e.g. Beck et al. 2013, Camargo-Sanabria et al. 2015, Kurten and Carson 2015), and by combinations of the two (Kurten et al. 2015). Nevertheless, the core questions of how forests are affected by hunting and what the role of seed dispersal, seed predation and browsing is, remains largely unanswered.

In this thesis I studied the effects of hunting on the tree species composition of forests in French Guiana. The study focused on three key questions (Figure 1): How does hunting affect vertebrate communities? (Chapter 2); How are vertebrates linked to fruits and seeds and how are these interactions affected by hunting? (Chapters 3 and 4), and; How does hunting affect the functional composition of tree recruit communities? (Chapter 5). The key findings of this thesis and the main conclusions and discussion points I link to these findings, are denoted in bold in the text below.



**Figure 1.** A conceptual model of how hunting may affect adult tree communities: Through hunting humans can affect vertebrate communities, causing changes in key ecological processes mediated by vertebrates, such as seed dispersal, seed predation and browsing. This in turn affects the communities of tree recruits, which over time leads to changes in the adult tree communities. The dashed boxes indicate which subject is covered in each chapter of this thesis.

### How does hunting affect vertebrate communities?

In the first step of the conceptual model (Figure 1) hunting affects vertebrate communities. It has been well established that hunting causes severe changes in the *species*

composition of these communities across the tropics (Redford 1992, Wright et al. 2000, Corlett 2007). For example, in the Amazonian rainforest game species such as peccary (*Dicotyles tajacu*, *Tayassu pecari*), brocket deer (*Mazama spp.*), tapir (*Tapirus terrestris*) and agouti (*Dasyprocta spp.*) are heavily hunted (Peres 2000, Richard-Hansen et al. 2019), which greatly affects the abundance of tapir and peccary, but less so of brocket deer and agouti (Peres and Palacios 2007, Endo et al. 2010).

However, hunting-induced changes in species composition is challenging to translate to changes in ecological processes (Figure 1). Due to the high biodiversity of tropical forests, it is simply not possible to study all vertebrate-mediated processes at species level. Furthermore, the roles of vertebrate species that are lost through hunting, such as tapir and peccary, may be mitigated by remnant vertebrate species with similar roles (Bueno et al. 2013). For these reasons I studied the impacts of hunting on the *functional* composition of vertebrates communities (Chapter 2). Functional traits dictate how species respond to changes in the environment (Luck et al. 2012), and thus changes in functional composition can be considered indicators for changes in ecological processes. Functional composition is strongly affected by hunting worldwide (Brodie et al. 2021), but reports on the impact of hunting on individual functional traits are rare (but see Bodmer et al. 1997, Rovero et al. 2020, Scabin and Peres 2021). In my study I explicitly included relationships between hunting and vertebrate traits so that they may be linked to the ecological processes of seed dispersal, seed predation and browsing (Chapter 2; Figure 1). The results revealed that **assemblages of hunted vertebrates exhibited smaller body size, a higher proportion of dichromacy (vision type), and a lower proportion of frugivory (diet)**, compared to non-hunted assemblages.

While previous studies have reported similar hunting-induced changes in body size and diet (Rovero et al. 2020, Scabin and Peres 2021), vision type has, to my knowledge, not been studied before. These changes may have severe impacts on seed dispersal, seed predation and browsing. For instance, reduced body size has been linked to reductions in the dispersal of large seeds (Brodie and Gibbs 2009), but might similarly be linked to reductions in seed predation. Birds and some primates are known to be more sensitive to certain colors due to their vision types, which affects their fruit selection (Lomáscolo and Schaefer 2010). Community wide changes in vision type may therefore have quantitative effects on vertebrate – fruit interactions based on fruit colors.

The relationships between vertebrate traits and fruit traits are largely unclear (Valenta and Nevo 2020). To translate hunting-induced changes in functional composition to

changes in ecological processes therefore required additional research, which was the focus of Chapters 3 and 4.

*How are vertebrates linked to fruits and seeds and how are these interactions affected by hunting?*

Functional traits of vertebrates are considered important indicators for their interactions with fruits (including seeds), however which traits are relevant and to what extent they determine vertebrate - fruit interactions, is still poorly understood. Ecologists often rely on dispersal syndromes, which are crude, lack detail, and are largely based on anecdotes (Valenta and Nevo 2020). Furthermore, interactions between vertebrates and fruits are mostly studied with a focus on fruit traits, while grouping animals, for example in feeding guilds (Gautier-Hion et al. 1985, Fischer and Chapman 1993). This approach largely ignores the importance of vertebrate traits, even though we know that they play an important role in fruit selection (Lomáscolo and Schaefer 2010, Melin et al. 2019).

I investigated trait - trait interactions between vertebrates and fruits (including seeds), to determine which traits of vertebrates and fruits are the best predictors for interactions, and which traits are not (Chapters 3 and 4). One of the most striking findings was that **body mass was *not* a good predictor for fruit length and seed mass** in vertebrate – fruit interactions (Chapter 4). Although the relationships were sometimes significant, the variance was very high, also within vertebrate groups (e.g. birds, primates). A positive relationship between vertebrate size and seed size is a fundamental assumption in many studies focusing on hunting, such as those that link hunting to reduced carbon storage in tropical forests (Bello et al. 2015, Peres et al. 2015, Osuri et al. 2016). Nevertheless, the results also revealed that **hunted vertebrate species interacted with fruits that were longer, had heavier seeds and were from species with a higher wood density**. So even though the fundamental assumption that hunted vertebrates are larger and therefore interact with larger seeds compared to non-hunted vertebrates is incorrect (Bello et al. 2015, Peres et al. 2015, Osuri et al. 2016), the outcome of the defaunation studies making these assumptions might still be similar.

**Vision type showed several significant relationships with fruit color.** For example tetrachromacy, which was mostly present in birds, was positively related to fruits that reflect blue light, in accordance with Lomáscolo and Schaefer (2010). This is however contrary to the general consensus, which is that birds prefer red and black fruits (Wheelwright and Janson 1985). Even though our data contained plenty of interactions between birds and red or black fruits, this did not significantly occur more often compared to other vision types. Furthermore, blue and purple are far less

common fruit colors in the Guianas (Chapter 3), and the relationship may therefore have previously been overlooked.

Many studies have focused on finding key traits that predict interactions between animals and fruits (Ramos-Robles et al. 2018, Bender et al. 2018), including my own research. However, **I hypothesize that ecological context plays a crucial role in fruit selection, and that relationships between vertebrates and fruits are context-dependent.** Research on ecological context-dependence in vertebrate – fruit interactions in the tropics is currently limited (Blendinger et al. 2016, Ramos-Robles et al. 2018), even though it is an important concept in ecology (Catford et al. 2022). For example, resource availability may influence the selection of floral traits in pollination (Sletvold 2019). Likewise, resource availability may also play an important role in vertebrate-fruit interactions in a spatial and temporal way. Firstly, the availability of fruits with the preferred traits within a vertebrate’s home range dictates the amount of interactions it may have with these fruits. When availability is low vertebrates may feed on fruits with less desirable traits. Secondly, the quantity of fruits with the preferred traits may vary over time, which in turn may dictate the amount of interactions between a vertebrate and its preferred fruits. This temporal variation in fruit availability could be linked to seasonal changes in precipitation or differences in fruit production between years.

*How does hunting affect the composition of tree recruit communities?*

Hunting-induced changes in ecological processes are not random as hunters prefer vertebrates with specific traits. This could have major consequences for the composition of tree recruit communities (Figure 1), which I investigated in Chapter 5. The results of Chapter 4 led me to hypothesize that changes in tree recruit communities following from changes in ecological processes must be related to fruit size and seed mass. However, I found that **defaunation**, expressed as the defaunation index (Giacomini and Galetti 2013), **was significantly related to leaf palatability (positive) and wood density (negative), and no significant relationships were found with fruit traits.** Our study was the first to reveal changes in leaf trait composition as a result of hunting. After Dirzo and Miranda (1991) demonstrated that large differences in browsing damage between a hunted and non-hunted forest, Kurten et al. (2015) were the first to investigate the relationship between hunting and leaf traits, but found no significant relationships. Multiple studies have shown that browsers can have a marked influence on the survival of recruits in tropical forests (Schupp 1988, Howe 1990, Molofsky and Fisher 1993, Osunkoya et al. 1993), and it is unclear why browsing received so little attention in hunting studies.

Even though I did not find a strong relationship between the level of defaunation and fruit traits, **it is unlikely that there are no changes in seed dispersal and seed predation**, as hunted vertebrates interact with larger seeds (Chapter 4), and considering the evidence from previous studies that found reduced dispersal of seeds, or increased clustering of recruits at hunted sites (Beckman and Muller-Landau 2007, Harrison et al. 2016, Bagchi et al. 2018). Unfortunately, due to a lack of data, we were unable to study relationships between defaunation and seed size or seed mass. However, the effects of reduced seed dispersal and seed predation on forest composition might also be weak.

**In this thesis I established that hunting-induced defaunation affects the composition of the tree recruit community, which will likely have a cascading effect on the adult community over time. Seed dispersal and seed predation will probably be affected, due to changes in vertebrate – fruit interactions, but how and to what extent changes in these ecological processes affect tree recruit communities remains unclear. It seems, however, that in earlier studies the impact of reduced seed dispersal may be overestimated, seed predation is understudied, and that the role of browsing has been underappreciated.**

## 2. IMPLICATIONS FOR CONSERVATION AND SOCIETAL RELEVANCE

Since long, hunting has been an important topic in nature conservation, but has generally focused on the consequences for vertebrate diversity (Balding and Williams 2016). **This research emphasizes the impact of hunting on tree communities.** Therefore, **I suggest that conservation of tree diversity should be included in hunting related conservation strategies.** Due to the slow rate of forest regeneration it may take centuries until the effects of hunting are measurable in the adult tree communities. In the meantime, other threats to forest diversity, such as deforestation and forest degradation may be considered as more pressing. **Herein lies the potential danger that the impacts of hunting on forests are overlooked and even forgotten in the long-term.** Future forests, of which adult tree communities have been altered through hunting, might even be considered to be in a natural state, in the same way we have long overlooked the influence of ancient human societies on the composition of the Amazonian forests (Levis et al. 2017).

**Conservation now is often focused on regulating hunting such that vertebrate populations remain at sustainable levels** based on carrying capacities, which can result in smaller but stable population sizes (Bennett and Robinson 2000, Milner-

Gulland et al. 2008). As Chapter 5 shows that tree recruit communities change linearly with increasing defaunation, **this strategy does not ensure the conservation of tree diversity. We revealed that tree species with high wood density, high leaf toughness and low SLA are vulnerable to hunting. Species with these traits, such as *Quararibea duckei*, *Protium apiculatum* and *Dicorynia guianensis*, should be considered in conservation strategies.** These strategies should focus on the conservation of browsers at undisturbed levels, and on the conservation of dispersers of the seeds of these tree species.

Hunting-induced reductions in the dispersal of large seeds has been connected to reduced carbon storage in tropical forest, due to the positive correlation between seed size, wood density and tree height. Models predict that the loss of large vertebrates in the Amazon basin could result in the loss of up to  $183 * 10^6$  Mg carbon (Peres et al. 2016). The research in Chapter 4 confirmed that **hunted vertebrates interact with larger seeds compared to non-hunted vertebrates. I also observed a lower mean wood density with increasing defaunation (Chapter 5). I was, however, unable to link this to reduced seed dispersal, but rather to reduced browsing.** A recent study in African rainforests has shown that forest elephants increase carbon stocks through preferential browsing on leaves from low wood density species in addition to the dispersal of large seeds (Berzaghi et al. 2023). Although elephant-sized vertebrates do not occur in the Amazonian rainforests, similar mechanism may play a role.

### 3. TOPICS FOR FUTURE RESEARCH

**This thesis has highlighted some important knowledge gaps.** Addressing these gaps, as well as improvements in the methodology to study these gaps, would improve our understanding of the impacts of hunting on tropical forests. Here I discuss four topics which I consider to be most valuable: **the impact of hunting on browsing; modern techniques for vertebrate surveys; context-dependence in vertebrate – fruit interactions; and disentangling seed predation and seed dispersal.**

Chapter 5 of this thesis, along with the research by Dirzo and Miranda (1991), present compelling results that underscore the **need for further study to deepen our understanding of the impacts of hunting on browsing.** While there are several studies on plant defenses against herbivory (Coley 1983, Coley and Barone 1996, Kursar and Coley 2003), there are surprisingly few studies on leaf trait – palatability relationships for vertebrates in the tropics (Lucas et al. 1998). These relationships are, however, crucial to understand and predict how hunting affects browsing. **Cafeteria experiments**, in which vertebrates are offered recruits varying in leaf traits may be used

**to investigate which leaf traits are preferred by vertebrates** (Pérez-Harguindeguy et al. 2003). Monitoring with camera traps allows for identifying differences in these relationships for different vertebrate species. An alternative approach for identifying leaf trait preferences is to **identify vertebrate species from the DNA in the saliva they leave at browsed twigs** (Nichols et al. 2015). Although the use of environmental DNA is promising, it is still a method in development (Zinger et al. 2020). Pilot studies in French Guiana have shown that the use of environmental DNA to detect and identify vertebrate species is challenging. However, an advantage of this approach would be that it provides insight into the impact that different vertebrate species have on recruit communities, and thus into how the loss of vertebrate species may affect browsing patterns.

**Line-transects with distance sampling is a widely used method for vertebrate surveys, and has major advantages** in that it has been well-studied and developed (Peres 1999, Buckland et al. 2005), which also makes it easier to compare with other studies. However, the human component in this method allows for limited amounts of data due to fatigue, and observer bias for example due to different levels of experience. New observation methods have been developed, which tackle these downsides of line transects (Zwerts et al. 2021). Particularly camera trapping is currently widely used after decades of development (Jansen et al. 2014, Rovero et al. 2014, Glover-Kapfer et al. 2019), but has mainly been proven suitable for ground-dwelling vertebrates and less for arboreal species (O'Brien and Kinnaird 2008, Zwerts et al. 2021). Acoustic monitoring, in which sounds are used to identify species, made its appearance relatively recently and is still in an early development phase (Blumstein et al. 2011, Sugai et al. 2019). Both camera trapping and acoustic monitoring are currently subject of methodological studies in French Guiana. All three methods are limited in the species they can observe, and accurate species density estimates is challenging for each method (Zwerts et al. 2021). **Camera trapping and acoustic monitoring are not a full replacement of line-transects, but may be used in addition to line transects.**

I have argued that **ecological context-dependence in time or space may play an important role in fruit selection by vertebrates**, and that this may explain how interactions do not always match the predicted preferences of vertebrates and thus diminishes the strength of statistical relationships between vertebrates and fruits. Blendinger et al. (2016) provide evidence to support this hypothesis for vertebrate - fruit interactions in Andean forests, where fruit selection changes over time and is mostly driven by the amount of pulp of the fruit. However, studies addressing this topic for tropical rainforests and for a wide variety of vertebrate species are missing. The investigation of the influence of annual phenology of fruiting is perhaps the easiest to achieve, considering that most tree species fruit during the main wet season and



least during the main dry season (Sabatier 1985, ter Steege and Persaud 1991). If the dataset with vertebrate – fruit interactions from Chapter 3, or similar datasets, would be supplemented with information on the time of the year in which the data were collected, we could **compare vertebrate fruit relationships between the wet and the dry season**. Spatial limitation (i.e. the availability of fruits within the home range) is probably more difficult to investigate, as this would require knowledge of all fruiting plants within a home range, but could perhaps be achieved at research stations where trees have been mapped and identified, such as at the Paracou research station in French Guiana.

**The loss of seed predation due to hunting has been the subject of relatively few empirical investigations** (Wright and Duber 2001, Beckman and Muller-Landau 2007, Dirzo et al. 2007, Rosin and Poulsen 2016) even though it has been acknowledged that the loss of seed predation might affect plant diversity (Wright 2003, Stoner et al. 2007). Although there is evidence that fungi and insects may offset reductions in seed mortality as a result of reduced vertebrate seed predation (Wright 2003, Williams et al. 2021), it is yet unclear to what extent reduced seed predation affects forest regeneration. On the other hand, there has been a great amount of attention for the loss of seed dispersal due to hunting. Some have predicted that the loss of seed dispersal might have major impacts on forest diversity (Bello et al. 2015, Peres et al. 2015, Osuri et al. 2016), even though studies (Bagchi et al. 2018, Hazelwood et al. 2020), including Chapter 5, have provided evidence that its importance might be overestimated.

A fundamental issue in assessing the roles of seed predation and seed dispersal in the context of hunting is that it is often unclear whether vertebrate – fruit interactions lead to seed predation or seed dispersal. Of the numerous studies collected for the seed interaction dataset (Chapter 3) there were plenty that provided information about seed fate. Among those are studies that identified seeds from vertebrate feces and tested them for viability (e.g. Janzen 1982, Lobova et al. 2003, Jerozolinski et al. 2009), an approach which could be repeated to gain more information. **A systematic review of such studies will provide much needed insights into the fate of seeds after vertebrate – fruit interactions.**

**In conclusion, it is without doubt that hunting has a major impact on vertebrate community composition, ecological processes and tree recruit community composition, which probably results into changes in adult tree community composition. In this study we showed that hunting affects the functional composition of vertebrate communities, that hunted vertebrates interact with different fruits**

compared to non-hunted vertebrates and that hunting-induced defaunation affects tree recruit community composition. However, this research also highlights some key questions that remain to be answered, particularly about how hunting-induced loss of browsers affects tree communities. Nonetheless, the new insights from this thesis can directly be implemented in strategies for the conservation of tropical forests.

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## SUMMARY

Vertebrates are hunted throughout the tropics, resulting in severe declines of their populations. These vertebrates play crucial roles in shaping tropical forests, through processes such as seed dispersal, seed predation and browsing, which affect the survival chances of seeds and tree recruits (i.e. seedlings and saplings). The loss of vertebrates is therefore thought to affect the composition of recruit communities, eventually resulting in compositional changes in adult tree communities. In the long-term this might affect the forest biodiversity, carbon sequestration and nutrient cycling.

Hunting is non-random, as vertebrates with a large body mass are the favored game species. Therefore hunting particularly affects populations of large vertebrate species. Body mass and other vertebrate functional traits, as well as functional traits of fruits, seeds and leaves, drive the interactions that lead to seed dispersal, seed predation and browsing. Therefore, hunting likely decreases survival changes for particular tree species, while increase them for others, depending on their functional traits. Consequently, hunting hypothetically affects the fruit, seed and leaf composition of tree recruit communities.

How hunting affects tropical forests remained largely unclear, and the aim of this research was to better this. Due to the importance functional traits in vertebrate – fruit and vertebrate – leaf interactions, the focus of this research lied mainly on functional traits and functional composition. First the research focused on looking at how hunting affects the functional composition of vertebrate assemblages, by comparing hunted and non-hunted assemblages across French Guiana. Next, the question was which vertebrate and fruit traits were important for vertebrate – fruit interactions, and if these relationships were different between hunted and non-hunted species. For this a large dataset was compiled, through a literature search, of fruit traits, vertebrate traits and vertebrate – fruit interactions. Finally, differences in functional composition of tree recruit communities in relation to the levels of hunting-induced defaunation were tested, for which data of eight tree recruit and adult communities across French Guiana were collected, each with its own level of defaunation.

This study showed that hunting affects the functional composition of vertebrate communities, and that hunted vertebrates interact with different fruits compared to non-hunted vertebrates. Furthermore, hunting-induced defaunation was found to be related to the functional composition of the tree recruit communities. However, these relationships were with leaf traits rather than with fruit and seed traits, suggesting that hunting strongly affects browsing. As browsing has so far received little attention in the context of hunting, this finding is a particularly important new insight. The



findings of this research provide new tools for nature managers and policy makers to formulate strategies for the conservation of tree communities of tropical forests.

## RÉSUMÉ EN FRANÇAIS

Les vertébrés sont chassés sous les tropiques, ce qui entraîne un déclin sévère de leurs populations. Ces vertébrés jouent des rôles cruciaux dans la formation des forêts tropicales, à travers des processus tels que la dispersion des graines, la prédation des graines et l'abroustissement, qui affectent les chances de survie des graines et des recrues d'arbres (i.e. semis et les jeunes arbres). On pense donc que la perte de vertébrés affecte la composition des communautés de recrues, entraînant éventuellement des changements dans la composition des communautés d'arbres adultes. À long terme, cela pourrait affecter la biodiversité forestière, la séquestration du carbone et le cycle des nutriments.

La chasse n'est pas aléatoire, car les vertébrés ayant une masse corporelle importante sont les espèces de gibier préférées. La chasse affecte donc particulièrement les populations de grandes espèces vertébrées. La masse corporelle et d'autres traits fonctionnels des vertébrés, ainsi que les traits fonctionnels des fruits, des graines et des feuilles, déterminent les interactions qui conduisent à la dispersion des graines, à la prédation des graines et à l'abroustissement. Donc, la chasse diminue probablement les chances de survie pour certaines espèces d'arbres, tandis qu'elle les augmente pour d'autres, en fonction de leurs caractéristiques fonctionnelles. Par conséquent, la chasse affecte hypothétiquement la composition en fruits, en graines et en feuilles des communautés de recrues arboricoles.

L'impact de la chasse sur les forêts tropicales reste largement flou, et le but de cette recherche était d'améliorer cette situation. En raison de l'importance des traits fonctionnels dans les interactions vertébrés – fruits et vertébrés – feuilles, cette recherche s'est principalement concentrée sur les traits fonctionnels et la composition fonctionnelle. Tout d'abord, la recherche s'est concentrée sur l'impact de la chasse sur la composition fonctionnelle des assemblages de vertébrés, en comparant les assemblages de populations en zones chassées et non chassées à travers la Guyane française. Ensuite, la question était de savoir quels traits des vertébrés et des fruits étaient importants pour les interactions vertébrés-fruits, et si ces relations étaient différentes entre les espèces chassées et non chassées. Pour cela, un vaste ensemble de données a été compilé, grâce à une recherche documentaire, sur les caractéristiques des fruits, les caractéristiques des vertébrés et les interactions vertébrés-fruits. Enfin, les différences dans la composition fonctionnelle des communautés de recrues d'arbres en relation avec le taux de défaunation induit par la chasse ont été testées, pour lesquelles des données de huit communautés d'arbres jeunes et adultes à travers la Guyane française, dans des sites ayant subi un niveau de défaunation variable.

Cette étude a montré que la chasse affecte la composition fonctionnelle des communautés de vertébrés et que les vertébrés chassés interagissent avec un ensemble de fruits différents par rapport aux vertébrés non chassés. De plus, la défaunation induite par la chasse s'est avérée être liée à la composition fonctionnelle des communautés de recrues d'arbres. Cependant, ces relations concernaient les caractères des feuilles plutôt que ceux des fruits et des graines, ce qui suggère que la chasse affecte fortement l'abrouissement. Comme l'abrouissement a jusqu'à présent reçu peu d'attention dans le contexte de la chasse, cette découverte constitue une nouvelle perspective particulièrement importante. Les résultats de cette recherche fournissent de nouveaux outils aux gestionnaires de la nature et aux décideurs politiques pour formuler des stratégies de conservation des communautés d'arbres des forêts tropicales.

## NEDERLANDSE SAMENVATTING

Door heel de tropen worden (gewervelde) dieren bejaagd, wat resulteert in een ernstige achteruitgang van hun populaties. Deze dieren spelen een cruciale rol bij de vorming van tropische bossen, via processen zoals zaadverspreiding, zaadpredatie en folivorie, die de overlevingskansen van zaden en jonge boompjes beïnvloeden. Men denkt daarom dat het verlies van dieren de samenstelling van gemeenschappen van jonge boompjes beïnvloedt, wat uiteindelijk resulteert in veranderingen in de samenstelling van volwassen boomgemeenschappen. Op de lange termijn kan dit gevolgen hebben voor de biodiversiteit van bossen, de koolstofvastlegging en de nutriëntenkringloop.

Jacht is niet willekeurig, aangezien dieren met een groot lichaamsgewicht de favoriete jachtsoorten zijn. Daarom heeft jacht vooral invloed op populaties van grote diersoorten. Lichaamsgewicht en andere functionele eigenschappen van dieren, evenals functionele kenmerken van vruchten, zaden en bladeren, zijn de drijvende kracht achter de interacties die leiden tot zaadverspreiding, zaadpredatie en folivorie. Daarom vermindert de jacht waarschijnlijk de overlevingskansen voor bepaalde boomsoorten, terwijl deze voor andere boomsoorten toeneemt, afhankelijk van hun functionele eigenschappen. Bijgevolg heeft de jacht hypothetisch invloed op de vrucht-, zaad- en bladsamenstelling van gemeenschappen van jonge boompjes.

Hoe jacht tropische bossen beïnvloedt was grotendeels onbekend, en het doel van dit onderzoek was om deze kennis te verbeteren. Vanwege het belang van functionele eigenschappen bij interacties tussen gewervelde dieren en vruchten of bladeren, lag de focus van dit onderzoek vooral op functionele eigenschappen en functionele samenstelling. In de eerste plaats concentreerde het onderzoek zich op hoe door jacht veroorzaakte verlies van dieren de functionele samenstelling van dierenpopulaties beïnvloedt, door bejaagde en niet-bejaagde populaties door heel Frans-Guyana te vergelijken. Vervolgens was de vraag welke eigenschappen van dieren en vruchten belangrijk waren voor interacties tussen dieren en vruchten, en of deze relaties verschillend waren tussen bejaagde en niet-bejaagde soorten. Hiervoor werd door middel van literatuuronderzoek een grote dataset samengesteld van vruchtkenmerken, kenmerken van dieren en interacties tussen dieren en vruchten. Ten slotte werden verschillen in functionele samenstelling van gemeenschappen van jonge boompjes in relatie tot de niveaus van jacht getest, waarvoor gegevens van acht gemeenschappen van jonge boompjes en volwassen gemeenschappen in Frans-Guyana werden verzameld, elk met zijn eigen niveau van jacht.

Deze studie toonde aan de door jacht veroorzaakte verlies van dieren de functionele samenstelling van gemeenschappen van dieren beïnvloedt, en dat bejaagde dieren

interacteren met andere vruchten in vergelijking met niet-bejaagde dieren. Bovendien bleek dat door de jacht veroorzaakte verlies van dieren verband hield met de functionele samenstelling van gemeenschappen van jonge boompjes. Deze relaties hadden echter betrekking op bladkenmerken en niet op vrucht- en zaadkenmerken, wat erop duidt dat jacht een sterke invloed heeft op folivorie. Omdat folivorie tot nu toe weinig aandacht heeft gekregen in de context van jacht, is deze bevinding een bijzonder belangrijk nieuw inzicht. De bevindingen van dit onderzoek bieden natuurbeheerders en beleidsmakers nieuwe instrumenten om strategieën te formuleren voor het behoud van boomgemeenschappen in tropische bossen.

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## ABOUT THE AUTHOR

Rens Vaessen was born on October 7th, 1986, in Heerlen, the Netherlands. He discovered his love for biology in the classrooms of the Erasmus College in Zoetermeer, where he completed his secondary education. He found his passion for plants and ecology while pursuing his Bachelor's degree Biology at Utrecht University. He obtained his Master's degree in Environmental Biology at Utrecht University, during which Rens embarked on an internship in Vietnam, where he investigated the biomass stored in forests. This experience ignited his love for tropical ecology. Before starting his PhD he co-founded the ecological research company Dactylis, and started as a teacher at Utrecht University.

In his pursuit of ecological research in the tropics he was guest researcher at Naturalis to investigate the number of known tree species in the Amazonian forests. It was after this research that his family definitively decided that his work consisted of counting trees. In 2015 Rens started his PhD funded by the Trésor foundation and Utrecht University.

During his time as a PhD-student Rens supervised over 10 bachelor's and master's theses, and 10 master's internships, of which eight joined him to French Guiana. Furthermore, every year he coordinated and taught most of the bachelors course *Nature conservation, sustainability and plant diversity*, while also making small contributions to several other courses.

Rens is currently working as ecologist and director at Dactylis. In his free time Rens likes to run, climb, or spend his time woodworking and gardening. Rens lives in Utrecht with his partner Gillian and daughter Laura.



