

**Seed dispersal mode and habitat connectivity underpin variation in carbon stocking
between Brazilian biomes.**

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Short running title: Landscape structure changes tree carbon stocks

Abstract

Landscape changes lead to direct and negative effects on zoochoric seed dispersal. The disruption of seed dispersal processes can significantly alter the long-term carbon storage potential in tropical forests. An important question is how landscape structure changes tree carbon stocks in different types of tropical vegetation and how variation is mediated by the dispersal mode of animal (zoochoric) or abiotic (non-zoochoric) seeds. We focused on tree plots at 126 sites in Brazil spanning four types of forest and savanna vegetation, and calculated carbon stored in zoochoric, non-zoochoric, and large frugivore-dispersed species. Our results showed that carbon stocks in zoochoric species and non-zoochoric species differ significantly among vegetation types, with rainforest having higher stocks in zoochoric species and semideciduous seasonally dry tropical forests having higher values in non-zoochoric species. A greater area of native vegetation promotes higher proportions of carbon stocks dispersed by large frugivore species, whereas a higher mean shape index reduces this proportion. This study highlights that seed-dispersal type underpins the variation in carbon stocks between vegetation types and that the maintenance of habitat of large dispersers and connectivity are key for retaining carbon stocks in zoochoric species, particularly in rainforest and cerrado sensu stricto.

Keywords: ecosystem functioning, ecosystem services, dispersal syndrome, fragmentation, habitat loss.

1. INTRODUCTION

In the Anthropocene, deforestation, fragmentation, and edge effects are the main drivers of carbon emissions (Achard et al. 2014; Baccini et al. 2012; Berenguer et al. 2014; Magnago et al. 2017, Pearson et al. 2014). These activities directly influence the landscape structure (organization and arrangement), creating landscape configurations with higher forest isolation, less forestry cover, and with different compositions, including agriculture, pastures, and urban infrastructure (Souza et al., 2020). These reduce the potential of landscapes to store carbon (Coelho et al. 2020; De Paula et al. 2011). In the remaining forest, fragmentation and edge effects usually create a hotter and less humid microclimate (Laurance et al. 2011, Murcia 1995), which leads to higher mortality of large tree species and thereafter to alterations in species composition, principally replacing late successional tree species with hardwood to softwood pioneer species (Laurance 1998, 2002, Matos et al. 2021). The combination of these factors is capable of releasing $425 \pm 92.0 \text{ Tg C year}^{-1}$ pantropically (Baccini et al. 2017). Other ecological processes, such as seed dispersal, can also be negatively impacted by changes in landscape structure, leading to changes in tree recruitment patterns (Terborgh et al. 2008; Emer et al. 2018). Change to the processes in the plant life cycle can significantly alter the long-term carbon storage potential in tropical rainforests (Bello et al. 2015, Brodie 2016, Brodie 2017, Osuri et al. 2016, Peres et al. 2016).

In tropical forests, most woody plant species (from 60 to 88%) depend on animal-plant interactions for dispersal (Howe & Smallwood 1982; Jordano 2000). Fruit size and seed mass are the main modulators of plant-disperser interaction networks (Donantti et al. 2011, Howe 2016, Valenta & Nevo 2020). These prevent some dispersal interactions, such as those of small vertebrates with large fruits (Fuzessya et al. 2018, Howe 2016, Leishman et al. 2000), promoting

dispersal by large vertebrates that have the ability to process fruits (Fuzessy et al. 2018, Valenta & Nevo 2020). Dependence on animal species for dispersal thus makes this interaction very fragile, especially in the face of anthropogenic land-use change and overhunting.

The decline or extinction of seed dispersers Influences the recruitment of tree populations (Redford 1992; Terborgh et al. 2008), and thus the composition of hardwood tree species (Bello et al. 2015; Culot et al. 2017). Following the overhunting and extirpation of large frugivores, large seeds may not be dispersed or are only dispersed rarely by the remaining secondary dispersers in the community, affecting seedling recruitment of these tree species (Donoso et al. 2017). Furthermore, seed size of tropical tree species has a positive correlation with individual longevity, wood density, and total height, all characteristics linked to carbon storage in above-ground biomass (Doughty et al. 2016, Moles & Westoby 2006). Consequently, the future carbon storage capacity of tree communities with large seeds becomes fragile due to the extinction of their major seed dispersers, potentially leading to long-term erosion of carbon stored in the tree community (Bello et al. 2015, Brodie 2016, Peres et al. 2016).

The plant-disperser relationship is mediated by environmental conditions and the community of animals present in the ecosystem (Nathan & Muller-Landau, 2000). For example, forest ecosystems have characteristics that contribute to more species being dispersed by animals, such as fleshy fruits (Galetti et al. 2011), refuge for reproduction, and security against predators (Keuroghlian & Eaton 2008). The opposite happens in ecosystems with more sparse vegetation, such as savannas and Caatinga, which facilitate dispersion by abiotic means, such as wind, while dispersal by animals is directed toward small and medium-sized seeds (<10mm) (Leal et al. 2017).

Savanna ecosystems tend to have patches larger than forest ecosystems (e.g., Atlantic Forest), although much of their native vegetation is covered in anthropic areas (Strassburg et al. 2017). Forest ecosystems have higher plant species diversity than more open savannas and dry forests (Mittermeier et al. 2011). Furthermore, they present arboreal species with higher tree heights, while savanna areas are dominated by small to medium tree species (IBGE 2012). Due to human pressure, all tropical forest biomes are highly fragmented and isolated (Rezende et al. 2018). Given these different characteristics, in terms of both tree composition and landscape structure, it is expected that carbon storage services will also reflect these differences.

Here, we focus on how landscape structure affects carbon storage in tree species with distinct dispersal characteristics in different vegetation types (forest and savanna formations). We hypothesize that: (a) forest vegetation types have proportionally more carbon stored in the biomass of species dispersed by animals than savanna vegetation formations, due to floristic differences and different landscape characteristics; and (b) changes in landscape structure related to increasingly severe deforestation and fragmentation have a more negative impact on carbon storage in tree species dispersed by animals, as habitat disruption negatively affect frugivores, especially the large ones.

2. MATERIALS AND METHODS

2.1. Study area

We selected 126 forest sites classified as Atlantic Forest (65 areas), Cerrado (43 areas), or Caatinga (18 areas), according to their geographic distribution and sampled between 1990 and 2018. Subsequently, we classified sites according to the vegetation type: 43 areas of cerrado sensu stricto (CE), 18 of seasonally dry tropical forest deciduous (SDTF_D), 59 of seasonally

dry tropical forest semideciduous (SDTF_SD), and 6 of rainforest (RF) (Figure 1, S1, S2, and Table S1) (in M).

The Atlantic Forest, one of the world's biodiversity hotspots (Mittermeier et al. 2011), currently occupies between 11% and 28% of its original area (Rezende et al. 2018). Its main vegetation types include rain forest (RF) and semi-deciduous seasonally dry tropical forest (SDTF-SD) (Morellato and Haddad 2000). It is characterized by medium to large trees, and woody and epiphytic vines (IBGE 2012). Animals are of fundamental importance for this biome, as they disperse 89% of tree species (Almeida-Neto et al., 2008). The Cerrado is a savanna ecosystem that presents a wide physiognomic variation, ranging from open fields to dense forests, such as the Cerrado sensu stricto (Oliveira & Marquis 2002; Ribeiro & Walter 2008). The Cerrado sensu stricto is characterized by savanna woodland grassy vegetation of low to medium size. About 70% of the tree species in this biome require plant-animal interactions for dispersal (Salazar et al. 2012). Caatinga is a little known biome that occupies 10.7% of Brazilian territory (Silva et al., 2017). It presents a long period of drought, which determines the prevalence of the seasonally dry deciduous tropical forest (SDTF-D; Silva et al. 2017). Abiotic dispersion syndrome is prevalent in this biome, being responsible for the dispersal of 70% of tree species (Leal et al. 2017).

Tree community data were obtained from the Minas Gerais Forest Inventory (Scolforo & Carvalho 2008) and the Federal University of Lavras – CONFLORA, which constitutes a robust set of data used in other publications (Scolforo et al. 2015; Terra et al. 2017). These areas have an extensive history of degradation, due to the strong anthropogenic pressure from different soil management practices such as pasture, agriculture, mining, and urban infrastructure (MapBiomas 2018).

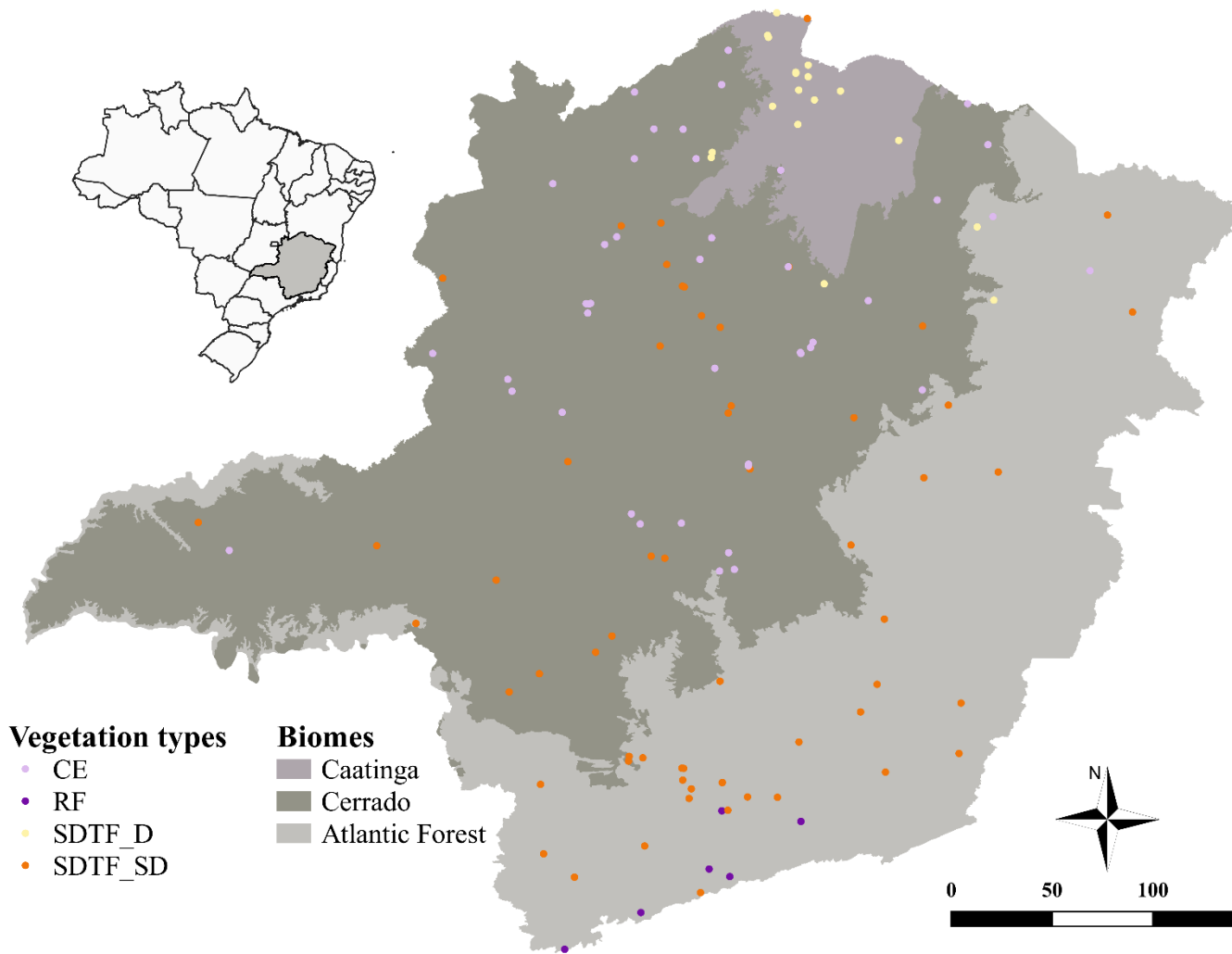


Figure. 1. Study area and location of the sampled sites in Minas Gerais State, Brazil. Cerrado sensu stricto (CE), rainforest (RF), seasonally dry tropical forest deciduous (SDTF_D) and seasonally dry tropical forest semi-deciduous (SDTF_SD).

We used a systematic sampling methodology for individual plots within sites of sizes ranging from 300, 400, and 1,000 m² according to the area of vegetation sampled. The total area sampled within a site ranged from 0.04 to 34.7 ha, with an average of 8.027 ha (Table S2). Within each plot, all tree species with diameter at breast height (DBH) <5 cm were sampled. Tree height data were obtained using a telescopic rod with a height of 5 m maximum. This method consists of placing the rod at the side of the tree and then extending it until it reaches the

height of the tree, and then the reading is done at the observer's line of sight (Scolforo et al. 2006). We adopted the APG III plant classification system and validated the names on the website “Flora do Brasil” (Flora do Brasil 2018).

2.2. CHARACTERIZATION OF COMMUNITY DISPERSION MODES

All tree species were classified into two major dispersal modes: zoochoric (species dispersed by animals) and nonzoochoric (species dispersed abiotically). This classification was based on characteristics related to fruit and seed morphology of the species: the presence of aril, pulp, elaiosome, viscous material, and colored coating (Barroso et al. 1999; Van der Pijl 1982). We consider dispersal to be the movement of seeds away from the parent plant, including consumption where the seeds are ingested and may occasionally be predated (Howe 2016, Howe & Smallwood 1982). Within zoochoric, the subset of tree species dispersed by large frugivores (mammals or birds) with large body mass (Figure. S3), based on the categorization of the dispersal mode per Bello et al. (2015), were termed ‘large-bodied frugivores’.

Seed diameter data for each species were collected from the literature (Bello et al. 2015), herbarium consultations, and the Species Link online platform (<http://splink.cria.org.br/>) (see Table S3). In previous studies on the Atlantic Forest (Bello et al. 2015; Galetti et al. 2013), the authors used the throat diameter of the largest frugivores to classify tree species according to their degree of threat. They classified all tree species that had a seed?? diameter <12 mm, as species that are dispersed by large frugivorous species (or threatened species), so we assumed this value for our investigation (Figure S4).

2.3. ESTIMATE OF BIOMASS AND CARBON STOCK

To estimate the above-ground biomass (AGB) of each individual tree, we used the allometric equation proposed by Chave et al. (2014) (Equation 1), where ρ is wood density (g.cm^{-3}), H is tree height (m) and D is the diameter at breast height (measured in cm at 1.3 m):

$$AGB_{est}: 0.0673 \times (\rho D^2 H)^{0.976}$$

(1)

Wood density values were obtained from the Global Wood Density Database (Zanne et al., 2009). As height was not taken for all trees sampled, we estimate the missing values by building diameter-height models for each vegetation type (Table S3). The models were built using the `nls2` function (Grothendieck 2013) in R software (R Core Team 2020) and selected based on the Akaike Information Criterion (AICc) (Akaike 1973).

The total AGB stock was calculated as the sum of the AGB values for all trees in each plot. For all sites, the biomass was estimated at 1 hectare. Tree species can vary in their amount of carbon stored in biomass, and these changes can be influenced by climatic gradients, edaphic changes, and age (Bordin et al. 2021). However, data on this are rare, and the 50% assumption is accepted for the different tropical biomes (IPCC 2003). Thus, we assumed that the amount of carbon corresponds to 50% of the estimated biomass. Individuals classified up to genus, family, or morphospecies (7.9% of the total individuals sampled) were not considered in the analyses of carbon storage of trees dispersed by animals, and species classified as dispersed by large frugivores.

2.4. ANTHROPOGENIC AND ENVIRONMENTAL VARIABLES

Landscape configuration and composition variables were obtained by processing the database provided by the online platform MapBiomass (2018), which contains information on

land cover and land use. We obtained the map in matrix format (30x30 m pixels) from the MapBiomass Project website, using data from 2004 because most of the vegetation community sampling took place at this time. The map was converted to a vector format, and 4x4 km square format buffers were generated, having as a central point the geographical coordinates of each sampled community. Several studies showed that different biodiversity and ecological parameters can be affected at different landscape scales (Walz 2011, Hagen et al. 2012, Martin et al. 2016; 'the scale of effect'). We selected the 4 km buffer size because: (i) most variation in tree structure and home ranges of large vertebrates is contained within these limits (Rocha-Santos et al. 2016, Thornton et al. 2011); (ii) most landscape studies used 4 km buffers (Matos et al. 2017, Ehlers Smith et al. 2017, Chen et al. 2021); and (iii) the buffer size for large seed dispersion was >1.6 km in Atlantic Forest Landscapes (Safar et al. 2022). Landscape variables were calculated using the V-late extensions (Lang & Tiede, 2003) and Patch Analyst (Rempel et al., 2012). All map processing and variables were obtained using the ArcGIS 10.5 program.

For each buffer, we calculated five variables related to landscape configuration: i) distance to nearest neighbour - returns the average distance value of the forest class considering all forest fragments within the buffer; ii) mean patch size - obtained by summing the size of forest/savanna patches divided by the number of forest/savanna patches; iii) edge density - returns the sum of all edges (ha) of the forest/savannah class divided by the total area (ha) of the landscape; iv) number of patches - a total number of forest/savanna class patches within the buffer; and v) mean shape index - values close to 1 indicate the forest/savanna patch has a circular shape and higher values higher denote a more irregular patch shape. We also calculated one composition-related variable: vi) native vegetation area – the sum of all areas of the forest/savanna class (Table S4). The normality of these variables was assessed graphically and

through the Shapiro-Wilk test (Figure S5). Given non-normality, we used Spearman correlation coefficient to assess the correlation between landscape variables. Edge density was strongly correlated with the number of patches and distance to the nearest neighbour, so it was excluded from the analysis (Table S5).

2.5. DATA ANALYSIS

First, we use generalized linear model analysis to test whether there are differences in seed size between vegetation types. We used a family of distributions of Gaussian errors seeking the best fit of the model, considering the non-normality of the seed diameter data. Second, to investigate how vegetation types differed in the proportion of carbon stored in all species dispersed by animals (zoochoric species), non-zoochoric species and species dispersed by large frugivorous species (tree species with seed diameter 12 mm), we used logistic regression models with beta error distribution family (proportion of continuous data), using the ‘betareg’ function (Ferrari & Cribari-Neto 2004).

We built generalized linear mixed models (GLMM) to investigate which explanatory variables (distance to nearest neighbor (m), mean patch size (ha), mean shape index, native vegetation area (ha), and number of patches) predict the proportion of carbon in three categories: carbon stored in all species dispersed by animals, carbon stored in non-zoochoric species and carbon stored in zoochoric trees dispersed by large frugivore species (tree species with seed diameter mm). We also incorporated an interaction term ‘vegetation types’ with four levels (Cerrado *sensu stricto*, Rain Forest, Seasonally Dry Tropical Forest deciduous, and Seasonally Dry Tropical Forest semideciduous). This addition allows us to explore potential differences in two aspects: (i) the relationship of each explanatory variable across all vegetation types; and (ii) the main effects specific to each vegetation type. For these models, we applied logistic regression

with the beta error distribution family using the function 'glmmTMB'. We tested overdispersion using the “simulateResiduals” function of the package “DHARMa” (Figure S6).

To control the effects of spatial autocorrelation in all models tested, we constructed a distance matrix (DM) for each response variable (total carbon (Mg ha^{-1}), carbon stored in animal dispersed species (%), carbon stored in dispersed by large frugivore species (%) and carbon stored in non-zoochoric species (%)) using the functions 'dnearneigh' and 'nb2listw' (Bivand & Wong 2018). For each of these response variables, a global model consisting of a response variable and six explanatory variables was constructed, including five landscape variables (distance to nearest neighbor (m), mean patch size (ha), mean shape index, native vegetation area (ha) and number of patches) and the distance matrix. These combinations were classified according to AICc, and models with $2 \leq \Delta\text{AICc} \leq 7$ have statistical support and, based on the analysis of the set of models under study, we defined as the best models those with $\Delta\text{AICc} \leq 4$ (Burnham et al. 2011). Inference by multiple models was made using the “model.avg” function based on the models that presented $\Delta\text{AICc} \leq 4$ values. We used the multcomp packages (Hothorn et al. 2008), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), MuMIn (Barton 2018), betareg (Cribari-Neto & Zeileis 2010) and ggplot2 (Wickham 2016).

3. RESULTS

3.1. CARBON STORAGE BY DISPERSAL MODE ACROSS VEGETATION TYPES

A total of 298,859 individuals comprising 1,316 tree species were sampled in our 126 forest and savanna communities (see Table S6). From the total of sampled species, 891 were classified as zoochoric and 425 as non-zoochoric (dispersed abiotically). Among all vegetation types, the majority of zoochoric species were found in the semideciduous SDTF (74%), Rain Forest (71%), and cerrado sensu stricto (63%). However, only 49% of the species were

zoochoric in the deciduous SDTF. The seed diameter of the zoochoric species ranged from 0.3 to 63.8 mm with an average of 7.4 mm and showed a wide variation between vegetation types (Figure 2). The vegetation type with the highest richness of species dispersed by large frugivores was semi-deciduous SDTF with 118 species (11%), followed by rainforest with 72 species (16%), SDTF deciduous with 28 species (7%), and cerrado sensu stricto with 23 species (4%). Zoochoric and non-zoochoric seed sizes differed among all types of vegetation (Table S7).

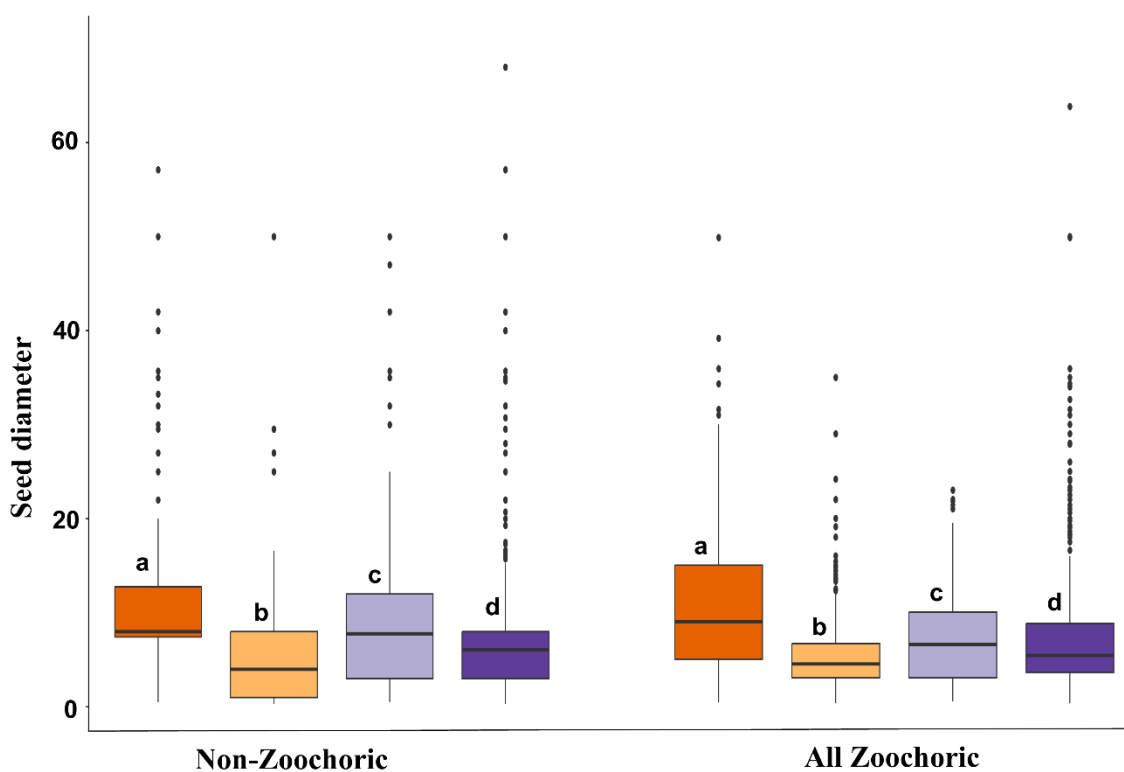


Figure 2. Average seed diameter (mm) of non-zoochoric species and zoochoric species (all species dispersed by animals) for each of the vegetation types in the study. The boxes show the median values. The points represent the discrepancies (outliers). Cerrado sensu stricto (CE) is represented by a dark orange color, Rain Forest (RF) by a light orange color, Seasonally Dry Tropical Forest deciduous (SDTF_D) by a light purple color, and Seasonally Dry Tropical Forest Semideciduous (SDTF_SD) by a dark purple color.

3.2. AMOUNT OF CARBON AMONG VEGETATION TYPES

We found significant differences among all types of vegetation in the proportion of carbon stored by zoochoric species ($p < 0.0001$, Figure 3A, Table S8) and non-zoochoric species per hectare ($p < 0.0001$, Figure 3B, Table S8). Deciduous SDTF had the lowest proportion of carbon stored in species dispersed by animals (14%) and the largest proportion of carbon stored in non-zoochoric species (83%), followed by cerrado sensu stricto (dispersed by animals: 37%; non-zoochoric: 55%), SDTF semideciduous (dispersed by animals: 55%; non-zoochoric: 36%) and Rain Forest (dispersed by animals: 63%; non-zoochoric: 31%). However, when looking at the proportion of carbon stored in species dispersed by large frugivores, the Rain Forest and SDTF deciduous have a similar pattern of carbon vulnerability, with 13% and 16% of carbon coming from these species (Figure 3C, S7, S8 and Table S8). The other vegetation types show significant differences. SDTF semideciduous with 18% and cerrado sensu stricto with 44% of carbon stored in species dispersed by large frugivores.

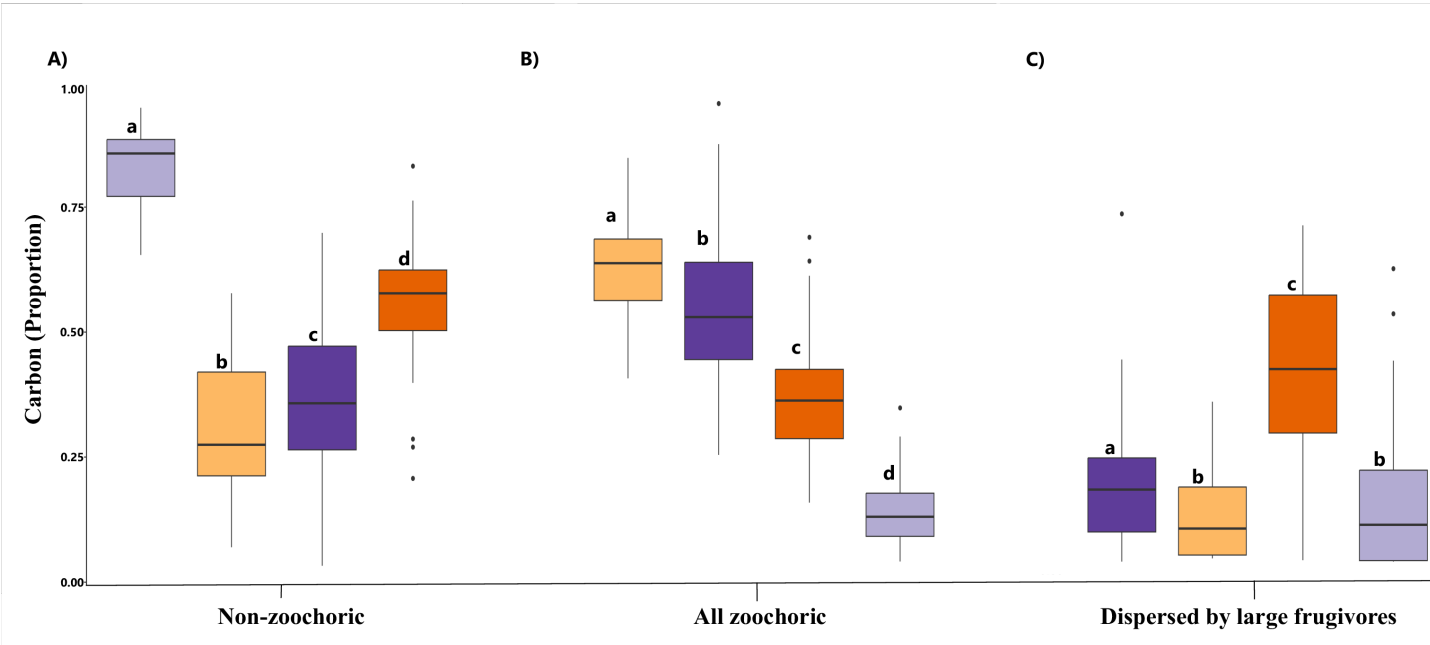
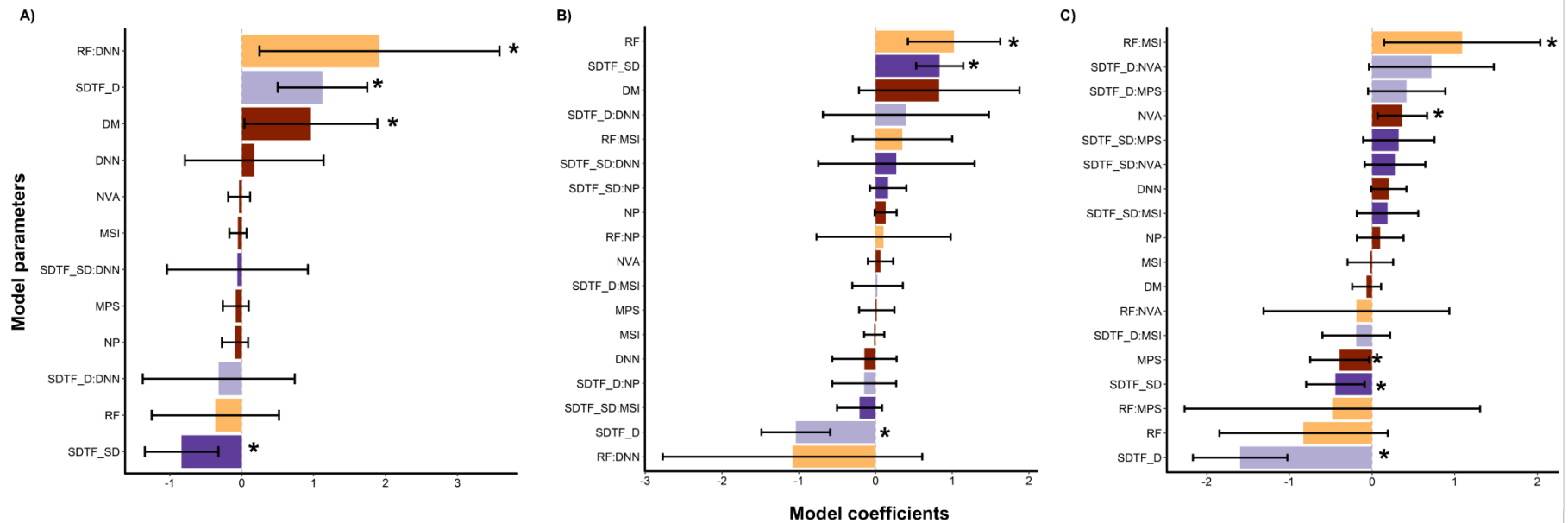


Figure. 3. Average proportion of carbon stored in non-zoochoric, all zoochoric and zoochoric species dispersed by large frugivores between the different vegetation types. Cerrado sensu

stricto (CE) is represented by a dark orange color, Rain Forest (RF) by a light orange color, Seasonally Dry Tropical Forest Deciduous (SDTF_D) by a light purple color, and Seasonally Dry Tropical Forest Semideciduous (SDTF_SD) by a dark purple color. Large frugivorous-dispersed species with seed diameter ≥ 12 mm. Different letters are significantly different at $p < 0.05$. Boxes show the median values. The points represent the discrepancies (outliers).

3.3. IMPACTS OF ANTHROPOGENIC VARIABLES ON CARBON

The multimodel inference showed that the proportion of carbon stored in zoochoric species is not related to the variables of the landscape structure variables (Figure 4A and Table S9). However, the models showed that the RF areas with a greater distance from the nearest patch (DNN) were responsible for the highest proportion of carbon stored in non-zoochoric species (Figure 4B and Table S9). Multimodel inference also showed that the proportion of carbon stored in tree species dispersed by large frugivores was positively driven by the native vegetation area around the sampled patches and was negatively affected by the mean shape index for the type of vegetation in the RF (Figure 4C and Table S9).



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296 **Figure 4.** Effect of environmental and distance variables on the proportion of carbon stored in (A) non-zoochoric species, (B) all
 297 zoochoric species, and (C) dispersed by large frugivore species (species with seed diameter ≥ 12 mm). DNN = Distance to the
 298 nearest neighbor, DM = distance matrix, MPS = mean patch size, MSI = mean shape index, NP = number of patches and NVA =
 299 native vegetation area. Rain Forest (RF) by light orange color, Seasonally Dry Tropical Forest Deciduous (SDTF_D) by light purple
 300 color, Seasonally Dry Tropical Forest Semideciduous (SDTF_SD) by dark purple color, and explanatory variables without the effect
 301 of interaction with vegetation types by dark red. The bars show the mean effect size (Model coefficients) of each explanatory variable
 302 on the carbon stock and whiskers representing the 95% confidence interval. The asterisk (*) indicates that $p < 0.05$. Cerrado sensu
 303 stricto (CE) does not appear here, as the proportions of the different carbon categories are not explained by the interaction with this
 304 type of vegetation.

4. DISCUSSION

Changes in landscape structure drive impacts on tropical forest carbon stocks (Bhan et al. 2021). We tackled the key question of how seed dispersal traits (zoochoric and abiotic dispersal types) mediate the resilience of carbon stocks in deforested and fragmented landscapes across a range of vegetation types. We find that the percentage of carbon stored in trees with seed dispersed by large-bodied frugivores differs between vegetation types, with cerrado sensu stricto having the highest percentage. Using a large spatial-scale assessment, our results reveal the importance of landscape composition and configuration for maintaining carbon stocks in the biomass of trees with different dispersal traits. In particular, we found that large amounts of native habitat in the landscape maintain the highest proportions of carbon per hectare stored in species dispersed by large frugivores and that this category is negatively affected by the mean patch size. This demonstrates the fragility of ecosystem functioning maintained by plant-animal interactions in a highly fragmented landscape.

4.1. CARBON STORAGE BY DISPERSAL MODE ACROSS VEGETATION TYPES

About 68% of the 1,316 species sampled are zoochoric, demonstrating the importance of maintaining plant-animal interactions for the continued functioning of the studied ecosystems and biomes (Bagchi et al. 2018, Caughlin et al. 2015, Farwig & Berens, 2012, Muñoz et al. 2017). Cerrado sensu stricto, SDTF semideciduous, and Rain Forest showed the highest dependence on seed-dispersal by large-bodied animals, supporting data described in the literature (Brancalion et al. 2018, Jardim & Batalha 2009, Sansevero et al. 2011). A different pattern was found for SDTF deciduous, which showed the lowest dependence on this seed-dispersal interaction because of its predominance of abiotically dispersed tree species (see Griz & Machado 2001, Leal et al. 2017).

SDTF_SD and RF show high richness and abundance of zoochoric species, but are directed toward species with small seeds (Staggemeier et al. 2016). This may be a result of the evolutionary reduction in seed size due to the loss of large frugivores over the century (Galetti et al. 2013; Jorge et al. 2013), explaining the low percentage of carbon stored in zoochoric species with large seeds and that similar percentage of carbon stored in zoochoric species with large seeds between these ecosystems. SDTF_D have the largest seed diameters directed towards non-zoochoric species, which dominate in terms of richness and abundance, supporting Leal et al. (2017). CE had the highest values of zoochoric seeds, although the abundance of these species was comparatively low. Despite the low abundance, these species store most of the carbon stocks of trees, reinforcing the importance of animals for the dispersal of these species in the CE and that CE presents a more moderate loss of animal dispersers when compared with RF and SDTF_SD (Carvalho et al., 2023).

4.2. PROPORTION OF ABOVE-GROUND CARBON AMONG VEGETATION TYPES AND DISPERSAL MODES

The proportion of carbon stored in zoochoric and non-zoochoric species was different among all vegetation types. SDTF_D had lower species richness and lower abundance of all types of zoochoric tree species (all zoochoric and zoochoric dispersed by large-bodied frugivores), shifting the largest amount of carbon stocks to non-zoochoric tree species. This finding is supported by the ecology of seed dispersal for SDTF_D, where abiotic seed dispersal predominates, with wind and gravity as the main agents (Leal et al. 2017).

4.3. VARIABLES THAT DRIVE ABOVE-GROUND CARBON

The proportion of carbon in all zoochoric species in vegetation types that occur in very deforested and degraded landscapes (about 9.52% of the remaining vegetation area in the study

area), such as SDTF_SD and RF, were not influenced by the variables we tested. This is probably because they have already gone through a process of directing zoochoric carbon toward species dispersed by small frugivores (Galetti et al. 2013), especially given high rates of loss of large frugivores (Bogoni et al. 2018). For SDTF_D, the landscape structure variables also did not significantly influence carbon in all zoochoric species, probably due to this vegetation presenting a reasonable area (~63% of native vegetation) of natural landscape (Souza et al. 2020). Furthermore, non-zoochoric dispersion predominates in their interactions, allowing dispersion to occur even with the landscape fragmented (Leal et al. 2017).

When looking at the relationship between landscape variables and non-zoochoric carbon, there is a positive relation with distance among forest patches in RF. RF areas with isolated patches in the landscape have a low percentage of frugivorous seed dispersers, resulting in a predominance of wind-dispersed tree species in the remaining patches (Molina et al. 2023; Jesus et al. 2012).

A higher proportion of carbon stored in zoochoric species dispersed by large frugivores is found in landscapes with large coverage of native vegetation, but in small forest patches. This result seems to reflect the anthropic action that has transformed natural landscapes (Souza et al. 2020) and restricted habitats for large frugivores (Galetti et al. 2021). For RF, in addition to the native vegetation area (NVA) and mean patch size (MPS), there is also the effect of the mean shape index, demonstrating that despite having a low proportion of carbon stored in species dispersed by large frugivores, it is concentrated in small patches with irregular shapes leading to a greater edge effect. This is a worrying pattern, as there is a negative relationship between edge effects and animal-dispersed seeds (Jesus et al. 2012). This reveals that, if in the long term this edge effect persists, the tendency is for species dispersed by large frugivores to become extinct

and if they cannot be replaced, the carbon stored in their biomass will be emitted into the atmosphere (also see Bello et al. 2015 and Osuri et al. 2015).

These conclusions are based on using a 4 km buffer, because this scale comprises variation in tree structure and large vertebrate home ranges (Rocha-Santos et al. 2016, Thornton et al. 2011), but there is the potential that the strength of some of our findings may vary if we used buffers at smaller or larger scales (i.e., variation in 'scale of effect') (Teng et al. 2020). Future work should investigate the optimal spatial scales for understanding such scales of effect.

5. CONCLUSIONS

Given the rapid fragmentation of tropical forests, we highlight the importance of conserving the largest area of native vegetation and landscape connectivity between patches. This will conserve zoochoric species, including species dispersed by large frugivores, as well as carbon storage in these species. By contrast, conserving isolated patches will lead to greater carbon storage in non-zoochoric species, which store less carbon in aboveground biomass.

Our study demonstrates the sensitivity of plant-animal interactions in areas that are currently under pressure from landscape conversion, such as the cerrado sensu stricto and Rain Forest. Covering about 9.48% (EC) and 0.38% (RF), respectively, it is precisely in these areas where 57% of the carbon stored in zoochoric species dispersed by large-bodied frugivores can be emitted into the atmosphere if these animals cannot be protected. These findings demonstrate the importance of turning our attention from conservation to understanding the ecological processes that are lost in different types of vegetation in the face of landscape changes in tropical ecosystems.

398 **Declarations**

399 **Declaration of Competing Interest**

400 The authors declare that they have no known competing financial interests or personal
401 relationships that could have appeared to influence the work reported in this paper.

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408 **Authors' contributions**

409 RMG, CBG and LFSM conceived the study; MAFL and RMS collected the data; RMG, MVP,
410 MP, DPE, and LFSM constructed the data metrics and performed the analysis; RMG, DPE, and
411 LFSM wrote the paper with contributions from all authors.

412 **References**

- 413 **Achard F, Beuchle R, Mayaux P, Stibig HJ, Bodart C, Brink A ... and Simonetti D** 2014
414 Determination of tropical deforestation rates and related carbon losses from 1990 to 2010.
415 *Global Change Biology*. **20**, 2540– 2554. <https://doi.org/10.1111/gcb.12605>
- 416 **Akaike H** (1973) Information Theory and an Extension of the Maximum Likelihood Principle.
417 In B N Petrov, and F Csaki (Eds.), *Proceedings of the 2nd International Symposium on*
418 *Information Theory* (pp. 267-281). Budapest: Akademiai Kiado.

- Aza A, Riccioli F and Di Iacovo F** (2021). Optimising payment for environmental services schemes by integrating strategies: The case of the Atlantic Forest, Brazil. *Forest Policy and Economics*, **125**, 102410. doi:10.1016/j.forpol.2021.102410
- Baccini A, Goetz SJ, Walker WS, Laporte NT, Sun M, Sulla-Menashe D, ... and Houghton, RA** (2012) Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Clim Change*, **2**, 3, 182–185. doi:10.1038/nclimate1354
- Baccini A, Walker W, Carvalho L, Farina M, Sulla-Menashe D and Houghton R A** (2017) Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science*, **358**(6360), 230–234. doi:10.1126/science.aam5962
- Bagchi R, Swamy V, Latorre Farfan J-P, Terborgh J, Vela CIA, Pitman NCA and Sanchez W G** (2018) Defaunation increases the spatial clustering of lowland Western Amazonian tree communities. *J. Ecol.*, **106**, 4, 1470–1482. doi:10.1111/1365-2745.12929
- Barroso GM, Morim MP, Peixoto AL and Ichaso CLF** (1999) *Frutos e Sementes, Morfologia aplicada a Dicotiledôneas* (3rd ed). Viçosa, MG: Ed. UFV.
- Bates D, Maechler M, Bolker B and Walker S** (2015) Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*, **67**(1), 1-48. doi:10.18637/jss.v067.i01.
- Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, Lima RAF ... and Jordano P** (2015) Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, 1(11), e1501105–e1501105. doi:10.1126/sciadv.1501105
- Berenguer E, Ferreira J, Gardner TA, Aragão LEOC, De Camargo PB, Cerri CE, Durigan M, Oliveira RCD, Vieira ICG and Barlow J** (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, **20**(12), 3713–3726. <https://doi.org/10.1111/gcb.12627>

442 **Bhan M, Gingrich S, Matej S, Fritz S and Erb KH** (2021) Land Use Increases the Correlation
 443 between Tree Cover and Biomass Carbon Stocks in the Global Tropics. *Land*, **10**, 1217.
 444 <https://doi.org/10.3390/land10111217>

445 **Bivand RS and Wong DWS** (2018) Comparing implementations of global and local indicators
 446 of spatial association. *TEST*, **27 (3)**, 716–748. doi:10.1007/s11749-018-0599-x

447 **Bordin KM, Esquivel-Muelbert A, Bergamin R S, Klipel J, Picolotto RC, Frangipani MA,**
 448 **and Müller S C** (2021) Climate and large-sized trees, but not diversity, drive above-ground
 449 biomass in subtropical forests. *Forest Ecology and Management*, 490, 119126.
 450 doi:10.1016/j.foreco.2021.119126

451 **Brancalion PHS, Bello C, Chazdon RL, Galetti M, Jordano P, Lima RAF ... and Reid JL**
 452 (2018) Maximizing biodiversity conservation and carbon stocking in restored tropical
 453 forests. *Conserv. Lett.* **11**(4), e12454. doi:10.1111/conl.12454

454 **Brodie JF** (2016) How Monkeys Sequester Carbon. *Trends Ecol Evol.* **31**(6), 414–416.
 455 doi:10.1016/j.tree.2016.03.019

456 **Brodie JF** (2017) Evolutionary cascades induced by large frugivores. *Proc. Natl Acad. Sci. USA.*
 457 **114**(45), 11998–12002. doi:10.1073/pnas.1710172114

458 **Burnham KP, Anderson DR and Huyvaert KP** (2011) AIC model selection and multimodel
 459 inference in behavioral ecology: some background, observations, and comparisons. *Behav.*
 460 *Ecol. Sociobiol.* **65**(1), 23–35. doi:10.1007/s00265-010-1029-6

461 **Carvalho RB, Malhi Y and Oliveras Menor I** (2023). Frugivory and seed dispersal in the
 462 Cerrado: Network structure and defaunation effects. *Biotropica*, **55**(4), 849–865.
 463 <https://doi.org/10.1111/btp.13234>

- Caughlin TT, Ferguson JM, Lichstein JW, Zuidema PA, Bunyavejchewin S and Levey DJ**
(2015) Loss of animal seed dispersal increases extinction risk in a tropical tree species due to
pervasive negative density dependence across life stages. *Proc. R. Soc. B*, **282**(1798),
20142095–20142095. doi:10.1098/rspb.2014.2095
- Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC ... and
Vieilledent G** (2014) Improved allometric models to estimate the aboveground biomass of
tropical trees. *Glob. Change Biol.*, **20**(10), 3177–3190. doi:10.1111/gcb.12629
- Coelho A J P, Magnago L F.S., Matos F A R, Mota N M, Diniz É S and Meira-Neto J A A**
(2020). Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado,
the Brazilian savanna. *Biodiversity and Conservation*. doi:10.1007/s10531-020-02013-6
- Cribari-Neto F and Zeileis A** (2010) Beta Regression in R. *J. Stat. Softw.* **34**(2), 1-24.
doi:10.18637/jss.v034.i02
- Culot L, Bello C, Batista JLF, do Couto HTZ and Galetti M** (2017) Synergistic effects of
seed disperser and predator loss on recruitment success and long-term consequences for
carbon stocks in tropical rainforests. *Sci Rep*, **7**(1). doi:10.1038/s41598-017-08222-4
- De Paula M D, Costa C P A and Tabarelli M** (2011). Carbon Storage in a Fragmented
Landscape of Atlantic Forest: The Role Played by Edge-Affected Habitats and Emergent
Trees. *Tropical Conservation Science*, **4**(3), 349–358. doi:10.1177/194008291100400310
- Donoso I, Schleuning M, García D and Fründ J** (2017). Defaunation effects on plant
recruitment depend on size matching and size trade-offs in seed-dispersal networks.
Proceedings of the Royal Society B: Biological Sciences, **284**(1855), 20162664.
doi:10.1098/rspb.2016.2664

486 **Doughty CE, Wolf A, Morueta-Holme N, Jørgensen PM, Sandel B, Violle C ... and Galetti**
487 **M** (2016) Megafauna extinction, tree species range reduction, and carbon storage in
488 Amazonian forests. *Ecography*, **39**(2), 194–203. doi:10.1111/ecog.01587

489 **Emer C, Galetti M, Pizo M A, Guimarães P R, Moraes S, Piratelli A and Jordano P** (2018).
490 Seed-dispersal interactions in fragmented landscapes - a metanetwork approach. *Ecology*
491 *Letters*, **21**(4), 484–493. doi:10.1111/ele.12909

492 **Farwig N and Berens DG** (2012) Imagine a world without seed dispersers: A review of threats,
493 consequences and future directions. *Basic Appl Ecol*, **13**(2), 109–115.
494 doi:10.1016/j.baae.2012.02.006

495 **Ferrari S and Cribari-Neto F** (2004) Beta Regression for Modelling Rates and Proportions. *J.*
496 *Appl. Stat.*, **31**(7), 799–815. doi:10.1080/0266476042000214501

497 **Flora do Brasil** (2020) under construction. *Jardim Botânico do Rio de Janeiro*. Available at: <
498 <http://floradobrasil.jbrj.gov.br/>>. Accessed on: 23 Mar. 2018

499 **Fuzessy LF, Janson C and Silveira F A** (2018) Effects of seed size and frugivory degree on
500 dispersal by Neotropical frugivores. *Acta Oecol.* **93**, 41–47. doi: 10.1016/j.actao.2018.10.004

501 **Galetti M, Gonçalves F, Villar N, Zipparro VB, Paz C, Mendes C, ...and Bovendorp R S**
502 (2021). Causes and Consequences of Large-Scale Defaunation in the Atlantic Forest. In:
503 Marques, M.C.M., Grelle, C.E.V. (eds) *The Atlantic Forest*. Springer, Cham.
504 https://doi.org/10.1007/978-3-030-55322-7_14

505 **Galetti M, Guevara R, Cortes MC, Fadini R, Von Matter S, Leite AB ... and Jordano P**
506 (2013). Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size.
507 *Science*, **340**(6136), 1086–1090. doi:10.1126/science.1233774

508 **Griz LMS and Machado ICS** (2001) Fruiting phenology and seed dispersal syndromes in
509 caatinga, a tropical dry forest in the northeast of Brazil. *J. Trop. Ecol.*, **17**(02), 303–321.
510 doi:10.1017/s0266467401001201

511 **Grothendieck G** (2013) nls2: Non-linear regression with brute force. *R package* version 0.2.
512 <https://CRAN.R-project.org/package=nls2>

513 **Hothorn T, Bretz F and Westfall P** (2008) Simultaneous Inference in General Parametric
514 Models. *Biometr. J.* **50**(3), 346–363. doi:10.1002/bimj.200810425

515 **Howe H F** (2016) Making dispersal syndromes and networks useful in tropical conservation and
516 restoration. *Glob. Ecol. Conserv.*, **6**, 152–178. doi:10.1016/j.gecco.2016.03.002

517 **Howe HF and Smallwood J** (1982) Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* **13**:201–
518 228.

519 **IEF/MG** (2023) Cobertura vegetal de Minas Gerais. *Instituto Estadual de Florestas*. Available
520 in: < <http://www.ief.mg.gov.br/florestas> > Accessed on: dec. 2023.

521 **IBGE** (2012) Manual Técnico da Vegetação Brasileira. 2ed.; Rio de Janeiro, *Instituto Brasileiro*
522 *de Geografia e Estatística-IBGE*, 91p.

523 **IPCC** (2003) Good Practice Guidance for Land Use, Land-Use Change and Forestry;
524 IPCC/OECD/IEA/IGES: Hayama, Japan,

525 **Jardim AVF and Batalha MA** (2009) Dispersal syndromes related to edge distance in cerrado
526 sensu stricto fragments of central-western Brazil. *Braz. Arch. Biol. Technol.* **52**(5), 1167–
527 1177. doi:10.1590/s1516-89132009000500014

528 **Jordano P** (2000) Fruits and frugivory. In M. Fenner (Ed.), *Seeds: The ecology of regeneration*
529 *in plant communities* (pp. 125–166). Wallingford, UK: CAB International.

530 **Jorge MLSP, Galetti M, Ribeiro MC and Ferraz KMPMB** (2013) Mammal defaunation as
531 surrogate of trophic cascades in a biodiversity hotspot. *Biol. Conserv.* **163**, 49–57.
532 doi:10.1016/j.biocon.2013.04.018

533 **Kuznetsova A, Brockhoff PB and Christensen RHB** (2017) “lmerTest Package: Tests in
534 Linear Mixed Effects Models. *J. Stat. Softw.*, **82**(13), pp. 1-26. doi: 10.18637/jss.v082.i13

535 **Lang S and Tiede D** (2003) *vLATE Extension für ArcGIS* - vektorbasiertes Tool zur
536 quantitativen Landschaftsstrukturanalyse, ESRI Anwenderkonferenz Innsbruck.

537 **Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM ... and**
538 **Lovejoy TE** (2011) The fate of Amazonian forest fragments: A 32-year investigation. *Biol.*
539 *Conserv.*, **144**(1), 56–67. doi:10.1016/j.biocon.2010.09.021

540 **Leal IR, Lopes AV, Machado IC and Tabarelli M** (2017) Plant–Animal Interactions in the
541 Caatinga: Overview and Perspectives. In: J M C. Silva, I R, Leal, M Tabarelli (Eds)
542 *Caatinga* (pp. 255–278). Springer, Cham. doi:10.1007/978-3-319-68339-3_9

543 **Leishman MR, Wright IJ, Moles AT and Westoby M** (2000) The evolutionary ecology of
544 seed size. *Seeds – the Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp.
545 31–57. CAB International, Walling-ford.

546 **Magnago LFS, Magrach oA, Barlow J, Schaefer CEGR, Laurance WF, Martins SV and**
547 **Edwards DP** (2017) Do fragment size and edge effects predict carbon stocks in trees and
548 lianas in tropical forests? *Functional Ecology* **31**:542–552

549 **Mittermeier RA, Turner WR, Larsen FW, Brooks TM and Gascon C** (2011) Global
550 Biodiversity Conservation: The Critical Role of Hotspots. In: F E Zachos and J C Habel
551 (Eds.), *Biodiversity Hotspots*, **3–22**. Springer, Berlin, Heidelberg. doi:10.1007/978-3-642-
552 20992-5_1

553 **Moles AT and Westoby M** (2006). Seed size and plant strategy across the whole life cycle.
554 *Oikos*, **113**(1), 91–105. doi:10.1111/j.0030-1299.2006.14194.x

555 **Molina M, Martins CPV, Raniero M, Fortes LS, Terra MFM, Ramos FN...and Hasui E**
556 (2023). Direct and indirect effects of landscape, forest patch and sampling site predictors on
557 biotic interaction and seed process. *Plant Ecol* **224**, 13–32. [https://doi.org/10.1007/s11258-](https://doi.org/10.1007/s11258-022-01276-z)
558 022-01276-z

559 **Muñoz MC, Schaefer HM, Böhning-Gaese K and Schleuning M** (2017) Importance of animal
560 and plant traits for fruit removal and seedling recruitment in a tropical forest. *Oikos*, **126**(6),
561 823–832. doi:10.1111/oik.03547

562 **Oliveira OS and Marquis RJ** (2002) *The Cerrados of Brazil. Ecology and natural history of a*
563 *neotropical savanna*. Columbia University Press, New York.

564 **Osuri AM, Ratnam J, Varma V, Alvarez-Loayza P, Hurtado Astaiza J, Bradford M ... and**
565 **Sankaran M** (2016). Contrasting effects of defaunation on aboveground carbon storage
566 across the global tropics. *Nat Commun*, **7**, 11351. doi:10.1038/ncomms11351

567 **Pearson TRH, Brown S and Casarim F M** (2014). Carbon emissions from tropical forest
568 degradation caused by logging. *Environmental Research Letters*, **9**(3), 034017.
569 doi:10.1088/1748-9326/9/3/034017

570 **Peres CA, Emilio T, Schietti J, Desmoulière SJM and Levi T** (2016) Dispersal limitation
571 induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci.*
572 **113**(4), 892–897. doi:10.1073/pnas.1516525113

573 **Projeto MapBiomias – Coleção 3.0 da Série Anual de Mapas de Cobertura e Uso de Solo do**
574 *Brasil*, accessed on October 22, 2018 through the link:
575 http://mapbiomas.org/pages/database/mapbiomas_collection

576 **R Core Team** (2020).R: *A language and environment for statistical computing*. Vienna, Austria:
577 R Foundation for Statistical Computing.

578 **Redford KH** (1992) The Empty Forest. *BioScience*, **42**(6), 412–422. doi:10.2307/1311860

579 **Rezende CL, Scarano FR, Assad ED, Joly CA, Metzger JP, Strassburg BBN ... and**
580 **Mittermeier RA** (2018). From hotspot to hopespot: An opportunity for the Brazilian
581 Atlantic Forest. *Perspectives in Ecology and Conservation*. doi:10.1016/j.pecon.2018.10.002

582 **Ribeiro JF and Walter BMT** (2008) Fitofisionomias do Bioma Cerrado. In: Sano, S M,
583 Almeida, S P, Ribeiro, J F. *Ecologia e flora* (pp. 152-212). Brasília: Embrapa.

584 **Rocha-Santos L, Pessoa MS, Cassano CR, Talora DC, Orihuela RLL, Mariano-Neto E ...**
585 **and Cazetta E** (2016) The shrinkage of a forest: Landscape-scale deforestation leading to
586 overall changes in local forest structure. *Biol. Conserv.* **196**, 1–9.
587 doi:10.1016/j.biocon.2016.01.028

588 **Sansevero JBB, Prieto PV, de Moraes LFD and Rodrigues PJP** (2011) Natural Regeneration
589 in Plantations of Native Trees in Lowland Brazilian Atlantic Forest: Community Structure,
590 Diversity, and Dispersal Syndromes. *Restor. Ecol.*, **19**(3), 379–389. doi:10.1111/j.1526-
591 100x.2009.00556.x

592 **Scolforo HF, Scolforo JRS, Mello CR, Mello JM and Ferraz Filho AC** (2015) Spatial
593 Distribution of Aboveground Carbon Stock of the Arboreal Vegetation in Brazilian Biomes
594 of Savanna, Atlantic Forest and Semi-Arid Woodland. *PLOS ONE*, **10**(6), e0128781.
595 doi:10.1371/journal.pone.0128781

596 **Scolforo JRS, Mello JM, Carvalho LMT, Oliveira AD, Castro CP, Borges LFR... and**
597 **Vargas Filho R** (2006) Procedimento do inventário florestal – flora nativa. In: Scolforo, J R,

598 Carvalho, L M T (Ed.). *Mapeamento e Inventário da Flora e dos Reflorestamentos de Minas*
599 *Gerais*. Lavras: UFLA, cap. 4, p.63-73.

600 **Scolforo JRS and Carvalho LMTde** (2008) *Inventário florestal de Minas Gerais:*
601 *Monitoramento da flora nativa*. 1. ed. Lavras-MG: Editora UFLA.

602 **Staggemeier VG, Cazetta E and Morellato, LPC** (2017), Hyperdominance in fruit production
603 in the Brazilian Atlantic rain forest: the functional role of plants in sustaining frugivores.
604 *Biotropica*, **49**: 71-82. <https://doi.org/10.1111/btp.12358>

605 **Souza CM Jr, Shimbo J Z, Rosa MR, Parente LL, Alencar A A, Rudorff BFT... and**
606 **Azevedo T** (2020) Reconstructing Three Decades of Land Use and Land Cover Changes in
607 Brazilian Biomes with Landsat Archive and Earth Engine - *Remote Sensing*, Volume 12,
608 Issue 17, 10.3390/rs12172735

609 **Strassburg BBN, Brooks T, Feltran-Barbieri R, Iribarrem A, Crouzeilles R, Loyola R ...**
610 **and Balmford A** (2017) Moment of truth for the Cerrado hotspot. *Nat. Ecol. Evol.* **1**(4),
611 0099. doi:10.1038/s41559-017-0099

612 **Terborgh J, Nuñez-Iturri G, Pitman NCA, Valverde FHC, Alvarez P, Swamy V ... and**
613 **Paine CET** (2008) Tree recruitment in an empty forest. *Ecology*, **89**(6), 1757–1768.
614 doi:10.1890/07-0479.1

615 **Terra MCNS, dos Santos RM, Fontes MAL, de Mello JM, Scolforo JRS, Gomide LR ...**
616 **and ter Steege H** (2017) Tree dominance and diversity in Minas Gerais, Brazil. *Biodivers*
617 *Conserv* **26**, 2133–2153. <https://doi.org/10.1007/s10531-017-1349-1>

618 **Thornton D, Branch L and Sunquist M** (2011) Passive sampling effects and landscape
619 location alter associations between species traits and response to fragmentation. *Ecol Appl.*
620 **21**(3), 817–829. doi:10.1890/10-0549.1

621 **Valenta K and Nevo O** (2020) The dispersal syndrome hypothesis: how animals shaped fruit
622 traits, and how they did not. *Functional Ecology* **34**: 1158–1169
623 **Van der Pijl L** (1982) *Principles of Dispersal in Higher Plants* (3rd ed.). Springer -Verlag
624 Berlin Heidelberg. doi: 10.1007/978-3-642-87925-8
625 **Wickham H** (2016) *ggplot2: Elegant Graphics for Data Analysis* (2nd ed.). New York:
626 Springer-Verlag. doi 10.1007/978-3-319-24277-4
627 **Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL and Chave J** (2009)
628 *Global wood density database*. Dryad. Identifier: <http://hdl.handle.net/10255/dryad.235>