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RESEARCH ARTICLE

Geographic patterns of tree dispersal modes in Amazonia and their ecological correlates

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Abstract

Aim: To investigate the geographic patterns and ecological correlates in the geographic distribution of the most common tree dispersal modes in Amazonia (endozoochory, synzoochory, anemochory and hydrochory). We examined if the proportional abundance of these dispersal modes could be explained by the availability of dispersal agents (disperser-availability hypothesis) and/or the availability of resources for constructing zoochorous fruits (resource-availability hypothesis).

Time period: Tree-inventory plots established between 1934 and 2019.

Major taxa studied: Trees with a diameter at breast height (DBH) ≥ 9.55 cm.

Location: Amazonia, here defined as the lowland rain forests of the Amazon River basin and the Guiana Shield.

Methods: We assigned dispersal modes to a total of 5433 species and morphospecies within 1877 tree-inventory plots across terra-firme, seasonally flooded, and permanently flooded forests. We investigated geographic patterns in the proportional abundance of dispersal modes. We performed an abundance-weighted mean pairwise

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distance (MPD) test and fit generalized linear models (GLMs) to explain the geographic distribution of dispersal modes.

Results: Anemochory was significantly, positively associated with mean annual wind speed, and hydrochory was significantly higher in flooded forests. Dispersal modes did not consistently show significant associations with the availability of resources for constructing zoochorous fruits. A lower dissimilarity in dispersal modes, resulting from a higher dominance of endozoochory, occurred in terra-firme forests (excluding podzols) compared to flooded forests.

Main conclusions: The disperser-availability hypothesis was well supported for abiotic dispersal modes (anemochory and hydrochory). The availability of resources for constructing zoochorous fruits seems an unlikely explanation for the distribution of dispersal modes in Amazonia. The association between frugivores and the proportional abundance of zoochory requires further research, as tree recruitment not only depends on dispersal vectors but also on conditions that favour or limit seedling recruitment across forest types.

KEYWORDS
Amazonian rain forests, anemochory, dispersal agents, disperser-availability hypothesis, endozoochory, flooded forests, hydrochory, resource-availability hypothesis, synzoochory, terra-firme forests

1 | INTRODUCTION

Seed dispersal is an essential ecological process (Howe & Smallwood, 1982; Jordano, 1995) that drives forest regeneration (Tabarelli & Peres, 2002; Wunderle, 1997) and can partly explain the spatial distribution of plants (Muller-Landau et al., 2008; Nathan & Muller-Landau, 2000). Through biotic (i.e., animals) and abiotic (i.e., wind, water, gravity) dispersal agents (Howe & Smallwood, 1982; Van der Pijl, 1982), plants can reach suitable habitat patches where they can establish (e.g., forest gaps or areas with particular soil types; Howe & Smallwood, 1982), avoiding the negative density-dependent effects that occur in proximity to parental plants (Comita et al., 2014; Connell, 1971; Janzen, 1970). The geographic distribution of tree dispersal modes (e.g., endozoochory and synzoochory, in which seeds are internally and externally dispersed by frugivores, respectively, as well as anemochory and hydrochory, in which seeds are dispersed by wind and water, respectively; Van der Pijl, 1982) is associated with other important components of biodiversity and ecosystem functioning. For instance, many large hardwood trees have large seeds dispersed by vertebrates (Aldana et al., 2017; Bello et al., 2015), and as a result, defaunation can decrease the recruitment of these trees and lead to the reduction of carbon stocks in tropical forests (Bello et al., 2015; Peres et al., 2016). Examining the underlying factors in the geographic distribution of tree dispersal modes can help to unravel the drivers of plant recruitment and biodiversity in the tropics.

Several geographic patterns of tree dispersal modes have been documented. Globally, the proportion of zoochory is highest in tropical areas (Chen et al., 2017; Moles et al., 2007). Within the tropics and subtropics, rainfall has been positively associated with the proportion of zoochory (Almeida-Neto et al., 2008; Butler et al., 2007; Correa et al., 2015; Tabarelli et al., 2003), and in the Neotropics, the dominance of endozoochory has been found to be higher in terra-firme forests compared to flooded forests (Umaña et al., 2011, 2018). Rainfall has been negatively associated with the proportion of abiotic dispersal modes (Correa et al., 2015; Massi et al., 2017; Tabarelli et al., 2003), while latitude (Chen et al., 2017; Moles et al., 2007), elevation (Albert et al., 2018; Chapman et al., 2016; Tovar et al., 2020), and hunting intensity (Nunez-Iturri et al., 2008; Peres et al., 2016; Terborgh et al., 2008; Wright et al., 2007) have been positively associated with their proportion. The ecological explanations of these patterns are still being discussed (Albert et al., 2018; Aldana et al., 2017; Carvalho et al., 2022; Chapman et al., 2016; Chen et al., 2017; Correa et al., 2015; Henneron et al., 2019; Massi et al., 2017; Peres et al., 2016; Tovar et al., 2020; Umaña et al., 2018; Vasconcelos et al., 2021).

Several non-mutually exclusive ecological hypotheses might explain the geographic patterns of tree dispersal modes. We focus on two of them: (a) the disperser-availability hypothesis, and (b) the resource-availability hypothesis. According to the disperser-availability hypothesis, the proportion of trees exhibiting a particular dispersal mode is associated with the availability of dispersal agents. Current geographic evidence has shown that in Neotropical forests the proportion of endozoochorous trees is positively associated with the biomass of primates (Correa et al., 2015), the proportion of anemochory with the occurrence of strong winds (Correa et al., 2015; Wright et al., 2016) and the proportion of hydrochorous trees with the presence of water bodies (Correa et al., 2015; Umaña et al., 2018). Based on the resource-availability hypothesis, the proportion of zoochorous

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trees, which have fruits that, in general, are metabolically more costly to plants compared to abiotically dispersed trees (because of having larger seeds and more nutritious fleshy structures that attract frugivores; Chen et al., 2017), increases in areas with high availability of resources for constructing zoochorous fruits (i.e., in areas with high and constant air temperature, high and constant water availability from rainfall, and fertile soils; Correa et al., 2015; Tabarelli et al., 2003; Willson et al., 1989). The broad-scale positive association between the proportion of zoochory and rainfall has been widely documented (Almeida-Neto et al., 2008; Butler et al., 2007; Correa et al., 2015; Tabarelli et al., 2003), but evidence supporting the role of air temperature or soil fertility in driving these patterns is still limited (Correa et al., 2015; Hughes et al., 1993; Willson et al., 1989).

With nearly 6 million km^2, Amazonia holds the largest tracts of relatively intact rain forests globally (Venter et al., 2016) and may contain more than 15,000 tree species (ter Steege et al., 2013, 2020). An examination of the patterns of tree dispersal modes and their ecological correlates, however, has not yet been undertaken in Amazonia. Recent studies show that ecological processes in the region can be explained by variations in climate and soils (Malhi et al., 2004; Quesada et al., 2012). The geographic distribution of dispersal modes in Amazonia could be also linked to the variation in dispersal agents and resources for constructing zoochorous fruits.

Using the largest database of tree-inventory plots in Amazonia [i.e., 1877 plots with 1,065,407 individuals corresponding to 5613 species and morphospecies; Amazon Tree Diversity Network (ATDN), 2020; ter Steege et al., 2020], we investigated the geographic patterns and ecological correlates in the distribution of the most common tree dispersal modes in the region (endozoochory, synzoochory, anemochory, hydrochory). We also examined if the proportional abundance of these dispersal modes could be explained by (a) the availability of dispersal agents (disperser-availability hypothesis) and/or (b) the availability of resources for constructing zoochorous fruits (resource-availability hypothesis). Based on the disperser-availability hypothesis, the proportion of endozoochorous trees would be positively associated with the availability of frugivorous primates (using them as a proxy of all frugivorous animals), the proportion of anemochorous trees with wind speed, and the proportion of hydrochorous trees with flooded forests. Based on the resource-availability hypothesis, the proportion of zoochorous trees would increase in areas with fewer restrictions for constructing zoochorous fruits, which would occur in areas with high and constant air temperature, high and constant water availability from rainfall, and fertile soils. Our analysis provides baseline information on the geographic patterns, ecological correlates, and possible environmental causes of the geographic distribution of the main dispersal modes in Amazonia, with implications for the conservation and management of its unique biodiversity.

2 | METHODS

We used tree-inventory plots with a standard tree-sampling methodology in Amazonia, here defined as the lowland rain forests of the Amazon River basin and the Guiana Shield. We selected plots where sampled trees had a minimum diameter at breast height (DBH; usually measured at 1.30 m aboveground) ≥ 9.55 cm. This led to a total of 1877 tree-inventory plots over a wide range of environmental conditions (Table 1). Of these plots, most were 1 ha (1282 plots), 490 had less area and 105 had more area. The plots were located across six Amazonian regions: central Amazonia (CA), eastern Amazonia (EA), Guiana Shield (GS), north-western Amazonia (NWA), southern Amazonia (SA) and south-western Amazonia (SWA), and included terra-firme forests and flooded forests. Terra-firme forests corresponded to white-sand podzol forests (PZ), terra-firme forests on the Brazilian Shield (TFBS), terra-firme forests on the Guiana Shield (TFGS), and terra-firme forests on the Pebas Formation (TFPB). The classification of terra-firme forests accounted for lithological differences that have been associated with the evolution of biodiversity in Amazonia (Hoorn et al., 2010; ter Steege et al., 2000). Flooded forests corresponded to seasonally flooded igapó forests (IG) along blackwater rivers, seasonally flooded várzea forests (VA) along whitewater rivers, and permanently flooded swamp forests (SW) (Figure 1).

We assigned a dispersal mode (anemochory, endozoochory, explosive dehiscence, hydrochory, myrmecochory, synzoochory or unassisted) to each species, based on the observation of diaspore morphology in herbaria exsiccates (virtual herbaria of the Chicago Botanic Garden CHIC, Instituto Amazónico de Investigaciones Científicas COAH, Universidad Nacional de Colombia COL, Royal Botanic Gardens K and The New York Botanical Garden NY) and information found in the scientific literature (Gentry & Vasquez, 1993; Stevenson et al., 2000; Van Roosmalen, 1985). Following Correa-Gómez et al. (2013) and Correa et al. (2015), anemochory was assigned to diaspores without fleshy structures that are reported to or can be dispersed by wind (i.e., having wings, kapok, or tufts of hair; Table 2). Endozoochory was assigned to diaspores with fleshy structures and mimetic seeds with seeds usually narrower than 2 cm, which are reported to or can be swallowed by frugivores in Neotropical forests including large primates, such as ateline monkeys (Fuzessy et al., 2018; Peres & Van Roosmalen, 2002; Stevenson et al., 2005). Explosive dehiscence was assigned to diaspores without fleshy structures that release seeds explosively. Hydrochory was assigned to diaspores without fleshy structures and with floating abilities that are reported to or can be dispersed by water, and with no obvious morphological adaptations to wind dispersal. Myrmecochory was assigned to diaspores with small seeds and associated elaiosomes. Synzoochory was assigned to fleshy or non-fleshy diaspores with seeds wider than 2 cm, which are not commonly ingested by frugivores but can be externally transported by rodents, bats and primates in Neotropical forests (Fuzessy et al., 2018; Jansen et al., 2012). The unassisted category included diaspores without any of the previous character combinations or any reported dispersal mode.

We also assigned dispersal modes to morphospecies identified to the genus level if no variation in dispersal modes was found for species within genera. Dispersal modes were assigned to a total of 1,019,946 individuals corresponding to 5433 species and morphospecies (i.e.,

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TABLE 1 Average and range of continuous variables included for the development of generalized linear models (GLMs) based on 1877 tree-inventory plots established in Amazonia

Type of variables	Variables	Variable abbreviation	Average	Range
Response variables	Proportional abundance of endozoochory (%)		58.4	0–98.1
	Proportional abundance of synzoochory (%)		14.7	0–97.8
	Proportional abundance of anemochory (%)		9.5	0–96.6
	Proportional abundance of hydrochory (%)		3.9	0–66.6
Elevation, latitude, longitude	Elevation (m a.s.l.)		148	0–976
	Latitude (°)		2.8 S	17.1 S–8.2 N
	Longitude (°)		61.3 W	78.8 W–46.1 W
Dispersal agent availability	Mean annual wind speed (m/s)	WS	1.3	0.7–3.1
	Biomass of frugivorous primates (kg/km^2)	BFP	112.2	12.2–408.7
Temperature	Mean annual temperature (°C)	MAT	26.1	21.9–27.7
	Annual range of temperature (°C)	ART	11.9	8.8–20.8
Water availability	Mean annual precipitation (mm)	MAP	2364	742–4285
	Precipitation seasonality (CV)	PS	49.5	12.4–87.2
Soil fertility	Soil cation exchange capacity (cmol$_c$/kg)	CEC	11.2	4.6–36
Productivity	Aboveground coarse woody biomass productivity (Mg C /ha/year)	AGWBP	5.6	4.2–7.9

Note: CV = coefficient of variation of precipitation seasonality. Units are shown in parentheses. The biomass of frugivorous primates (BFP) was calculated for 25 sites.

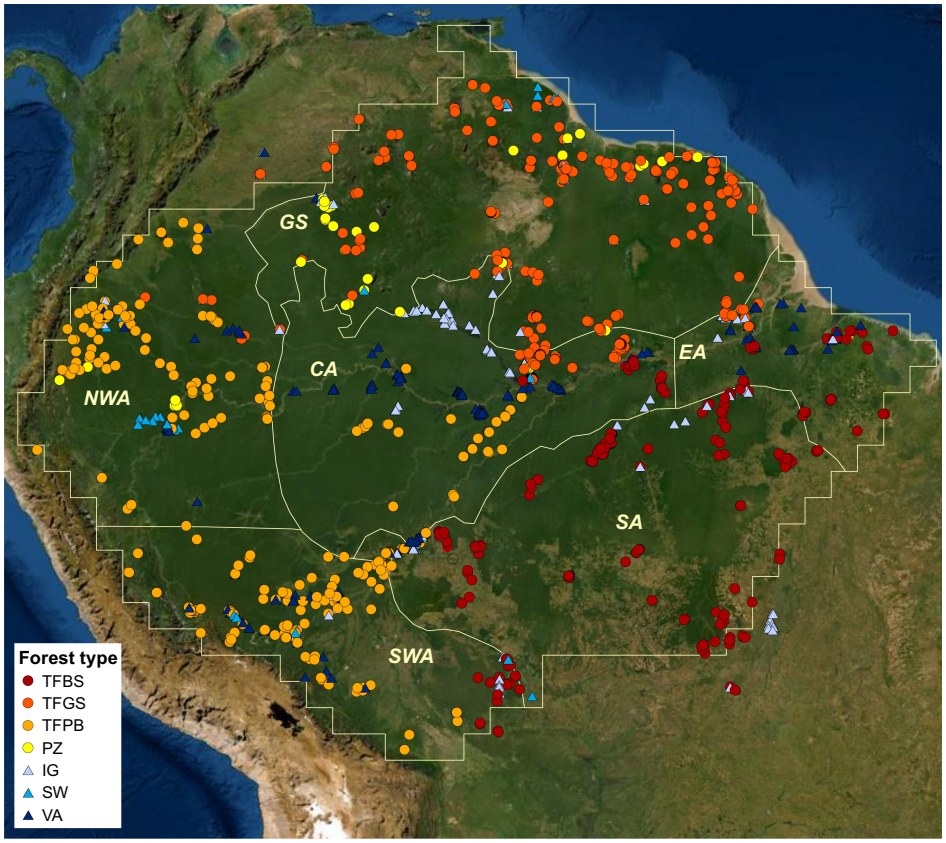

FIGURE 1 Location of 1877 tree-inventory plots within Amazonian regions classified by forest type. Terra-firme forests represented by circles: white-sand podzol forests (PZ), terra-firme forests on the Brazilian Shield (TFBS), terra-firme forests on the Guiana Shield (TFGS), terra-firme forests on the Pebas Formation (TFPB). Flooded forests represented by triangles: seasonally flooded igapó forests (IG), seasonally flooded várzea forests (VA) and permanently flooded swamp forests (SW). Amazonian regions: central Amazonia (CA), eastern Amazonia (EA), Guiana Shield (GS), north-western Amazonia (NWA), southern Amazonia (SA) and south-western Amazonia (SWA).

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TABLE 2 Classification of dispersal modes following Correa-Gómez et al. (2013) and Correa et al. (2015)

Dispersal mode	Description
Anemochory	Diaspores without fleshy structures that are reported to or can be dispersed by wind (i.e., having wings, kapok, or tufts of hair)
Endozoochory	Diaspores with fleshy structures and mimetic seeds with seeds usually narrower than 2 cm
Explosive dehiscence	Diaspores without fleshy structures that release seeds explosively
Hydrochory	Diaspores without fleshy structures and with floating abilities that are reported to or can be dispersed by water, and with no obvious morphological adaptations to wind dispersal
Myrmecochory	Diaspores with small seeds and associated elaiosomes
Synzoochory	Fleshy or non-fleshy diaspores with seeds wider than 2 cm
Unassisted	Diaspores without any of the previous character combinations or any reported dispersal mode

96 and 97% of total individuals and species/morphospecies within the 1877 plots, respectively).

Our analyses were based on the most common dispersal modes found in the tree-inventory plots, corresponding to two biotic dispersal modes (endozoochory and synzoochory) and two abiotic dispersal modes (anemochory and hydrochory). These dispersal modes represented 87 and 92% of total individuals and species/morphospecies among plots, respectively, with the highest percentage for endozoochory (i.e., 61 and 68% of total individuals and species/morphospecies, respectively), followed by synzoochory, anemochory and hydrochory (i.e., 14 and 7%, 9 and 13%, 3 and 4% of total individuals and species/morphospecies for synzoochory, anemochory and hydrochory, respectively).

2.1 | Response and explanatory variables

As the response variable, we used the proportional abundance of dispersal modes per plot (i.e., the percentage of endozoochory, synzoochory, anemochory and hydrochory based on the total number of individuals per plot). To test the disperser-availability hypothesis, we used three variables representing the availability of dispersal agents, corresponding to the availability of frugivorous primates (i.e., the biomass of frugivorous primates), wind (i.e., mean annual wind speed), and water (i.e., forest types that flood seasonally such as IG and VA, and that are permanently flooded such as SW). We obtained the biomass of frugivorous primates (BFP), as a proxy of all frugivorous animals that would influence the proportional abundance of endozoochory, from 154 sites (Stevenson, 2016). We assigned the BFP to a subset of 110 tree-inventory plots (out of the selected 1877 tree plots) by averaging the biomass values within a 20-km buffer centred in each plot classified by forest type. To avoid pseudoreplication, we averaged response and explanatory variables among nearby plots (i.e., clusters of plots within 20 km of each other classified by forest type that are assumed to share frugivorous primate communities), leading to a subanalysis with 25 sites. The biomass of other key taxonomic groups of frugivores, such as tapirs, scatter-hoarding rodents, birds, bats and fishes, was not available and thus not included in the present study; however, primates are a key taxonomic group for seed dispersal in the Neotropics (Fuzessy et al., 2016; Link & Di Fiore, 2006). We obtained the mean annual wind speed, which could influence the proportional abundance of anemochory, from the WorldClim v.2 dataset at a 1-km spatial resolution (Fick & Hijmans, 2017) for each plot. We obtained flooded forest types from direct observations for each plot.

To test the resource-availability hypothesis, we obtained climatic and soil fertility variables from rasters at a 1-km spatial resolution for each plot. These variables represent the availability of resources for constructing zoochorous fruits (i.e., high and constant air temperature, high and constant water availability from rainfall, and fertile soils; Correa et al., 2015; Tabarelli et al., 2003; Willson et al., 1989). Climatic variables corresponded to the mean annual temperature (MAT), annual range of temperature (ART), mean annual precipitation (MAP) and precipitation seasonality (PS) obtained from the WorldClim v.2 datasets (Fick & Hijmans, 2017). Soil fertility was measured in terms of the soil cation exchange capacity (CEC) at a depth of 0–1 m, obtained from the SoilGrids datasets (Hengl et al., 2017). We also included forest types as a proxy of soil fertility (where PZ, IG and SW are considered to have low soil fertility, TFGS and TFBS intermediate soil fertility, and TFPB and VA high soil fertility).

To account for the potential effects of forest productivity on the geographic distribution of dispersal modes, we obtained the aboveground coarse woody biomass productivity (AGWBP) from a raster at a 0.5° spatial resolution for each plot (Coelho de Souza et al., 2019; Malhi et al., 2004). The AGWBP is considered proportional to the total aboveground wood productivity and has been found to be positively correlated with litterfall production (Malhi et al., 2004).

2.2 | General geographic patterns

We created maps to visualize the geographic distribution of endozoochory, synzoochory, anemochory and hydrochory, by averaging the proportional abundance of dispersal modes among plots within a

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4°×4° grid. We examined changes in dispersal modes among forest types through boxplots. To detect statistically significant differences among forest types, we created homogeneous subsets based on multiple comparison tests (Fisher's least significant difference procedure with Bonferroni corrections) following Kruskal–Wallis tests. Maps were developed in ArcGIS v. 10.7.1. Statistical analyses were undertaken in the software environment R v. 4.1.3 (R Core Team, 2022). The package "agricolae" (de Mendiburu, 2020) was used to create homogeneous subsets in boxplots.

The degree of similarity in dispersal modes among forest types was evaluated using an abundance-weighted mean pairwise distance (MPD) test (Tucker et al., 2017). MPD is a metric used to determine the degree of similarity in a given trait (in this case, dispersal mode) across species. We used the Gower dissimilarity coefficient (Podani, 1999) to calculate trait dissimilarity. We calculated MPD for all plots and conducted a null model analysis to standardize the metric [standardized effect size (SES) MPD] across plots with different species richness. The null model consisted of shuffling trait values (dispersal modes) 999 times across the entire dataset and re-calculating MPD. Then, we calculated the SES MPD by subtracting the mean of the null distribution from the observed value and dividing it by the standard deviation. Negative SES MPD indicates that the differences in dispersal modes within a given plot are lower than expected given the observed species richness (i.e., a clustering in dispersal modes), while positive SES MPD indicates the opposite (i.e., a higher dissimilarity in dispersal modes). We fit regression lines to illustrate the changes in SES MPD as a function of latitude and longitude. We also examined changes in the SES MPD values among regions and forest types through boxplots. To detect statistically significant differences among regions and forest types, we created homogeneous subsets based on multiple comparison tests (Fisher's least significant difference procedure with Bonferroni corrections) following Kruskal–Wallis tests. Analyses were undertaken in the software environment R v. 4.1.3. The package "FD" (Laliberté et al., 2020) was used to construct the dissimilarity matrix of dispersal modes, the package "picante" (Kembel et al., 2010) was used to calculate the MPD in dispersal modes per plot, and the package "agricolae" (de Mendiburu, 2020) was used to create the homogeneous subsets in boxplots.

2.3 | Disperser-availability and resource-availability hypotheses

We fit generalized linear models (GLMs) to explain the proportional abundance of dispersal modes as a function of the availability of dispersal agents and the availability of resources for constructing zoochorous fruits. The potential effect of forest productivity on the geographic distribution of dispersal modes was tested by including AGWBP. First, we fit GLMs using all plots and all variables but without including the biomass of frugivorous primates, which was only calculated for 25 sites. The inclusion of all variables in the GLMs allowed the evaluation of the two tested hypotheses (disperser-availability hypothesis and resource-availability hypothesis) as well as the direct comparison of the effect of each variable on the geographic distribution of dispersal modes. Then, we fit GLMs using the 25 sites that were assumed to share frugivorous primate communities and all variables. We applied a GLM framework because it offers the advantage of accounting for the mean–variance relationship in the response variables and increasing the statistical power of tests when the response variables have low variance, aspects that are often overlooked in the traditional distance-based multivariate analysis methods (Wang et al., 2012). To achieve this, a single GLM was fit to each response variable with a common set of predictor variables, and a resampling method was used to test for significant associations with the explanatory variables at both the community level and at each response variable level. A negative binomial regression model was specified to account for a quadratic mean–variance relationship and the log-linear relationship between dispersal modes and the explanatory continuous variables, after checking for the absence of obvious patterns in each of the GLM residuals. To account for the correlation between dispersal modes, we tested the significance of explanatory variables by resampling 999 times (based on the probability integral transform PIT-trap resampling method) and using a Wald statistic (Warton, 2011). First, we tested the significance at the community level, and then, for each response variable using univariate tests. The PIT-trap resampling method does not assume an identical distribution of residuals and offers reliable Type I error rates from bootstrapped residuals (Warton et al., 2017). We checked for collinearity in GLMs using a variance inflation factor (VIF), which measures how much the variance of an independent variable is inflated by its correlation with another independent variable. When GLMs were collinear, we undertook a backward elimination procedure by sequentially removing variables with VIF higher than 5 until regression models showed little collinearity. We found little collinearity in the GLMs based on total plots. In the GLMs that included the biomass of frugivorous primates, we eliminated the variables representing region and forest type, which showed high collinearity (Supporting Information Tables S3 and S4). Analyses were undertaken in the software environment R v. 4.1.3 using the package "mvabund" (Wang et al., 2012). We additionally fit a locally weighted regression (Loess) model to visualize the variation of endozoochory as a function of the BFP, using the software environment R v. 4.1.3 (R Core Team, 2022).

3 | RESULTS

3.1 | General geographic patterns

Both endozoochory and anemochory increased southward and westward, while both synzoochory and hydrochory increased northward and eastward (Figure 2, Supporting Information Figures S1 and S2). A higher dissimilarity in dispersal modes per plot was found towards the north and east (Figure 3a,b), with significantly higher SES MPD values in eastern Amazonia (EA) and the Guiana Shield (GS) (Figure 3c), as well as in flooded and podzol (PZ) forests (Figure 3d).

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Significantly lower SES MPD values were found in terra-firme forests (excluding podzols).

3.2 | Disperser-availability hypothesis

Anemochory was significantly, positively associated with mean annual wind speed (WS) and hydrochory was significantly higher in flooded forests, with a maximum coefficient in the seasonally flooded igapó (IG) and várzea (VA) forests (Table 3). No significant associations were found between endozoochory and the biomass of frugivorous primates (BFP; Figure 4, Supporting Information Table S5), despite the initial positive correlation between these variables (Supporting Information Figure S4).

3.3 | Resource-availability hypothesis

Endozoochory was significantly, positively associated with mean annual precipitation (MAP), precipitation seasonality (PS) and annual

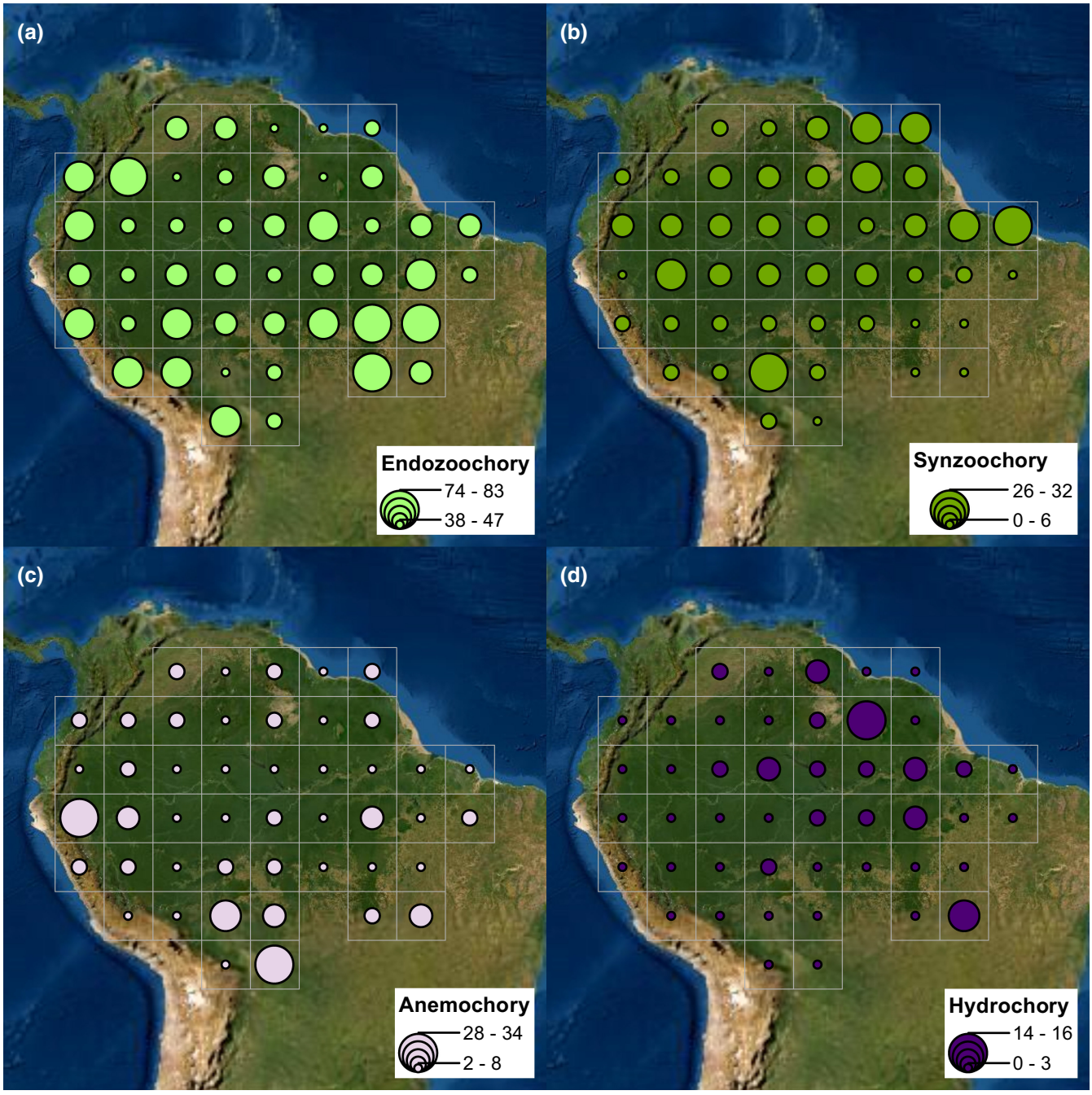

FIGURE 2 Average proportional abundance of dispersal modes (%) within a 4°×4° grid across Amazonia based on 1877 tree-inventory plots. (a) Endozoochory, (b) synzoochory, (c) anemochory and (d) hydrochory.

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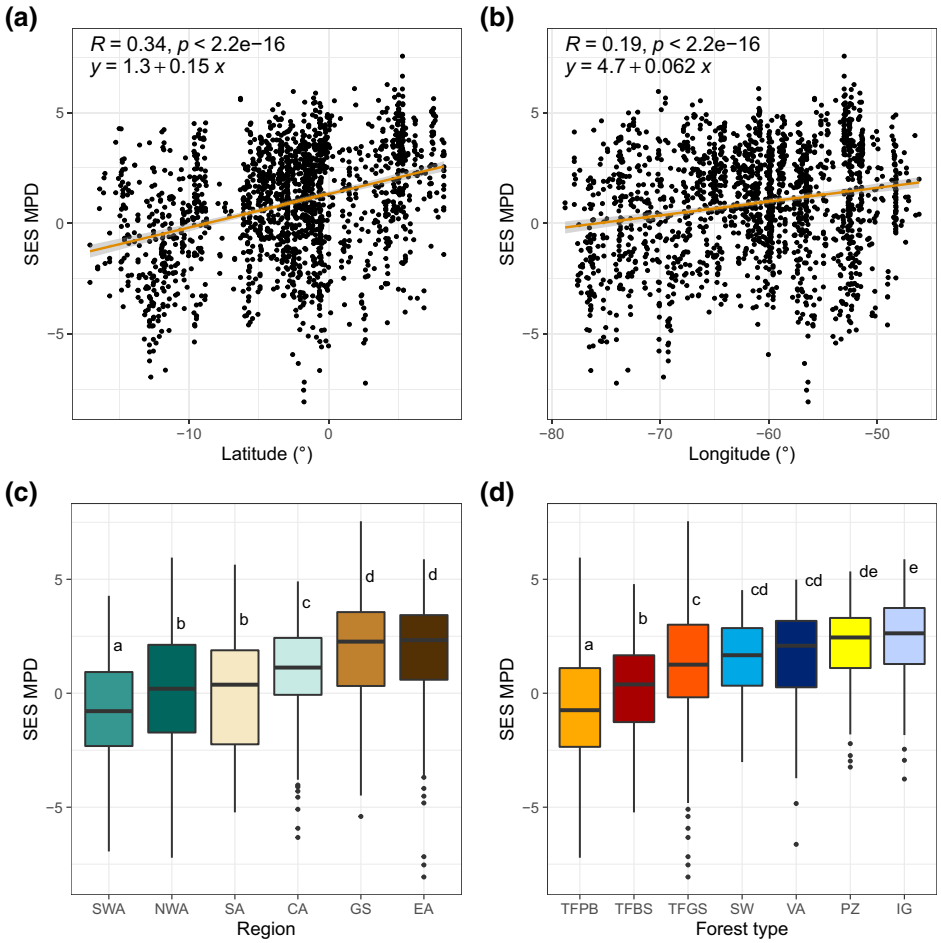

FIGURE 3 Regression lines on the similarity of tree dispersal modes (standardized effect size mean pairwise distance, SES MPD) as a function of (a) latitude and (b) longitude. Boxplots illustrating the similarity of dispersal modes (SES MPD) among (c) regions and (d) forest types. Regions: central Amazonia (CA), eastern Amazonia (EA), Guiana Shield (GS), north-western Amazonia (NWA), southern Amazonia (SA) and south-western Amazonia (SWA). Forest types: white-sand podzol forests (PZ), terra-firme forests on the Brazilian Shield (TFBS), terra-firme forests on the Guiana Shield (TFGS), terra-firme forests on the Pebas Formation (TFPB), igapó forests (IG), várzea forests (VA), swamp forests (SW). Lower-case letters show homogeneous subsets based on multiple comparison tests (Fisher's least significant difference procedure with Bonferroni corrections) following Kruskal–Wallis tests.

range of temperature (ART), as well as significantly, negatively associated with soil cation exchange capacity (CEC) (Table 3). Synzoochory was significantly, positively associated with mean annual temperature (MAT) and MAP and was significantly, negatively associated with ART. Anemochory was significantly, positively associated with ART and more fertile soils in terms of CEC, as well as negatively associated with MAP and PS.

Using the terra-firme forests on the Brazilian Shield (TFBS) as a reference level for statistical analyses, endozoochory was significantly higher in terra-firme forests on the Pebas Formation (TFPB) and significantly lower in igapó (IG), podzol (PZ), and swamp (SW) forests (Table 3). Synzoochory was significantly higher in SW and significantly lower in PZ and IG. Anemochory was significantly higher in PZ, SW, and IG. Boxplots show the variation in dispersal modes among forest types (Figure 5).

Synzoochory and anemochory were significantly, positively associated with aboveground coarse woody biomass productivity (AGWBP), while endozoochory was significantly, negatively associated with this variable.

4 | DISCUSSION

4.1 | Disperser-availability hypothesis

Our analyses suggest that dispersal agents are important factors shaping the proportional abundance of anemochory and hydrochory (Table 3). Agreeing with other studies undertaken in tropical forests, anemochory was significantly, positively associated with mean annual wind speed (Correa et al., 2015) and hydrochory was significantly higher in seasonally or permanently flooded forests (Correa et al., 2015; Umaña et al., 2018). Our results suggest that changes in wind speed resulting from climate change (Kling & Ackerly, 2020) could alter the dispersal and recruitment of anemochorous trees. Likewise, decreases in the intensity and extent of flooding regimes resulting from climate change (Arnell & Gosling, 2013; Langerwisch et al., 2013) or the construction of dams (Schöngart et al., 2021; Timpe & Kaplan, 2017) could alter the dispersal and recruitment of hydrochorous trees.

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TABLE 3 Statistically significant variables associated with the proportional abundance of dispersal modes (%) in Amazonia (ordered by decreasing Wald value) based on 1877 tree-inventory plots

Dispersal mode	Variable	Coefficient	Wald value
Endozoochory	Igapó (IG)	-2.47×10^{-1}	8.65***
	Mean annual wind speed (WS)	-1.48×10^{-1}	6.76***
	Podzol (PZ)	-2.35×10^{-1}	6.15***
	Mean annual precipitation (MAP)	9.89×10^{-5}	5.32**
	Precipitation seasonality (PS)	3.34×10^{-3}	4.76***
	Swamp (SW)	-2.22×10^{-1}	4.18***
	Terra-firme Pebas Formation (TFPB)	1.05×10^{-1}	3.79**
	Annual range of temperature (ART)	1.70×10^{-2}	3.60***
	Soil cation exchange capacity (CEC)	-7.25×10^{-3}	3.21**
	Aboveground coarse woody biomass productivity (AGWBP)	-2.47×10^{-2}	2.04*
Synzoochory	Annual range of temperature (ART)	-1.12×10^{-1}	10.06***
	Mean annual temperature (MAT)	2.07×10^{-1}	7.51***
	Aboveground coarse woody biomass productivity (AGWBP)	1.53×10^{-1}	5.47***
	Podzol (PZ)	-3.84×10^{-1}	4.36***
	Mean annual wind speed (WS)	1.95×10^{-1}	3.80**
	Swamp (SW)	3.95×10^{-1}	3.35**
	Mean annual precipitation (MAP)	1.27×10^{-4}	2.92**
	Igapó (IG)	-1.67×10^{-1}	2.52*
Anemochory	Mean annual precipitation (MAP)	-3.03×10^{-4}	6.21**
	Annual range of temperature (ART)	6.89×10^{-2}	5.54***
	Soil cation exchange capacity (CEC)	2.73×10^{-2}	4.78***
	Podzol (PZ)	4.57×10^{-1}	4.74***
	Mean annual wind speed (WS)	2.42×10^{-1}	4.35***
	Precipitation seasonality (PS)	-7.19×10^{-3}	3.92**
	Swamp (SW)	3.67×10^{-1}	2.78*
	Igapó (IG)	1.89×10^{-1}	2.59*
	Aboveground coarse woody biomass productivity (AGWBP)	8.41×10^{-2}	2.66*
Hydrochory	Igapó (IG)	1.52×10^{0}	14.27***
	Soil cation exchange capacity (CEC)	6.91×10^{-2}	8.29***
	Várzea (VA)	8.15×10^{-1}	7.24***
	Mean annual precipitation (MAP)	-3.90×10^{-4}	5.13**
	Mean annual wind speed (WS)	-4.62×10^{-1}	5.00***
	Swamp (SW)	9.44×10^{-1}	4.89***
	Annual range of temperature (ART)	-7.46×10^{-2}	3.82***
	Aboveground coarse woody biomass productivity (AGWBP)	-1.51×10^{-1}	3.17*

Note: *p*-values of univariate tests were calculated by resampling 999 times (based on the probability integral transform PIT-trap resampling method; Wang et al., 2012) and using a Wald statistic (Warton, 2011).

*$p<.05$.; **$p<.01$.; ***$p<.001$.

The disperser-availability hypothesis was not well supported for endozoochory. The influence of frugivores on the geographic distribution of zoochorous trees requires further investigation, as our study was limited to a small subset of 25 sites and included only primates as a proxy of all frugivorous animals (Figure 4). While primates are effective dispersal agents of endozoochorous trees in the Neotropics (Fuzessy et al., 2016; Link & Di Fiore, 2006), further analyses including information on the biomass of birds, bats, tapirs and fishes may give more insights on the role of frugivores in the distribution of endozoochory in Amazonia. The influence of scatter-hoarding rodents also requires further investigation, as they are considered very important for dispersing large seeds (many of them synzoochorous) in the Neotropics (Jansen et al., 2004, 2012). It is also known that when the size

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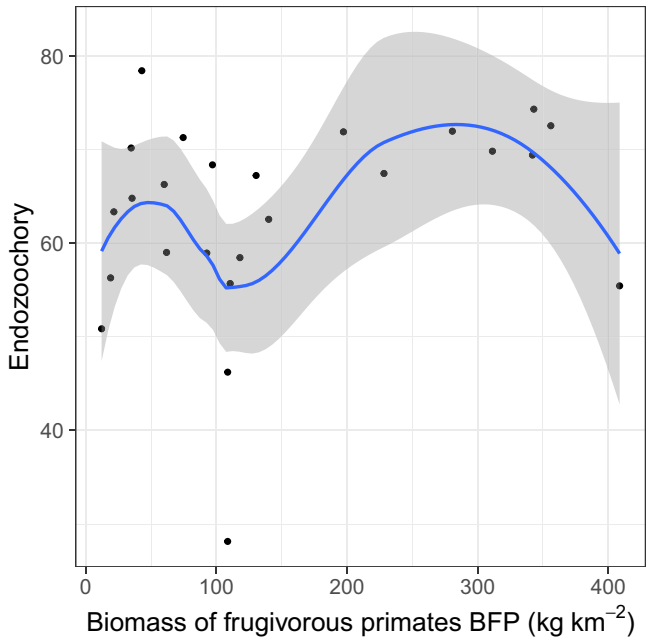

FIGURE 4 Loess regression illustrating the proportional abundance of endozoochory (%) as a function of the biomass of frugivorous primates (BFP) based on 25 sites. The 95% confidence interval is shown in grey shading.

of frugivorous communities declines as a result of hunting or deforestation (i.e., defaunation), the dispersal and recruitment of zoochorous trees can decrease, particularly for large-seeded species (Beck et al., 2013; Gardner et al., 2019; Muller-Landau, 2007; Stevenson, 2011; Terborgh et al., 2008). Our study did not explicitly consider the effects of defaunation on the geographic distribution of dispersal modes, but we suggest this is a key factor to consider in future studies given the increased rates of defaunation in tropical forests (Gardner et al., 2019).

4.2 | Resource-availability hypothesis

The resource-availability hypothesis was not well supported in our analysis. As predicted by this hypothesis we found a significant, positive relationship between zoochory (i.e., endozoochory and synzoochory) and mean annual precipitation. In agreement with this hypothesis, we also found significant, positive associations between endozoochory and fertile forest types (i.e., terra-firme Pebas Formation) as well as negative associations between zoochory and less fertile forest types (i.e., endozoochory and igapó, podzol and swamp forests, as well as synzoochory and podzol and igapó forests). However, only synzoochory (but not endozoochory) was significantly, positively associated with mean annual temperature and negatively associated with annual range of temperature. Also, contrary to the prediction, endozoochory was significantly, positively associated with precipitation seasonality and annual range of temperature, as well as significantly, negatively associated with soil fertility in terms of soil cation exchange capacity. Contrary to the prediction, synzoochory was significantly, positively associated with the less fertile swamp forests.

On the other hand, anemochorous species were hypothesized to need fewer resources than zoochorous species for constructing their comparatively smaller seeds and dry diaspores (Tabarelli et al., 2003; Willson et al., 1989). In agreement with this hypothesis, we found a significant, positive association between anemochory and annual range of temperature, a significant, negative association with mean annual precipitation, and a significant increase in the less fertile podzol, swamp and igapó forests. However, contrary to the prediction, anemochory showed a significant, positive association with fertile soils in terms of soil cation exchange capacity, as well as a significant, negative association with precipitation seasonality. These trends suggest that the availability of resources for constructing zoochorous fruits does not adequately explain the proportional abundance of dispersal modes in Amazonia.

4.3 | Potential relationships between dispersal modes and forest dynamics

Changes in forest dynamics, resulting from climatic and soil fertility gradients, could affect the distribution of dispersal modes in Amazonia. In western Amazonia, more fertile soils in proximity to the Andean mountain range (Malhi et al., 2004; Quesada et al., 2012) would drive higher forest turnover (ter Steege et al., 2006). A higher forest turnover could increase the frequency of forest gaps that offer advantageous conditions for the recruitment of trees with small and medium seed sizes (many of them anemochorous and endozoochorous), as these can outcompete larger seeds under favourable germination conditions (Westoby et al., 2002). This could explain the westward increase in anemochory and endozoochory, as well as the significant, positive association of endozoochory with fertile forest types (i.e., terra-firme Pebas Formation) and the positive association of anemochory with fertile soils in terms of soil cation exchange capacity and productive areas in terms of aboveground coarse woody biomass productivity. On the other hand, a lower forest turnover in eastern Amazonia would favour the recruitment of large-seeded trees (many of them synzoochorous; ter Steege et al., 2006), as large seeds have competitive advantages in shady (Baraloto & Forget, 2007) and nutrient-deprived environments (Parolin, 2000; Westoby et al., 2002). This could explain the eastward increase in synzoochory. More fertile soils in western Amazonia could also increase fleshy fruit productivity per unit area and thus the availability of frugivores (Stevenson, 2001) that act as effective dispersers of endozoochorous trees in the Neotropics (Nunez-Iturri et al., 2008; Peres & Van Roosmalen, 2002). The hypothesized set of relationships that could drive the recruitment of anemochorous and endozoochorous trees in Amazonia is shown in Figure 6: high soil fertility would increase forest turnover and favour the

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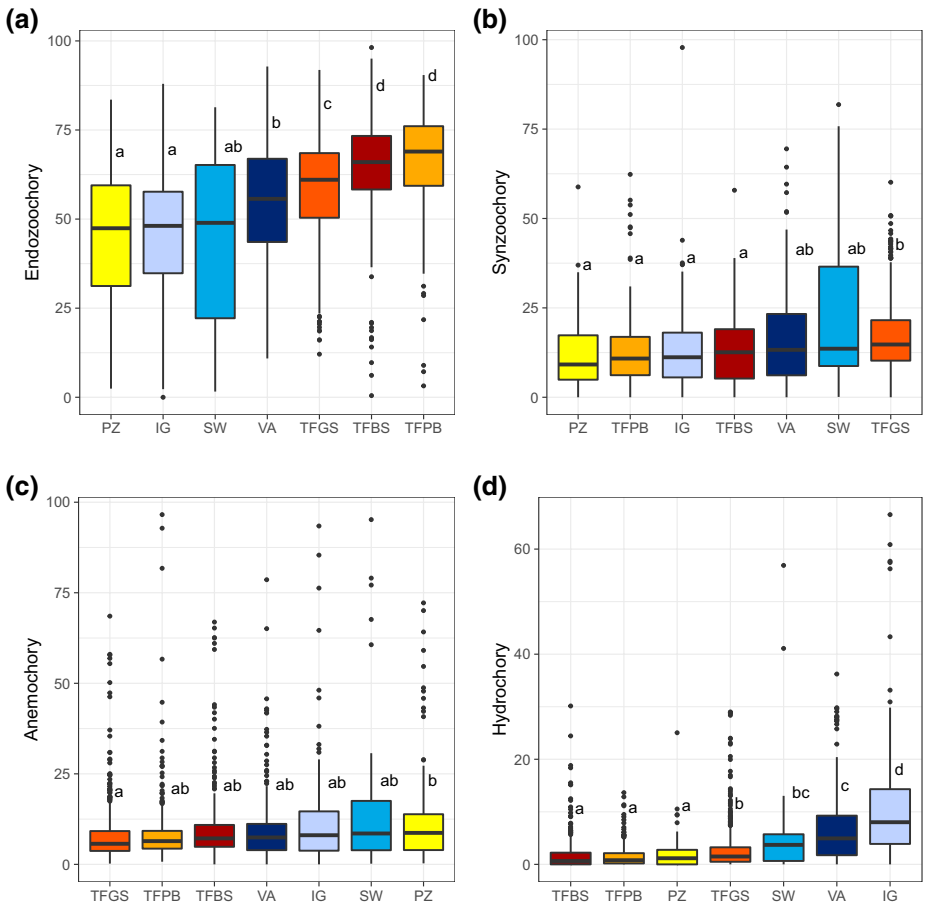

FIGURE 5 Boxplots illustrating the proportional abundance (%) of (a) endozoochory, (b) synzoochory, (c) anemochory and (d) hydrochory among forest types. Forest types: white-sand podzol forests (PZ), terra-firme forests on the Brazilian Shield (TFBS), terra-firme forests on the Guiana Shield (TFGS), terra-firme forests on the Pebas Formation (TFPB), igapó forests (IG), várzea forests (VA), swamp forests (SW). Lower-case letters show homogeneous subsets based on multiple comparison tests (Fisher's least significant difference procedure with Bonferroni corrections) following Kruskal–Wallis tests.

recruitment of trees with small and medium seed sizes (many of them anemochorous and endozoochorous), and also high soil fertility would increase fleshy fruit productivity per unit area and as a result increase the availability of frugivores that enhance the recruitment of endozoochorous trees.

Gradients in mean annual precipitation could further affect the distribution of dispersal modes in Amazonia. The higher occurrence of deciduous trees in drier forests (Ouédraogo et al., 2016; Van der Sande et al., 2016) would result in seasonal leaf shedding that has been shown to increase the dispersal distance of anemochorous seeds (Nathan & Katul, 2005). Seasonal leaf shedding would also favour the recruitment of trees with small seed sizes (many of them anemochorous) under advantageous germination conditions from increased access to sunlight (Moles & Westoby, 2004; Westoby et al., 2002). This could explain the significant, negative association between anemochory and mean annual precipitation. More fertile soils could also support the occurrence of deciduous trees, as opposed to evergreen trees that need to retain leaves with their nutrients in less fertile environments (Goldberg, 1982; Ouédraogo et al., 2016), which would enhance the recruitment of anemochorous trees in more fertile areas.

4.4 | Dispersal modes and forest types

Anemochory was significantly higher in swamp and igapó forests (as opposed to endozoochory in both forest types, as well as synzoochory in igapó forests). More open canopies in flooded forests (Alvarenga et al., 2018; De Almeida et al., 2016; Haugaasen & Peres, 2005) could favour the recruitment of anemochorous trees. Restricted mobility of terrestrial frugivores throughout the year in flooded forests (Alvarenga et al., 2018; Haugaasen & Peres, 2007) could also potentially decrease the dispersal of zoochorous trees in these forest types. On the other hand, synzoochory was significantly higher in swamp forests, which could be explained by the effective dispersal and recruitment of palm trees, many of them synzoochorous, in permanently flooded areas (ter Steege et al., 2019). The highly dynamic conditions of flooded forests would diversify dispersal modes and explain the high dissimilarity of tree dispersal modes (SES MPD) in these forest types compared to terra-firme forests (excluding podzols), the latter of which showed the highest dominance of zoochory (Supporting Information Table S6).

We also found that endozoochory and synzoochory were significantly lower in podzol forests while anemochory was significantly

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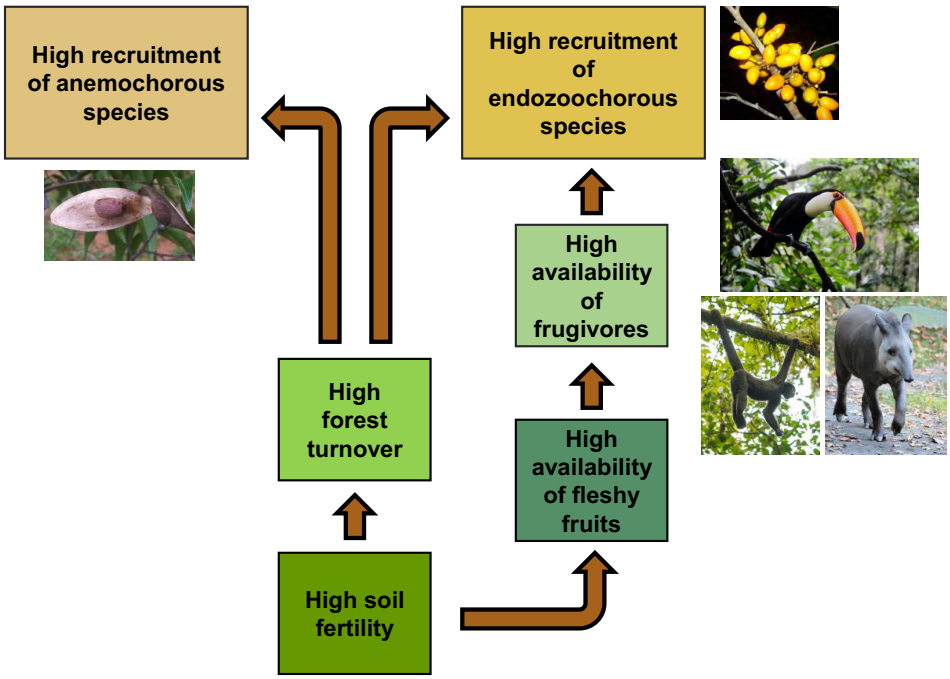

FIGURE 6 Diagram of potential causal relationships in the recruitment of anemochorous and endozoochorous trees in Amazonia. Soil fertility would affect plant recruitment by increasing forest turnover, favouring the recruitment of trees with small and medium seed sizes (many of them anemochorous and endozoochorous). More fertile soils would also increase fleshy fruit production per unit area and thus frugivore availability, favouring the recruitment of endozoochorous trees. Photos by Carmel Arquelau (Unsplash – toucan), Tomás Pinzón (Universidad de los Andes, Colombia – woolly monkey), Dušan Veverkolog (Unsplash – tapir) and DFC (first author – fruits).

higher in this forest type. Podzol forests are limited by water and nutrients in soils (Aragão et al., 2009). How these limitations affect fleshy fruit productivity, frugivore availability and/or the recruitment of zoochorous trees, requires further investigation. Trees with different dispersal modes would be able to recruit in podzol forests, explaining the high dissimilarity of dispersal modes (SES MPD). In contrast, less dissimilarity occurred in other terra-firme forests (excluding podzols), where zoochory showed the highest values.

4.5 | Anthropogenic influence on the geographic distribution of dispersal modes

Mounting evidence shows that Amazonian rain forests have been modified by humans and that their impact persists in current plant communities (Clement et al., 2015; Levis et al., 2017). Thus, the geographic distribution of dispersal modes may have also been influenced by the cultivation of domesticated species by pre-Columbian populations. Domesticated plants are particularly present in southwestern Amazonia and mainly consist of palm trees and species with fleshy fruits for human consumption (Levis et al., 2017), potentially explaining the high synzoochory values in the Llanos de Mojos, one of the most densely populated areas inhabited by the pre-Columbian Casarabe culture (Prümers et al., 2022). Furthermore, the geographic distribution of dispersal modes can be impacted by hunting and the subsequent defaunation, which may limit the recruitment of large-seeded trees (many of them synzoochorous; Nunez-Iturri et al., 2008; Peres et al., 2016; Terborgh et al., 2008; Wright et al., 2007). We currently lack information on the relative contributions of each of these impacts upon the distribution of dispersal modes in Amazonia.

4.6 | Caveats and future research

In our study, dispersal modes were mainly defined based on diaspore morphology. We assumed that the most common dispersal mode in a particular species can be inferred from a combination of diaspore traits that are related to their most frequent dispersal agent (Table 2). However, the distribution of several species might result from less frequent dispersal agents and/or stochastic events (e.g., long-distance dispersal events that might not be mediated by a morphology-inferred dispersal agent; Green et al., 2021; Nathan et al., 2008). We encourage the development of experimental studies that correlate diaspore morphology with their most efficient dispersal mode, particularly within the tropics where ecological information of thousands of tree species remains limited. In addition, it would be more realistic to address that in some cases seeds may be dispersed by different dispersal agents (e.g., *Spondias* seeds may be swallowed or dropped by monkeys, swallowed by tapirs, and secondarily dispersed by water).

Plant functional traits (such as dispersal mode, seed size, leaf size, tree size, and wood density) covary (Westoby et al., 2002) and correlate with geographic and ecological factors (McGill et al., 2006). Our analyses were restricted to dispersal modes, but further exploring

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the relationships between dispersal modes and other plant functional traits (e.g., leaf size, tree size, wood density), and how these traits vary geographically and within communities, may shed light on the drivers of the distribution of tree dispersal modes in Amazonian and other tropical forests. Explaining the geographic distribution of dispersal modes would benefit from exploring the geographic and within-community variation in plant functional traits associated with dispersal modes (e.g., seed size) and how they associate with frugivore functional traits (e.g., body and gape size).

The connections between dispersal modes, and other components of biodiversity and ecosystem services, in the face of increasing anthropogenic disturbance (from climate change, deforestation, soil erosion, construction of dams, and hunting), require further investigation. For instance, hunting in tropical regions can drive forest defaunation (Benítez-López et al., 2017), decreasing the dispersal and recruitment of zoochorous trees (Bello et al., 2015; Donoso et al., 2017) as well as the distance their seeds can reach (Fricke et al., 2022). This alters forest tree composition (Beck et al., 2013) and drives cascading effects that include reductions in forest carbon stocks (Bello et al., 2015; Dirzo et al., 2014; Gardner et al., 2019; Peres et al., 2016) and in the ability of species to adapt to climate change (Fricke et al., 2022).

5 | CONCLUSIONS

Examining the main underlying factors resulting in the geographic distribution of tree dispersal modes is important to unravel the drivers of plant recruitment, biodiversity persistence, and delivery of ecosystem services in Amazonian and other tropical forests. Here, we tested two hypotheses to explain the distribution of dispersal modes in Amazonia. We found partial support for the disperser-availability hypothesis given the limited dataset to analyse the effect of frugivores, and no strong support for the resource-availability hypothesis. These results highlight that forest types are important in the distribution of dispersal modes in Amazonia, and that the geographic distribution of abiotic dispersal modes can be predicted by considering the mean annual wind speed (for anemochory) and the presence of flooded areas (for hydrochory). On the other hand, it is hypothesized that higher soil fertility could increase the occurrence of anemochory and endozoochory in western Amazonia via increased forest turnover, and for endozoochory also through increased availability of frugivores. In contrast, synzoochory (characterized by the largest seed sizes among dispersal modes) could be favoured in the less fertile and hence more stable environments in eastern Amazonia. Anemochory could be favoured where more open canopies facilitate the recruitment of their comparatively smaller seeds (i.e., in drier forests, flooded forests and podzol forests) or where frugivores are limited. It is also possible that the high values of synzoochory found in south-western Amazonia reflect the pre-Columbian cultivation of domesticated palm trees in the region. Current anthropogenic activities might disrupt ecological interactions that drive the recruitment of trees based on their dispersal mode, with potentially disastrous consequences for the resilience of Amazonian forests. Further studies on the role of ongoing human-driven anthropogenic degradation (e.g., considering climate change, large-scale deforestation and soil erosion, construction of dams, and uncontrolled hunting) in the distribution of dispersal modes could lead to the implementation of better management practices and policies for the conservation of Amazonia.

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[Correction added on 24 November 2022, after first online publication: Projekt CAUL funding statement has been added.]

DATA AVAILABILITY STATEMENT

The percentages of dispersal modes per plot are included as Supporting Information (Table S7, based on 5433 species and morphospecies within 1877 tree-inventory plots across terra-firme, seasonally flooded, and permanently flooded forests in Amazonia). The dispersal modes assigned to these 5433 species and morphospecies are also included as Supporting Information (Table S8).

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ATDN is a network of over 200 botanists, zoologists, anthropologists and ecologists that share data of over 2000 Amazonian tree plots to jointly study all aspects of the Amazon Tree Flora.

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