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Original Article

Plant dispersal strategies in post-mining restoration areas in the Eastern Amazon

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ABSTRACT

Mining activities in the Amazon result in significant environmental damage to mined areas. Natural regeneration through seed dispersal is a crucial process that aims to reintegrate those mined areas into the native vegetation nearby. In this study, our main objective was to compare seed and fruit dispersal strategies that occur in the vertical stratification in altered primary forest (APF) and natural regeneration (NR) areas after bauxite mining. The results indicate that zoochory was the most frequent dispersal syndrome in APF areas, with fleshy fruits being the most frequent. The NR areas exhibited greater variation in dispersal syndromes, with zoochory, anemochory, and autochory being the most representative, with a predominance of dry fruits. The differences in dispersal modes between APF and NR areas are within the patterns already expected and previously found in other studies on fruit dispersal. These findings emphasize that understanding how species composition and dispersal strategies are influenced by environmental and anthropogenic impacts is crucial for the restoration of these areas. This knowledge helps identify which dispersal mechanisms are best adapted to degraded areas, enabling more effective recovery strategies through planting species with similar dispersal mechanisms, particularly in regions impacted by mining.

Keywords: dry fruits; dispersal patterns; fleshy fruits; mining; natural regeneration.

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Introduction

The dispersal of diaspores involves their removal, transport, and release at various distances from the mother tree (Beckman & Sullivan, 2023), and is considered effective when new adults are produced (Schupp *et al.*, 2010; Howe, 2016; Beckman & Sullivan, 2023). Furthermore, diaspores dispersal plays an important role in ecosystems by assisting in the natural regeneration of degraded areas and maintaining populations and communities of plant species (Benedicto-Royuela *et al.*, 2024; Lussier *et al.*, 2025).

Plants produce diaspores with adaptations in their morphology and nutritional content for protection and dispersal. Van der Pijl (1982) classified dispersal syndromes according to fruit types and associated them with dispersing agents, into: zoochory (including endochory and exochory/epizoochory); anemochory (by wind); hydrochory (by water); autochory (by the plant itself through explosive mechanisms); and barochory (due to the plant's weight). More specific terminologies and subgroups were later used (Beckman & Sullivan, 2023).

In tropical mature forest ecosystems, zoochory predominates, where dominant plants produce larger, heavier, fleshy fruits with vibrant colors (Valenta & Nevo, 2020; Gonçalves *et al.*, 2024). This pattern contrasts with that observed in degraded tropical forest ecosystems, where plants with lighter fruits and adaptations for wind dispersal, such as wings and fibers, increase their relative abundance (Correa *et al.*, 2023; Benedicto-Royuela *et al.*, 2024; Gonçalves *et al.*, 2024). Although this pattern is well documented (Galetti, 2013; Hawes *et al.*, 2020), understanding how the functional characteristics of plants, especially reproductive characteristics such as fruit and seed types, and seed dispersal mode respond to environmental degradation is important for defining appropriate restoration strategies that consider all biodiversity.

Mining, as well as water pollution, soil erosion, and a decrease in air quality, is one of the main anthropogenic impacts that cause abrupt changes in mature ecosystems, consequently altering dispersion patterns and the way in which these areas will recover (Sengupta, 2021; Branco *et al.*, 2022). The state of Pará hosts two of the largest mineral deposits in the Northern Region of Brazil: the Oriximiná deposit (bauxite mining) and the Serra dos Carajás deposit (mining of manganese, copper, bauxite, gold, nickel, tin, and iron, which is the largest amongst all mineral deposits), with bauxite accounting for up to US$ 276 million in the mineral export industry in Pará (Simineral, 2022). Excessive levels of toxic waste can negatively impact the local biota (Dey *et al.*, 2023), affecting the establishment of populations and communities in regeneration areas (Crespo-Lopez *et al.*, 2023). Restoring vegetation cover is one of the first steps to recover post-mining areas, and one of the essential aspects is the arrival of seeds from the surrounding areas, which often depends on the presence of animals (Howe & Miriti, 2004; Souza *et al.*, 2006).

The *Programa de Recuperação de* Áreas *Degradadas* (PRAD, Program for the Recovery of Degraded Areas) is recognized as a fundamental public policy for mitigating the impacts of vegetation loss in the Amazon (Sampaio *et al.*, 2021). It employs different approaches, including passive and assisted intervention methods (such as natural regeneration) and active methods (such as seedling planting and nucleation) (Restrepo-Carvajal *et al.*, 2025). Assisted natural regeneration, which uses complementary techniques to control biotic and abiotic disturbance factors (such as weed spread, livestock grazing, and fire), has demonstrated greater success in ecological restoration than active approaches, especially for increasing biodiversity and vegetation structural complexity (Crouzeilles *et al.*, 2017). Seed sources for regeneration can be present in the soil seed bank or can come from dispersal from neighboring plants (Chazdon & Guariguata, 2016). This source is highly influenced by the number and location of forest fragments and biological corridors around the restored area, as well as the abundance and diversity of seed dispersers (McAlpine *et al.*, 2016). Thus, seed dispersal as an ecosystem service is a process that should be considered in the restoration programs for degraded areas, especially in post-mining regeneration areas (Krauss *et al.*, 2024), where all vegetation and soil that support the seed bank are completely suppressed (Gastauer *et al.*, 2019).

Our main objective was to compare seed and fruit dispersal strategies that occur in altered primary forest (APF) and natural regeneration (NR) areas after bauxite mining. We also aimed to (a) understand the role of plant richness and community structure in the functional groups (*i.e.*, dispersal syndromes and zoochoric dispersal types) in both APF and NR environments; (b) evaluate whether dispersal syndromes differ between strata within each environment and between them; and (c) evaluate whether the distribution of species abundance varies according to the type of dispersal syndrome and the type of fruit. We hypothesize that autochoric/anemochoric species would predominate in NR areas, while zoochoric species would predominate in APF areas. Consequently, we expected that dry fruits (typically anemochorous or autochorous) would be more abundant in areas of natural regeneration, while fleshy fruits would predominate in areas of altered primary forest.

Material and Methods

Study area

The study was conducted in Paragominas, Pará state, Brazil (Fig. 1), on a private property of the mining company Norsk Hydro ASA, whose main economic activity is bauxite mining. The property is located in the Miltônia 3 plateau, with an approximate latitude of 02°59'45" S and longitude of 47°21'10" W (IBGE, 2015). The climate, according to the Köppen-Geiger classification, is predominantly hot and

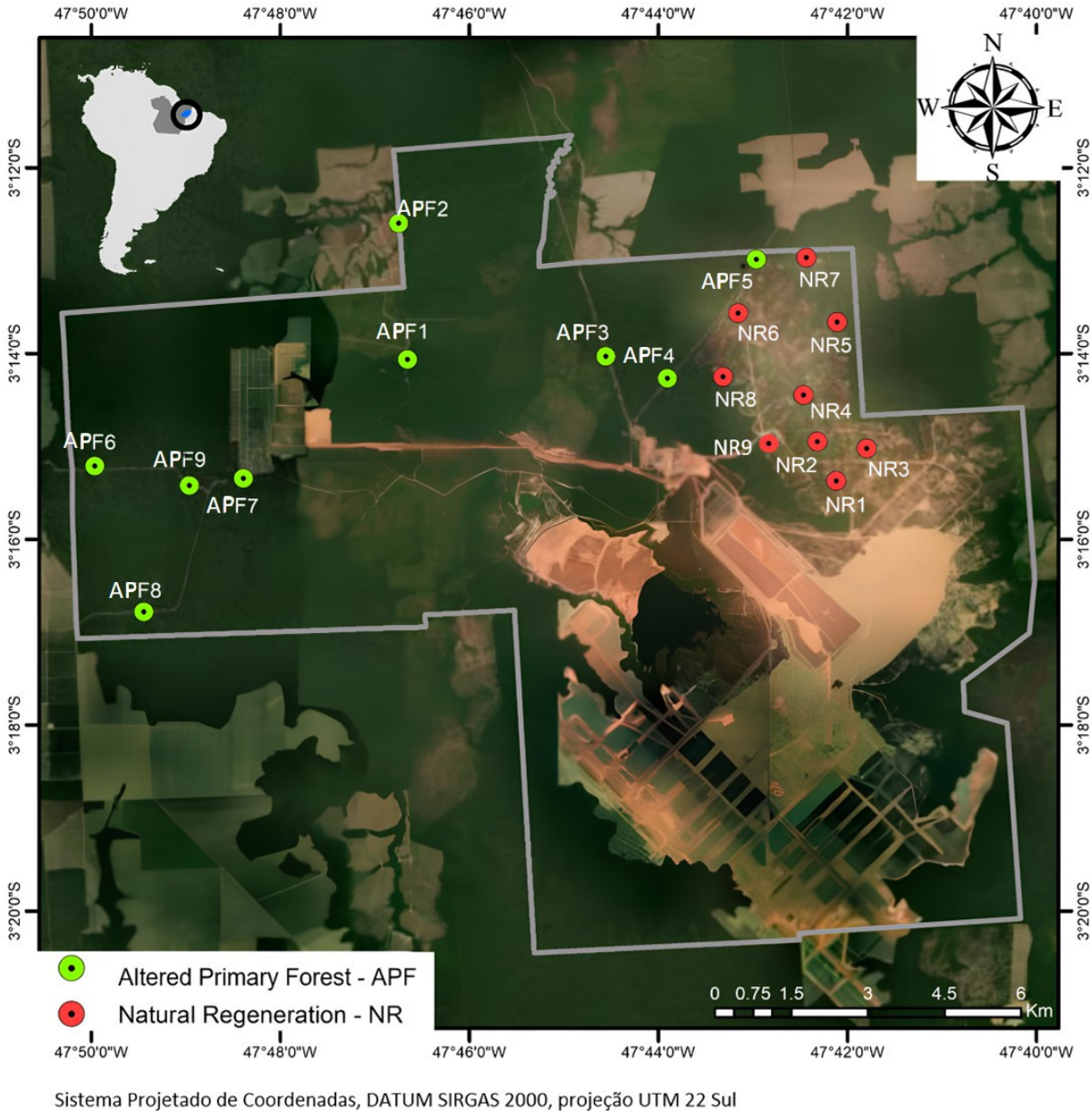

Figure 1. Location of the Hydro mining area (Paragominas, PA), with the sampling points in red representing the natural regeneration areas (NR1-NR9) and in blue the altered primary forest areas (APF1-APF9).

humid (Aw), with marked seasons (Alvares *et al.*, 2013). The average annual temperature is 26.3°C, relative humidity of 81 %, and average annual precipitation of 1,800 mm, with the rainiest months from December to May and the driest from June to November (Pinto *et al.*, 2009).

The region's predominant soils are yellow latosol, yellow argisol, plinthosol, gleissol, and neossol, characterized by low concentrations of calcium, magnesium, phosphorus, nitrogen, and high aluminum saturation (Rodrigues *et al.*, 2003). The original vegetation is represented mainly by dense ombrophilous forest physiognomy (low plateaus, dissected plateaus, and high plateaus) (Watrin & Rocha, 1992). The remaining forest areas within the project's influence area have been altered, either by fire, timber extraction, or mining (Hydro, 2003). A large part of these areas is in advanced successional stages, with a well-formed canopy, being classified as altered primary forest, according to Salomão *et al.* (2024). However, these areas have abundant tree vegetation and a well-structured canopy, with taxa typical of mature and stable forests, such as *Lecythis, Eschweilera*, and *Neoptychocarpus* (Cerqueira *et al.*, 2021).

In the Forest Restoration Program (PRAD), three restoration techniques were implemented: nucleation, seedling planting, and natural regeneration. Only areas

under natural regeneration were studied here, as NR presented a significant number of areas to establish at least nine plots. The technique consists of inducing natural regeneration (assisted) through the backfilling and grading of the terrain and the return of plant residues and topsoil previously removed during mining (Martins *et al.*, 2018). The studied areas have been undergoing the NR process since 2014. These areas currently contain early successional species, with low floristic and structural diversity, an open canopy, and a predominance of herbaceous and shrub species (Cerqueira *et al.*, 2022). The company conducts assessments and enrichment in areas undergoing restoration, in accordance with targets proposed by regulatory agencies. However, at the time of this study, only spontaneously regenerating native species remained alive. This is evidenced by the low species richness and dominance of certain species, like *Croton matourensis* Mart., *Vismia guianensis* (Aubl.) Choisy, *Solanum crinitum* Lam., and *Cecropia* spp. (see Cerqueira *et al.*, 2021; 2022).

Data collection

The data analyzed were collected between 2018 and 2020 during a floristic inventory and phytosociological survey. For this study, we analyzed the data collected by Cerqueira *et al.* (2021), where canopy species (Layer 1) were sampled in plots measuring 250 m × 40 m, considering tree species with a DBH ≥ 10 cm. For understory species (Layer 2), we analyzed data obtained by Cerqueira *et al.* (2022), which included treelets and shrub species with a DBH between 10 cm and 3.0 cm, sampled in plots of 2 m × 20 m. Finally, for forest floor species (Layer 3), we considered species with a DBH ≤ 3.0 cm, sampled in 1 m × 10 m plots, notably shrubs and herbaceous species (unpublished data). In total, data from 18 sampling areas were analyzed, encompassing the three vertical strata characteristic of the studied environments: RN (n = 9) and APF (n = 9) (Fig. 1). Vouchers information is available in Cerqueira *et al.* (2021, 2022).

Characterization of plant species

Characteristics related to plant habit, taxonomic categories, dispersal syndromes, and fruit types were based on information obtained from the Flora and Funga do Brasil website (2022) and literature (Lorenzi, 1992; Judd *et al.*, 2009). Dispersal syndromes were classified as biotic (zoochory - ZOO) and abiotic (anemochory - ANE, autochory - AUT, hydrochory - HYD, and barochory - BAR), as proposed by Van der Pijl (1982). Some species were classified by two types of dispersal syndromes when they exhibited both primary and secondary dispersal (*e.g.*, barochory and zoochory - BAR_ZOO, respectively). Fruit types were classified as dry - DRY (non-succulent pericarp) or fleshy - FLE (thick and succulent pericarp) (Vidal & Vidal, 2003), according to the descriptions presented in Table 1, suggested by Judd (1985), Spjut (1994), Judd *et al.* (2009), and Souza *et al.* (2013).

Data analysis

We used a Principal Coordinate Analysis (PCoA) based on a Bray-Curtis dissimilarity matrix computed from species abundance data to compare the species composition between both environments (APF and NR). First, species abundance was aggregated at the sampling areas (Fig. 1), resulting in a site-by-species matrix. The Bray-Curtis dissimilarity matrix was calculated using the vegan package. The absence of negative eigenvalues confirmed the suitability of the dissimilarity matrix for PCoA. A PCoA was then performed using the cmdscale() function, retaining the first two principal coordinate axes. Next, to confirm the pattern observed in the ordination, we performed a PERMANOVA (Permutational Multivariate Analysis of Variance) with 999 permutations using the same distance matrix. To verify the assumption of homogeneity of multivariate dispersion required by PERMANOVA, we applied the betadisper() function followed by an ANOVA on the distances to group centroids.

Additionally, to investigate patterns in species richness and the abundance of functional groups across sampling areas from the two environments, we constructed a summary dataset based on sampled point levels. For each sampled area, we summarized species richness and aggregated species abundances according to multiple biological classifications, including dispersal syndromes (abiotic, biotic, or both) and zoochory dispersal types (mammaliochory, ornithochory, chiropterochory, or not classified). These numeric summary variables were standardized to unit variance and centered before performing Principal Component Analysis (PCA), to account for differences in scale and units among variables. We selected the PCs with eigenvalues higher than 1 according to the Kaiser criterion. All the above-cited analyses were performed using the *vegan* package (Oksanen *et al.*, 2020).

Next, to investigate whether species abundance and richness differed between environments for each dispersal syndrome type, we fitted separate generalized linear mixed models (GLMMs) for species classified as abiotic, biotic, or both. Models included the environment (NR and APF) and the vegetation layer as fixed effects, and sampled areas as a random effect to account for repeated sampling within the environment. For each model, abundance or richness was used as a response variable, and models were fitted using Poisson or negative binomial distributions, depending on the presence of overdispersion. Model diagnostics were assessed by calculating the overdispersion statistic using Pearson residuals, and model selection was based on the Akaike Information Criterion (AIC). When the estimated variance of a random effect was zero, indicating no contribution to the model, the random effect was removed, and the model was refitted using a GLM.

Table 1. Classification and description of the fruit types found in the study area according to the literature.

Fruit Type	Description	Author
Achene (ACH)	Small, indehiscent and dry fruit, with a single seed protected by a thin, adpressed wall.	Judd (1985); Judd *et al*. (2009).
Berry (BER)	Indehiscent, fleshy fruit with one or a few to many seeds.	Judd (1985); Judd *et al*. (2009).
Capsule (CAP)	Dry fruit, rarely fleshy, formed by a bicarpellate to multicarpellate gynoecium that opens in different ways to release the seeds.	Judd (1985); Judd *et al*. (2009).
Caryopsis (CAR)	Dry, small, indehiscent fruit with a thin wall partially fused to a single seed.	Judd (1985); Judd *et al*. (2009).
Drupe (DRU)	Fleshy and indehiscent fruit, in which the external part is more or less soft.	Judd (1985); Judd *et al*. (2009).
Schizocarp (SCH)	Dry fruit, rarely fleshy, derived from a gynoecium with two or more carpels that divide into segments (mericarps) with one or a few seeds each.	Judd (1985); Judd *et al*. (2009).
Follicle (FOL)	Dry fruit, rarely fleshy, derived from a simple carpel and which opens along a single longitudinal slit.	Judd (1985); Judd *et al*. (2009).
Legume (LEG)	Fruit derived from a single carpel that opens along two longitudinal slits.	Judd (1985); Judd *et al*. (2009).
Loment (LOM)	Dry fruit derived from a single carpel that fragments transversely into one-seeded segments.	Judd (1985); Judd *et al*. (2009).
Nut (NUT)	Dry, indehiscent, and relatively large fruit, with a thick and stony part surrounding a single seed.	Judd (1985); Judd *et al*. (2009).
Syncarpous (SYN)	Fruit with its carpels fused to a greater or lesser degree into a single ovary.	Font Quer (2001).
Samara (SAM)	Dry, indehiscent, winged fruit, usually containing one seed (rarely two).	Judd (1985); Judd *et al*. (2009).
Silique (SIL)	Fruit derived from a bicarpellate gynoecium, in which the two valves separate from a persistent central septum (arranged around a frame-like structure, the replum, to which the seeds are attached).	Judd (1985); Judd *et al*. (2009).
Pyxis (PYX)	Capsule-type fruit with dehiscence by a lid (operculum), or a common pore encircling all carpels.	Spjut, R. W. (1994).
Pseudofruit (PSE)	Structure not derived from the ovary but from other parts of the flower, referred to as an "accessory fruit".	Souza *et al*. (2013).

Since the environments in this study exhibit very distinct plant abundances, as previously described by Cerqueira *et al*. (2021; 2022), we evaluated the floristic composition in three vegetation strata based on the relative abundance of each dispersal syndrome and fruit type. To this end, we used GLMMs (with the sampled area attributed as a random factor) or GLMs, depending on the best fit of the model to the data, using betabinomial and quasibinomial distributions. Models were fitted using the proportion of individuals within each sampled area belonging to a given dispersal syndrome or fruit type as the response variable. The main predictor used in these models was a categorical variable named 'group', which represents the combination of environment (NR or APF) and syndrome or fruit type. This allowed us to compare relative abundances across all combinations of categories. Proportion data were used in the models to avoid false trends created by absolute values, aiming to compare the proportion of each dispersal syndrome and fruit type across the two environments. After fitting the models, we performed a pairwise comparison with Tukey adjustment using the *emmeans* package (Lenth, 2021) and the *dabest* package to plot the mean difference based on the 95 % confidence interval of the abundance proportion between the environments (Ho *et al*., 2019).

Additionally, for each environment, we evaluated whether the distribution of species abundance varied according to dispersal syndrome type and fruit type using GLMMs with a negative binomial distribution. Dispersal syndrome and fruit type were used as fixed factors in the models, while vegetation layer was included as a random effect to account for stratification in the sampling design. All selected models showed overdispersion values between 1 and lower than 1.3, indicating an acceptable fit. Model diagnostics were assessed using residual dispersion and inspection of residuals through the *DHARMa* package (Hartig, 2024). All statistical analyses were performed in R software version 4.2.2 (R Core Team, 2023).

Results

Among the 373 plant species sampled in this study, dispersal syndromes were classified for 295 species found in APF, 50 in NR, and 19 present in both environments (Fig. 2).

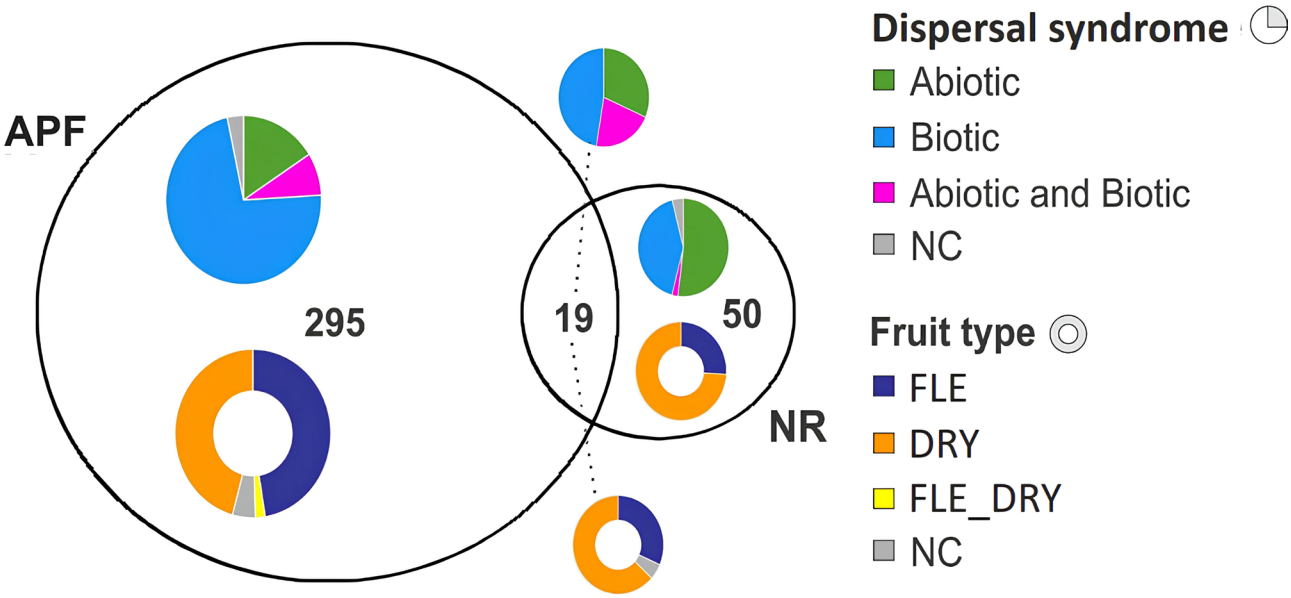

Figure 2. Number of plant species present in the studied environments and their respective proportions according to dispersal syndrome and type of fruit. NR = Natural Regeneration; APF = Altered Primary Forest; FLE = Fleshy fruit; DRY = Dry fruit; FLE_DRY = Fleshy and/or dry fruit; NC = Not classified.

The PCoA ordination based on species composition showed a clear distinction between APF and NR areas (Fig. 3A). The first two axes together accounted for 50.21 % of the variance in species abundance. This differentiation between environments was confirmed by PERMANOVA, which indicated that species composition differed significantly between APF and NR ($F = 8.53$, $R^2 = 0.348$, $p = 0.001$). However, multivariate dispersion also differed between the two environments (betadisper ANOVA: $F = 33.14$, $p < 0.001$), with NR exhibiting greater within-group variation. These results suggest that differences in community composition may be partially influenced by greater heterogeneity in species distribution within natural regeneration areas.

In addition, the PCA ordination based on summary-level variables per sampling area (*i.e.*, species richness and the abundance of dispersal syndrome types) showed that APF areas had a higher abundance of species with biotic dispersal syndromes and were associated with higher species richness, whereas NR areas were predominantly associated with abiotic dispersal syndromes. The first principal component (PC1) captured 55.4 % of the total variance (eigenvalue = 4.99), while the second axis (PC2) accounted for 19.3 % (eigenvalue = 1.74), summing to 74.7 % of the total data variability (Fig. 3B). No overlap between the two environments was observed using centroid buffers in the PCA, suggesting distinct groupings according to the summary variables. The longest vectors in the biplot (R = richness, BIO, ABI_BIO, and ABI) indicated that the richness and abundance of species classified within each dispersal syndrome category were important variables to distinguish the two environments (Fig. 3B).

For species classified under abiotic dispersal syndromes, sampling areas from NR showed higher abundance compared to APF (estimate = 0.71, $p = 0.047$, Poisson-GLMM), but a 0.18-fold lower richness (estimate = -1,70, $p < 0.001$, Poisson-GLM). For species with biotic dispersal syndromes, abundance (estimate = –0.70; $p < 0.001$; Poisson GLMM) and richness (estimate = -3.03, $p < 0.001$, Negative binomial - GLMM) were lower in NR plots compared to APF. For species classified as both abiotic and biotic, no significant difference in abundance was found between environments (estimate = –0.34; $p = 0.231$; Negative Binomial GLMM). However, NR showed fewer species classified both as abiotic and biotic than APF (estimate = -1.91, $p < 0.001$, Poisson-GLM). Absolute values are available in Table S1.

Although the absolute abundance values differed between the two environments with respect to the dispersal syndrome, when we evaluated the proportion of individuals in each category, APF and NR had a similar proportion of individuals with ANE syndrome ($p = 0.99$, pairwise contrasts from a beta-binomial GLMM). Despite the lack of significance ($p = 0.71$ for ZOO and $p = 0.41$ for BAR_ZOO, pairwise contrasts from a beta-binomial GLMM), the effect analysis through the confidence interval showed that the proportion of ZOO and BAR_ZOO plants (biotic syndrome) in layer 1 of the NR areas was higher than the average proportion observed in the APF areas (Fig. 4A). A result contrary to that observed with the absolute abundance value (Fig. 3). A significant difference in the proportion of dispersal syndrome was observed in layer 3. The NR showed 30 % more specimens of autochoric syndrome than APF ($p = 0.036$), and on average, 20 % fewer plants of zoochoric syndrome ($p < 0.001$) (Fig. 4C).

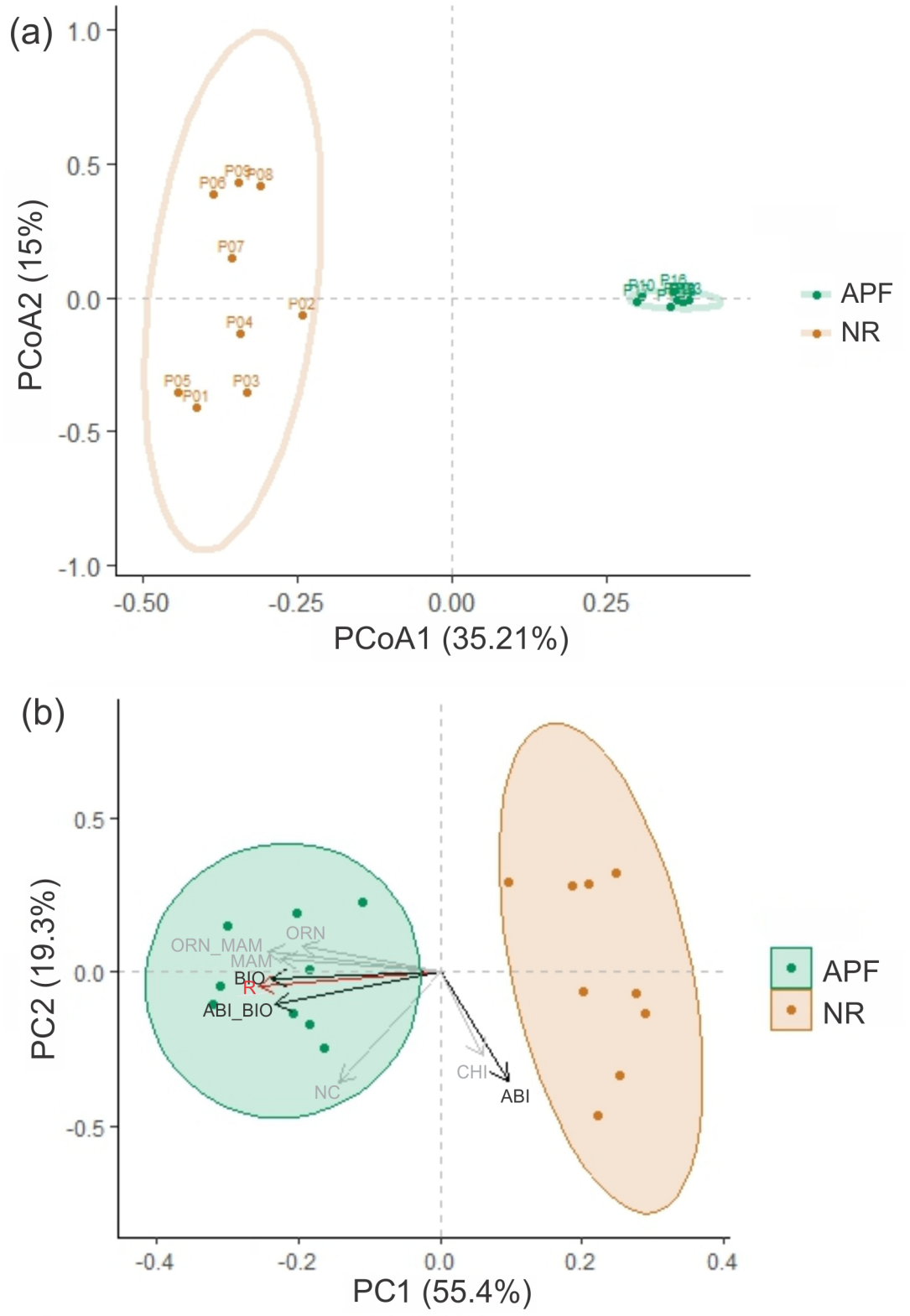

Figure 3. Spatial ordination of sampling areas across two environments, Altered Primary Forest (APF) and Natural Regeneration (NR). (A) Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarity of species abundance matrix. (B) Principal Component Analysis (PCA) biplot based on summary variables, including species richness and the abundance of different dispersal syndrome types per sampling area. The PCA was based on standardized (scaled) variables using scaling = 2. Points represent the sampled areas. Black arrows show the variables of dispersal syndrome. Gray arrows indicate the "zoochory dispersal". BIO = Biotic; ABI = Abiotic; ABI_BIO = Abiotic and biotic; MAM = Mammaliocoria; ORN = ornithochory; CHI = Chiropterochory; NC = not classified; R = richness.

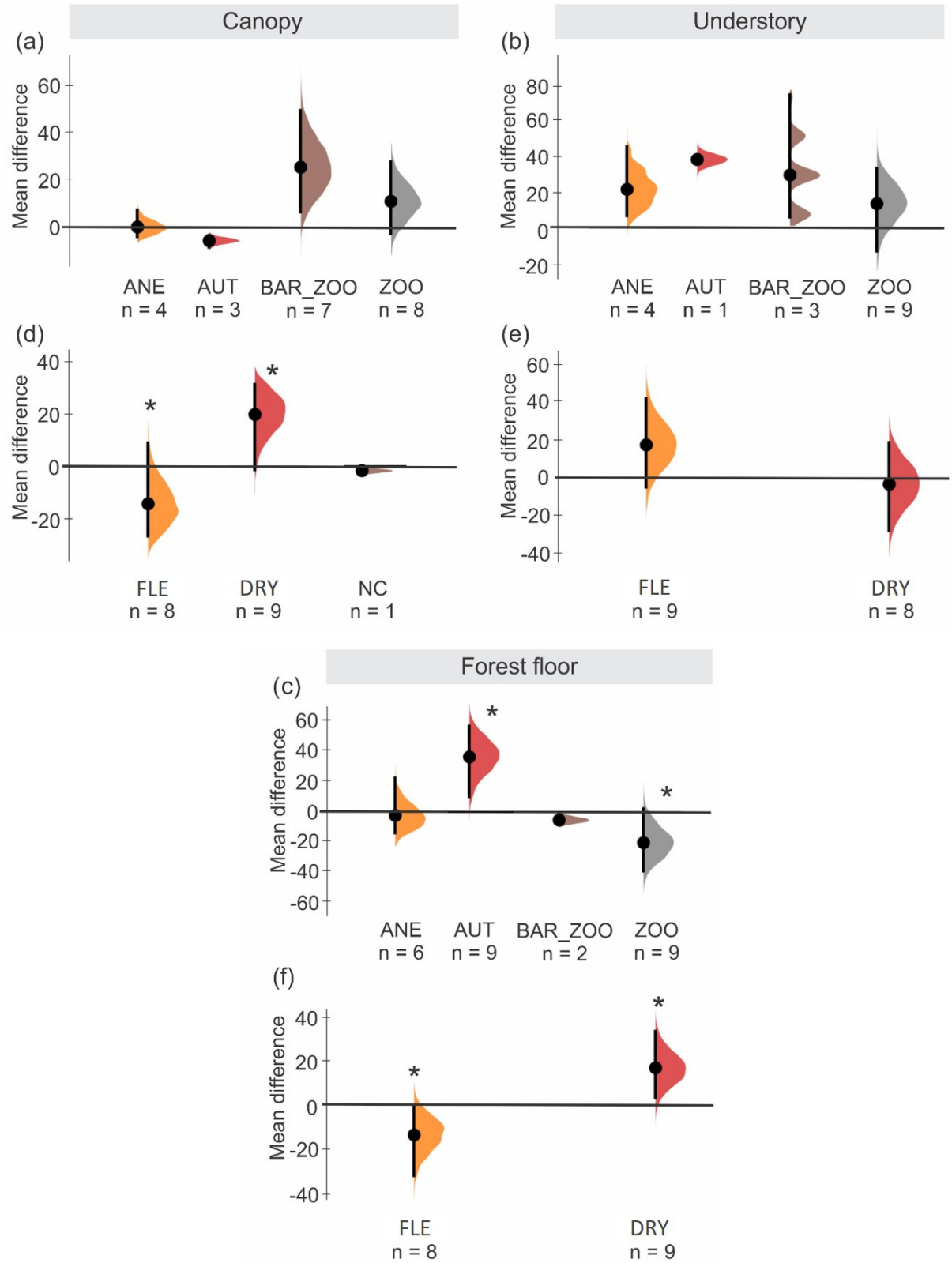

Figure 4. Mean difference between the proportion of plants distributed in dispersal syndrome and fruit type between Altered Primary Forest and Natural Regeneration areas. The vertical black line represents the reference value for APF for each dispersal syndrome or fruit type. Values above the black line indicate higher proportions in NR, while values below indicate higher proportions in APF. Relative abundance of the most common dispersal syndrome in the following forest layers: (A) canopy; (B) understory; (C) forest floor. Relative abundance of fruit type in the following forest layers: (D) canopy; (E) understory; (F) forest floor. * $p < 0.05$. ANE = Anemochory; AUT = Autochory; BAR = Barochory; ZOO = Zoochory; FLE = Fleshy fruit; DRY = Dry fruit; NC = Not classified.

Considering the proportion of individuals classified by fruit type, on layer 1 (canopy), NR showed 10 % fewer plants with fleshy fruits (p = 0.02) and 20 % more plants with dry fruits than APF (p = 0.006) (Fig. 4D). On layer 2 (understory), the proportion of individuals with fleshy fruits (p = 0.55) and with dry fruits (p = 0.99) was similar between the two environments (Fig. 4E). The same trend observed in layer 1 (canopy) was observed in layer 3 (forest floor) (Fig. 4F).

The species abundance within APF plots was distributed differently according to the dispersal syndrome and fruit type (Fig. 5A). In terms of dispersal syndrome, ANE_ZOO, AUT_HYD, NC, and ZOO_AUT had lower abundance than the ANE dispersal syndrome (reference level), while BAR_ZOO and ZOO showed higher abundance. No difference in the abundance of species by fruit types FLE and DRY was observed in the APF. However, species with fruits classified as FLE_DRY and the NC showed lower abundance than the FLE fruits (reference level) and other fruit types. Differently, in the NR areas, the abundance of species with AUT, BAR_ZOO, and ZOO dispersal syndromes increased when compared with the abundance of species of ANE dispersal syndromes (Fig. 5B). Nonetheless, in NR areas, the abundance of DRY fruits increased compared to FLE fruits.

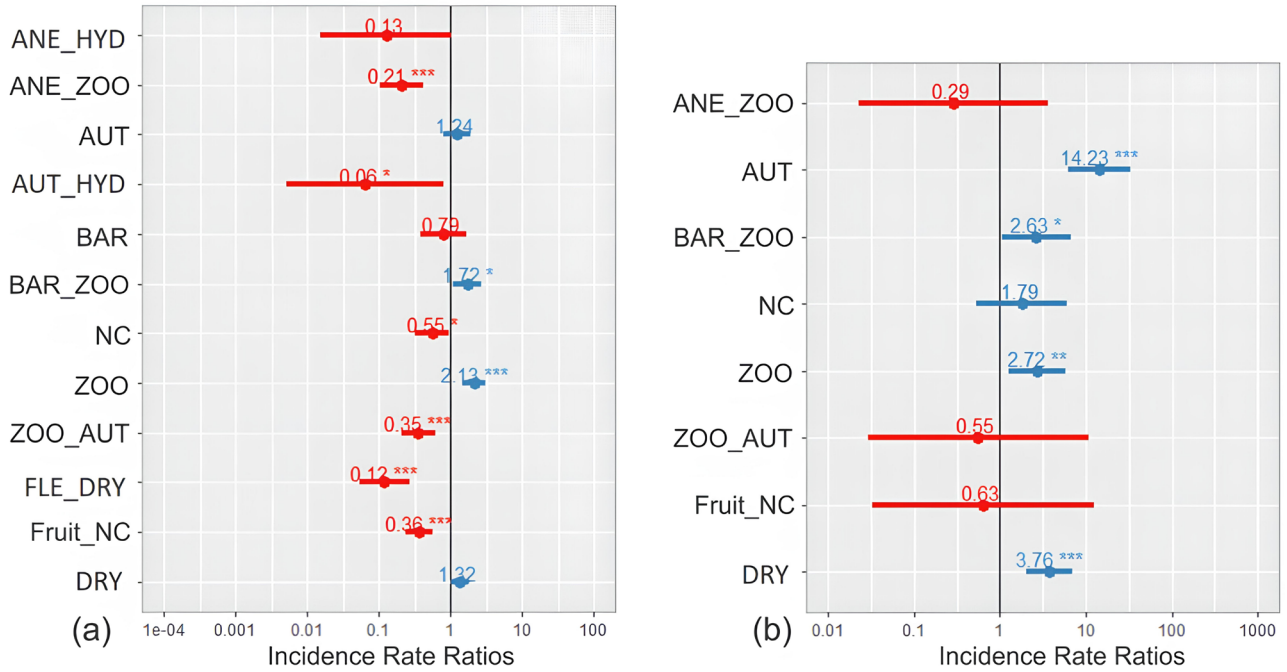

Figure 5. Incidence rate ratios from GLMMs showing the total abundance of species classified within each dispersal syndrome category and fruit type. Incidence Rate Ratios indicate the coefficient of reduction (red values) or increase (blue values) on abundance value using the abundance of anemochory syndrome as reference (vertical black line). (A) Altered Primary Forest; (B) Natural Regeneration. * p < 0.05; ** p < 0.01; *** p < 0.001. ANE = Anemochory; AUT = Autochory; BAR = Barochory; HYD = Hydrochory; ZOO = Zoochory; FLE = Fleshy fruit; DRY = Dry fruit; NC = Not classified.

Discussion

The study's results reveal significant insights into how different environments influence the composition and abundance of plant species, particularly regarding dispersal mechanisms. The clear distinction between APF and NR areas suggests that environmental changes, such as forest degradation, can affect not only the species present but also the strategies they use to disperse their propagules.

Although PERMANOVA detected compositional differences between environments that were statistically significant, the test for homogeneity of dispersion (betadisper) included in the analysis determined greater variation in the natural regeneration group. This result suggests that part of the compositional difference observed can be explained by greater heterogeneity in these sampling areas, possibly due to more variable successional processes or habitat conditions between regenerating forests. The NR areas, although they present the same restoration technique, have different distances from the forest matrix and, consequently, from a possible dispersing and pollinating fauna, which we suggest can be assisted as a facilitator in the regenerative process of the trained sites (Chazdon *et al.*, 2009). Fenner (1985) also notes that areas with developed vegetation and greater complexity attract a diversity of birds, thus accelerating the entry of seeds from this source into the area.

The predominance of species with biotic (zoochoric) dispersal syndromes in APF areas indicates that these environments still maintain characteristics that favor interactions with dispersing animals, which may be crucial for maintaining local and regional diversity. Conversely, the greater abundance of species with abiotic syndromes in NR may reflect an adaptation to distinct regeneration conditions, where wind dispersal becomes more prevalent. The same trend was observed in the study of Carvalho (2010), who compared the proportions of dispersal syndromes of propagules between secondary and preserved ombrophilous forests, and concluded that the areas differed significantly in the richness and density of species with biotic dispersal. Hawes *et al.* (2020) classified the dispersal mode and seed size of material from regenerating secondary forests and disturbed primary forests affected by burning and selective extraction in Pará. These authors found that disturbance reduced species diversity, increased the number of tree species with small seeds, and those consumed by animals, while reducing those dispersed by other mechanisms, such as wind.

Species with fleshy fruits were more abundant in APF areas, mainly in the canopy and forest floor, while species with dry fruits predominated in NR areas, also in the canopy and forest floor. Animals are responsible for dispersing the vast majority of plants within communities, differing in the quantity and quality of dispersal, as well as in the form and distance over which the seeds can travel from the source (Brockelman *et al.*, 2022). Zoochory plays a structuring role in tropical forests, allowing the movement of propagules away from conspecific adults and influencing the maintenance and richness of species in the seed bank (Valenta & Nevo, 2020). Furthermore, most trees in tropical forests produce fleshy fruits intended for consumption by animals (Sinnott-Armstrong *et al.*, 2022). Thus, these factors likely contributed to the richness and abundance of fleshy fruits in altered primary forest areas. However, frequent disturbance environments, such as NR areas, generally present a greater dominance of ruderal plant species (R-strategy), as this ecological strategy facilitates the expansion of the distribution area of these species (Liao *et al.*, 2021). Because they exhibit several traits that enhance their survival and rapid spread, these species are considered highly efficient seed producers and dispersers, with typically small and light seeds characteristic of dry fruits (Carvalho, 2013).

As expected, species with fleshy fruits exhibit zoochory as the primary dispersal mechanism. However, species with dry fruits also showed zoochory as the primary dispersal mechanism, with autochory and anemochory exhibiting similar but lower values. These results align with those found by Silva Júnior *et al.* (2020) when comparing dispersal syndrome patterns in three types of forests in the Amazon region, where 72 % of the species analyzed exhibited zoochoric dispersal syndrome and 14.5 % exhibited autocoric dispersal syndrome. Species with zoochoric dispersal, in theory, have fewer chances of having their diaspores dispersed randomly (Giehl *et al.*, 2007), and zoochory is described as the primary dispersal syndrome found in various studies related to dispersal in the tropics (Carvalho, 2010; Beaune *et al.*, 2013; Silva Júnior *et al.*, 2020). This pattern may be related to the long distance reached by propagules dispersed by animals such as birds, mammals and invertebrates, whether through the digestive tract (*i.e.*, being regurgitated or expelled through feces) or attached outside of the animal's body (*i.e.*, exochory or epizoochory), which can reach up to 10 km (Roth, 1987; Corlett, 2009).

In NR areas, species with anemochory as their main dispersal syndrome were mostly related to dry fruits, while in APF areas, anemochory was not significantly related to dry fruits. Wind-dispersed species tend to produce small fruits and morphological appendages (wings, feathers, etc.) to facilitate the dispersal process (Seale & Nakayama, 2020). These species easily colonize disturbed habitats, as they do not depend on the presence of dispersers, but rather on the amount of wind and the efficiency of their dispersal appendages (Bacles *et al.*, 2006). According to Vieira *et al.* (2002), anemochoric species are more important in open areas, which may influence the fact that NR areas have a higher number of species with this type of dispersal.

Species dispersed by two mechanisms were observed in both environments analyzed, especially in APF areas, mostly related to species in the Lecythidaceae family. More than one dispersal mechanism can operate simultaneously or sequentially for certain plant species (Howe, 2016), which is commonly observed in species with large fruits. Plants with large fruits tend to have barochory as the primary dispersal mechanism and zoochory as secondary (Santos *et al.*, 2024). This is the case for some species in the Lecythidaceae family, where the fruits or seeds initially fall from the mother trees and are later carried and buried by small rodents in various locations in the forests, thus increasing the dispersal distance and allowing the development of these propagules (Vilela *et al.*, 2012; Cerqueira *et al.*, 2021).

Species with fruits of the berry, drupe, capsule, and legume types were the most commonly recorded in APF areas, while species with fruits of the capsule, berry, achene, and caryopsis types were the most commonly recorded in NR areas. The difference between the fruit types recorded in APF and NR areas is likely related to the particular characteristics of the sampled environments. Hawes *et al.* (2020) found that fruits of the berry, capsule, and drupe types differ significantly between the fragments studied at different successional stages in the northwest of Pará state. The authors found that in more disturbed areas (plots in disturbed forests), compound fruits (such as those from the Moraceae, Siparunaceae, and Urticaceae families) and syncarpous (such as those from the Annonaceae family) predominated, while in these environments, fruits of the berry and capsule types were reduced.

Among the 50 species recorded in NR areas, those from the Asteraceae, Urticaceae, and Poaceae families made up a representative fraction of the collected plants. These families are characterized by fruits of the achene and caryopsis types, commonly found in open environments with drier climates (Judd *et al.*, 2009). Preserved areas are characterized by a closed canopy and shaded understory, providing a humid microclimate with lower temperatures, favorable to fleshy fruits due to high water availability (Jara-Guerrero *et al.*, 2011). In contrast, degraded areas have a dry and hot climate due to reduced vegetation cover and increased solar incidence, accelerating the dehydration of dry fruits and the opening of their diaspores (Kuhlmann & Ribeiro, 2016). Furthermore, changes in land use (*e.g.*, mining) lead to significant changes in the physical, chemical, and biological characteristics of the soil, influencing the quality and quantity of fruit resources (Carvalheiro *et al.*, 2021), which may explain the different patterns of fruit types recorded between the NR and APF areas.

Zoochory was the most frequent dispersal syndrome, both in APF areas and in NR areas, with fleshy fruits (berry and drupe) being the most frequent in APF areas and dry fruits (capsule, achene, and caryopsis) in NR areas. These differences in dispersal modes between APF and NR areas are within the patterns already expected and previously found in other studies on fruit dispersal. Dry fruits exhibited zoochory, autochory, and anemochory as the main dispersal syndromes. Furthermore, NR areas contain a greater number of species with abiotic dispersal mechanisms (*i.e.*, anemochory and autochory) and dry fruits. This type of vegetation formation exhibited a greater diversity of dispersal syndromes than altered primary forest areas. This suggests that species developing in disturbed areas have more strategies for their dispersal, whereas less disturbed areas favor the dispersal of fleshy fruits by animals, reinforcing the relative importance of these fruits in forest areas.

In conclusion, this work demonstrates the importance of understanding how species composition and dispersal strategies are influenced by environmental conditions and anthropogenic impacts to which they are subjected. Furthermore, the study allows us to assess which dispersal mechanisms are best adapted to degraded environments under strong anthropogenic pressure. This knowledge can enable more effective implementation of recovery strategies, for instance, by prioritizing the planting of species with similar dispersal mechanisms for the colonization and subsequent restoration of degraded areas, especially in areas impacted by mining.

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Supplementary Material

The following online material is available for this article:

Table S1 – Richness and abundance of species present in the APF and NR areas of the mining company Hydro, Paragominas, Pará, according to the dispersal mechanism, fruit type, and dispersal syndrome. The values in parentheses correspond to the percentage (%).

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Authors' Contribution

The conceptualization, supervision, and management of the research project were carried out by Marlúcia B. Martins and Roberta M. Cerqueira. Data collection and the first version of the manuscript were done by Fabiane Barral Sampaio and Roberta M. Cerqueira. Data analysis was conducted by Rafaela Tadei and Claudia I. Silva. The text translation and final revision were done by Matheus Marques Bitencourt. All authors contributed to the writing, read, and approved the final manuscript.

Conflicts of Interest

We declare that we have no conflict of interest (personal, scientific, commercial, political, or financial) in the submitted manuscript.

Data Availability

Datasets related to this article will be available upon request to the corresponding author.

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