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RESEARCH ARTICLE

Landscape features predict broad-scale seed rain patterns across fragments of the Brazilian Atlantic Forest

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Abstract

1. The seed rain, that is, the flux of seeds landing on a given location, is a fundamental ecological process driving community assembly and forest regeneration. Because seed rain studies usually focus on a particular site, the influence of

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landscape features—such as deforestation and fragmentation—on seed dispersal remains poorly understood at the broad scale.

2. We investigated how patch size, forest cover, number of patches, precipitation and latitude influence seed rain parameters (proportion of zoochorous species, seed density, species richness and within-site spatial turnover) spanning a latitudinal gradient from 7°S to 29°S in a highly fragmented global biodiversity hotspot: the Brazilian Atlantic Forest. This is the first study to synthesize seed rain patterns across such a large extent.
3. We compiled a database from 1905 seed traps in 52 study patches. Over 1.3 million seeds were sampled and 1029 taxa were identified to at least the family level.
4. Total precipitation and forest cover were the most important predictors for the proportion of zoochorous species. Seed density increased with the number of patches (fragmentation) for both zoochorous and non-zoochorous species. Species richness and turnover were strongly predicted by forest cover; therefore, increasing with habitat amount, especially in sites with higher precipitation levels.
5. *Synthesis*. Along with precipitation, forest cover emerges as a fundamental driver of alpha and beta diversity in the seed rain. This highlights the role of habitat amount at the landscape level over patch-level features, like patch size, for seed dispersal. However, increased seed density can be related to higher dispersal rates in forest borders. Understanding these drivers of seed rain can help predict forest regeneration trajectories that shape the future configuration of fragmented landscapes.

KEYWORDS
Atlantic Forest, broad-scale patterns, dispersal modes, landscape metrics, macroecology, species richness, turnover

1 | INTRODUCTION

Forest regeneration demands the coupling of seed-dispersal and seedling-establishment processes (Hampe et al., 2008; Howe & Miriti, 2004; Schupp & Fuentes, 1995), which drive plant recruitment, gene flow and community assembly (Beckman & Sullivan, 2023; Howe & Smallwood, 1982; Rogers et al., 2019). The assembled communities and the successional pathways that emerge are largely driven by landscape context, including landscape composition and configuration, as well as previous land-use history (Arroyo-Rodríguez et al., 2017; Martínez-Ramos et al., 2016; Mesquita et al., 2015). These factors, therefore, shape forest regeneration, as well as the environmental conditions (such as temperature and precipitation) under which succession unfolds (Nepstad et al., 1996).

The seed rain (i.e. the flux of seeds landing on a given location) is composed of seeds shed from trees overhead, as well as those disseminated from distant sources, arriving via zoochorous (animal-dispersed) and non-zoochorous dispersal agents (Levin et al., 2003; Nathan & Muller-Landau, 2000). At the patch level, the seed rain tends to show higher species richness (i.e. alpha diversity) as the size of forest patches increase (Freitas et al., 2013; Knörr & Gottsberger, 2012) and forest canopies close (Acosta-Rojas et al., 2023). At the landscape level, forest cover—a proxy for habitat amount—is a strong predictor of successful successional trajectories, that is, that do not result in alternative, stagnant, undesirable states (Arroyo-Rodríguez et al., 2023). In contrast, the seed rain in small and isolated forest patches often show higher abundances of dominant pioneer species (Jesus et al., 2012), which are typically small-seeded (Tabarelli et al., 2010), maintaining these fragments as showing initial successional features (Pütz et al., 2011).

Thus, highly fragmented and deforested landscapes with reduced diversity, low forest cover and/or increased edge effects can be dominated by virtually identical suites of pioneer species, resulting in floristic homogenization (Arroyo-Rodríguez et al., 2013; Lôbo et al., 2011). In a practical sense, we would have a low species replacement among sampling units (low spatial turnover), which is a component of beta diversity according to Baselga's partitioning approach (Baselga, 2010). Low spatial turnover in the seed rain may occur due to two contrasting features: (1) low species richness or (2) high activity of dispersal agents that mix seeds among sites. Hence, when dispersal agents are present, they spatially spread the seeds, thereby tending to homogenize species composition in regenerating communities (Wandrag et al., 2017).

Tropical forests are predominantly composed of zoochorous species, as warm and moist environments provide plants with plentiful resources to produce fleshy fruits that attract birds and other vertebrates (Almeida-Neto et al., 2008; Chen et al., 2017; Correa et al., 2015). Reciprocally, the proportion of non-zoochorous species, including anemochorous and autochorous dispersal, increases in cooler and drier environments, such as mountain tops (Buitrón-Jurado & Ramírez, 2014; Chapman et al., 2016). Although large latitudinal and altitudinal gradients have been used to characterize dispersal mode across sites, such data have been mostly drawn from standing community surveys (Almeida-Neto et al., 2008), rather than from seed trap samplings. In fact, seed rain studies in the Neotropics commonly focus on a single forest patch (Capellesso et al., 2015; Melo et al., 2006; Perini et al., 2019; Rother et al., 2009; Silva et al., 2018; Zimback et al., 2023) or on different forest patches within a study site (Freitas et al., 2013; Jesus et al., 2012; Knörr & Gottsberger, 2012; Marques & Oliveira, 2008). This limits our understanding of how the interactions between climate and landscape features drive seed rain patterns at the broad (continental) scale, or how a region's evolutionary and land-use history mould the successional pathways promoted by seed dispersal.

The Atlantic Forest is one of the most deforested, fragmented and overexploited tropical forests (de Lima et al., 2024). It originally covered between 1.01 and 1.62 million km^2, extending from the northeastern to southern Brazilian coast (spanning approximately 30° of latitude) and into parts of Argentina and Paraguay (Marques et al., 2021; Muylaert et al., 2018). Currently, the conservation status of the Atlantic Forest is critical, with only ~23% of its original forest cover remaining (Vancine et al., 2024), mostly in isolated patches smaller than 50 ha (Ribeiro et al., 2009). Due to its immense biodiversity and the severe threats from rapid habitat loss and the erosion of ecosystem services, this tropical forest is recognized as a global hotspot for biodiversity conservation (Mittermeier et al., 2011; Myers et al., 2000; Ribeiro et al., 2011) and a priority for forest restoration (Brancalion et al., 2019; Rezende et al., 2018; Strassburg et al., 2020).

Contrary to the classical richness-latitude gradient, tree species richness is lower in the northern and southern regions of the Atlantic Forest, and peaks in the mid-portion of the biome, from São Paulo to Bahia (Zwiener et al., 2020). Moreover, the vast latitudinal gradient of the Atlantic Forest results in contrasting north–south temperature patterns and an east–west variation in precipitation (Cruz et al., 2009; Figure 1). Given the available data from multiple seed rain studies and the ubiquity of forest fragmentation throughout this extensive vegetation domain, the Atlantic Forest is an ideal model to evaluate the combined role of landscape features and climate variables in shaping seed rain parameters in fragmented tropical forests.

In the present study, we compiled seed rain data from 52 forest patches across the Atlantic Forest in Brazil to investigate how patch size, forest cover, number of patches, precipitation and latitude affect seed rain patterns across a high latitudinal gradient. Specifically, we addressed the following questions: (1) What is the main driver of seed rain parameters related to dispersal mode, including the proportion of zoochorous species and seed density per dispersal mode—local (patch), regional (landscape) or broad (climatic) scale features? Which of those features better explain alpha and beta diversity patterns (species richness and turnover) across the landscape? We expect the relative proportion of zoochorous species to be strongly influenced by climate variables, as the occurrence of fleshy fruits increases with precipitation (Almeida-Neto et al., 2008). We also expect seed density to be greater in more fragmented patches, due to a higher dispersal rate in forest borders (Knörr & Gottsberger, 2012; Tabarelli & Peres, 2002), which may also depend on forest cover and connectivity. Finally, we anticipate an increase in species richness with patch size and forest cover, showing a negative relationship with deforestation (Costa et al., 2012; Melo et al., 2006). The loss of large-bodied frugivores in fragmented landscapes can jeopardize the dispersal of zoochorous large-seeded species (Bello et al., 2015; Fricke et al., 2025; Galetti et al., 2013; Marjakangas et al., 2020; Rogers et al., 2021). Therefore, fragmented areas are likely to show a decrease in species turnover, leading to floristic homogenization as a result of low species diversity.

2 | MATERIALS AND METHODS

2.1 | Database compilation

We assembled a database containing information on seed rain studies conducted across a large latitudinal gradient in the Atlantic Forest (latitudes from 7°S to 29°S) between 1987 and 2021. The studies were primarily compiled from three major scientific databases: the Brazilian Bank of Thesis and Dissertations (https://catalogodeteses.capes.gov.br/), Web of Science and Scopus. From this initial pool of studies, we gathered the raw data from 52 study patches (provided by their respective data owners). Vegetation within the study patches encompassed closed-canopy, well-established rainforest and seasonal forests ('forest formations', MapBiomas class 3; see https://mapbiomas.org/). We also included the arboreal *restinga* ('wooded sandbank vegetation', MapBiomas class 49; see Vancine et al., 2024), which shows a closed canopy and woody vertical structure, functionally working as a forest formation. Studies conducted in open systems, planted areas, restoration/management projects or focusing exclusively on a single dispersal mode (e.g. only zoochory) were not considered.

We organized the datasets for all patches with each row representing a seed trap, each column a study species (or morphospecies) and each cell containing the number of seeds found per trap for each species. Additionally, for each patch, we had GPS coordinates, number

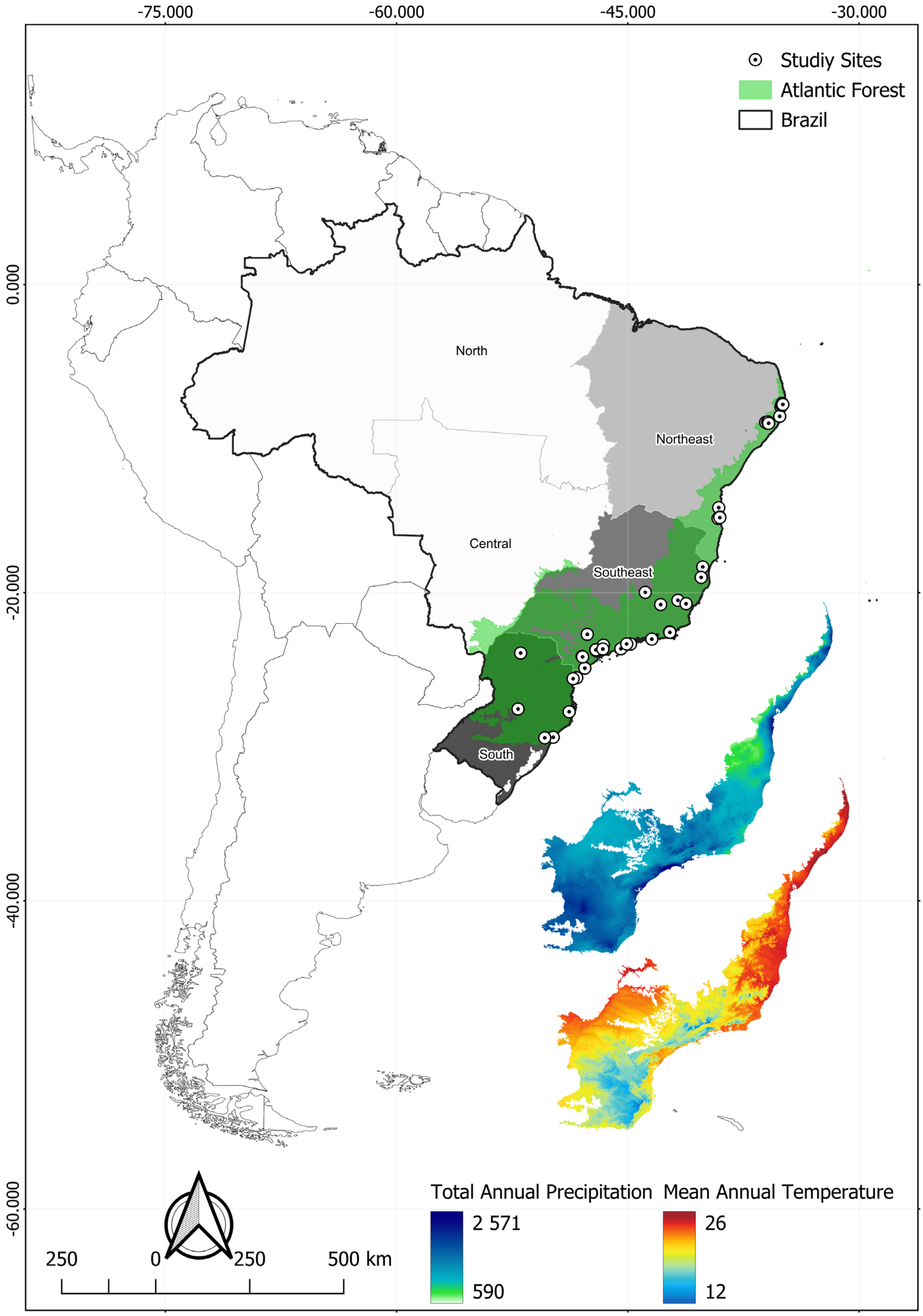

FIGURE 1 Distribution of study patches where seed rain data was collected across the Brazilian Atlantic Forest.

of traps used, trap size (m^2) and total sampling duration (months). Most studies focused on a single forest patch, but in cases where multiple patches were sampled in a larger study site (e.g. Freitas et al., 2013; Jesus et al., 2012; Knörr & Gottsberger, 2012), we ensured that each forest patch had its own specific patch size and other landscape spatial features for use in the analyses (see Figure 1; Table S1).

2.2 | Proportion of zoochorous species and seed density per dispersal mode

We considered two dispersal mode categories: zoochorous (Zoo, animal-dispersed species) and non-zoochorous (Non-Zoo, wind-+self-dispersed species). Because the proportions of these classes in the communities are essentially reciprocal of each other, we evaluated only the proportion of Zoo species in the analysis. For seed density, however, we evaluated both dispersal modes separately. Only the patches where at least 50% of the species were identified to at least the family level (i.e. 41 patches; see Figure S1) were included in the proportion of Zoo species and seed density calculations. Moreover, the proportion of Zoo species was calculated by pooling the data from the total number of identified taxa within each patch, resulting in a single adjusted per-patch value for this metric. We determined seed density per dispersal mode for the same subset of patches (see below). Because trees represented ~80% of species across patches (Figure S2), the type of growth form (trees, shrubs, lianas, herbs) was not included in the analyses.

Dispersal mode data was obtained from the TreeCo Project (Neotropical Tree Communities database) for 703 identified species across all compiled studies (de Lima et al., 2020). For an additional 400 taxa, including IDs at species, genus and family level, we surveyed the literature to determine their dispersal mode. These classifications were made according to van der Pijl (1982), categorizing the taxa as Zoo for species with fleshy fruits or arylated seeds, attractive to the fauna and as Non-Zoo when they showed winged diaspores, fruits with palps or fruits/seeds lacking specialized dispersal structures. Taxa identified only to family level were generally assigned as 'undetermined'. Exceptions were made for morphospecies from the Myrtaceae and Lauraceae families, which typically bear zoochorous fleshy fruits in the Neotropical region, for which we assigned a Zoo dispersal mode (Galetti et al., 2011; Gressler et al., 2006; Pizo, 2002).

Given studies varied in the number (9 to 144 traps/study) and size (0.2 to 1.1 m^2) of traps, as well as sampling duration (12 to 36 months, with a single exception sampled for only 6 months, see Table S1), we calculated seed density as the number of seeds per square meter, obtained as the total number of seeds divided by the total trap area in each study patch. Although some studies may have counted fruits or fruit parts as 'seeds', which could lead to slight underestimation of absolute seed density, we consider this metric generally reliable for estimating the number of seeds captured per sampling unit. This value was standardized per sampling duration time (months)—so the final metric for seed density was assessed as $N_{seeds}\ m^{-2}\ month^{-1}$.

2.3 | Species richness and turnover

Due to the differences in the number and size of sampling units (traps) among studies, we estimated species richness by standardizing the sampling effort at each site to an equal level of completeness (or coverage, see Chao et al., 2020; Roswell et al., 2021). Sampling completeness was established based on the asymptote/stabilization of species accumulation curves, extrapolating the point at which sites were sufficiently sampled. To achieve this, we used species incidence data to plot rarefaction and extrapolation curves, estimating sample completeness from the frequency of rare species to ensure a similar base coverage level across all study patches (97.5%; see Chao et al., 2014). Species richness ($q=0$) for each study patch was then obtained using the *estimateD* function from the *iNEXT* package (Hsieh et al., 2016), following the 'true' diversity framework of (Jost, 2007).

Given the differences in experimental design and taxonomic precision of species identification across studies, we assessed spatial turnover (beta diversity) by calculating species replacement among traps only *within* each forest patch. Spatial turnover was calculated using the Sorensen index of similarity with the *beta.multi* function from the *betapart* package (Baselga & Orme, 2012).

2.4 | Patch size and landscape-level metrics

We obtained a patch-level variable (patch size, in hectares), as well as two landscape-level metrics: forest cover (%) and number of patches. All these parameters were extracted using the *landscapemetrics* package (Hesselbarth et al., 2019, 2023). We used the base map of the MapBiomas Collection 8, with a 10 × 10 m per pixel spatial resolution and a Brazilian territory scale of 1:5000 (Souza Jr. et al., 2020). Patch size represents the total area of the study patches and was calculated using the function *lsm_p_area*; directions were set as 8 (queen's case), which indicates the number of directions in which patches could be connected. Forest cover (an indicator of deforestation level) and number of patches (a proxy for fragmentation) represent different aspects of forest composition and configuration (Fletcher & Fortin, 2018; Metzger, 2006). Forest cover is a landscape composition metric, which corresponds to the percentage of cover of a given vegetation class, that is, MapBiomas classes 3 and 49 (see above), thus representing the overall proportion of woody vegetation surrounding each study patch, calculated using the function *lsm_c_pland*. The number of patches is a landscape configuration metric, which consists of a simple counting of the number of forest fragments (patches) at the landscape level, using the same vegetation classes, calculated at the landscape level using the function *lsm_p_np*. We also extracted the data for edge density, which equals the sum of all edges of a given class in relation to the landscape area (m/ha). Nonetheless, because edge density was 85%–94% correlated with the number of patches (Figure S3), we only kept the latter in the final version of the analyses (see Section 2.5 below).

Landscape-level metrics were extracted considering four different buffer sizes (spatial scales of 500 m, 1 km, 2 km and 5 km radius), with the buffer centre set as the centroid of the polygon where the traps were installed at each study patch. Since distinct seed rain parameters might be affected differently by landscape features, we previously tested in separate which buffer size was most strongly related to forest cover and number of patches using model selection based on Akaike Information Criterion (Burnham & Anderson, 2002). The best models were chosen based on the lowest AIC scores and then used in the final statistical models (see Table S2). Because the influence of landscape composition and configuration on ecological processes often varies with spatial extent, this multi-scale approach allowed us to identify the scale at which landscape effects on seed rain patterns were strongest (Martin & Fahrig, 2012).

Finally, we obtained the average of mean annual temperature and the average of total annual precipitation (climate variables) for all study sites. These variables were extracted using the *WorldClim* database (package *geodata*, Hijmans et al., 2023). Because mean temperature varied with the latitudinal gradient (73% of correlation, see Figure S3), we only kept latitude as a covariate in the final statistical models.

2.5 | Data analyses

Generalized linear models (GLMs) were constructed separately for each response variable (proportion of Zoo species, seed density per dispersal mode, total species richness and spatial turnover) using patch size, forest cover, number of patches, precipitation and latitude as predictors. Patch size was log-transformed in the analyses and all predictor variables were standardized using the 'scale' function to improve model convergence. The best buffer sizes explaining the response variables differed: 5 km for both forest cover and number of patches for the proportion of Zoo species; 500 m for both metrics for seed density (Zoo); 500 m for forest cover and 5 km for number of patches for seed density (Non-Zoo); 500 m for forest cover and 2 km for number of patches for species richness; 1 km for both metrics for turnover (Table S2). Seed density was log-transformed for the analysis and modelled assuming a Gaussian distribution. Species richness was modelled using a Gamma error distribution with a log link function, which is appropriate for positive continuous values and accounts for heteroscedasticity through its mean–variance relationship. An ordbeta distribution was used for the proportion of Zoo species and turnover values, which varied between zero and one, allowing for flexible variance and non-normal error distribution. The full models (i.e. for each response variable) included each predictor, as well as plausible interactions between them, with the following structure:

$$
\begin{aligned}
Yi = {} & \beta_0 + \beta_1(\text{patch\_size})_i + \beta 2(\text{forest\_cover})_i + \beta 3(\text{n\_patch})_i \\
& + \beta 4(\text{total. prec})_i + \beta 5(\text{latitude})_i + \beta_6(\text{patch\_size} \times \text{n\_patch})_i \\
& + \beta_7(\text{forest\_cover} \times \text{n\_patch})_i + \beta_8(\text{patch\_size} \times \text{total. prec})_i \\
& + \beta_9(\text{forest\_cover} \times \text{total. prec})_i + \beta_{10}(\text{n\_patch} \times \text{total. prec})_i \\
& + \epsilon_i
\end{aligned}
$$

where Y_i is the response variable, representing the outcome for the *i*-th observation. β_0 is the intercept, representing the baseline value of the response variable when all predictors are zero. β_1(patch_size)$_i$, β_2(forest_cover)$_i$, β_3(n_patch)$_i$, β_4(total.prec)$_i$ and β_5(latitude)$_i$ are the fixed effects (coefficients) of the predictors, with some interactions between them included. Each β represents the strength and direction of the relationship between the predictor and the response variable, while ϵ_i is the residual error or noise, capturing unexplained variation in the response for the *i*-th observation.

Because the full model would likely be overfitted, with too many predictors relative to the number of observations, we reduced model complexity using AIC-based model selection. To do so, we built a series of models considering each variable separately. These models used latitude as a control variable in order to consider the vast extension of the Atlantic Forest in the analyses (patch_size + lat; forest_cover + lat; n_patch + lat; total.prec + lat; latitude). The respective interactions were also considered in separate models, avoiding patch_size × forest_cover due to collinearity; models always included latitude as a control variable (patch_size × n_patch + lat; forest_cover × n_patch + lat; patch_size × total.prec + lat; forest_cover × total.prec + lat; n_patch × total.prec + lat). We also built a null model for comparison. We then conducted AIC model selections and all models with delta (Δ) AIC <2 were considered equally plausible (Burnham & Anderson, 2002). Models were fitted using the package *glmmTMB* (Brooks et al., 2023) and all analyses were conducted using the R software (R Core Team, 2025). To check for collinearity between predictor variables, we checked VIF values (variance inflation factor) and R^2 for the selected models using the *performance* package (Lüdecke et al., 2021). Model predictions for the most plausible models were plotted with *ggeffects* package (Lüdecke, 2018). We also considered the spatial autocorrelation among sampling sites, given some patches were not fully independent—often nested in a given study area. To do so, we calculated Moran's *I* index for the residuals of the selected models using the *ncf* package (Bjornstad & Cai, 2022), and plotted correlograms for each of them across distance classes. Positive Moran's *I* values indicate spatial clustering, while negative values indicate spatial dissimilarities.

3 | RESULTS

Over 1.3 million seeds were sampled across the 52 study patches, including information from 1905 seed traps (Figure 1; Table S1). Approximately 1000 taxa (1029) were identified to at least the family level, 698 of them to species, representing ~100 botanical families.

Total precipitation was the strongest predictor of the proportion of Zoo species (Figure 2; Table 1; see also Table S3). The model with forest cover × precipitation was considered equally plausible, with the proportion of Zoo species also increasing in parallel with forest cover. Latitude had little to no effect on this response variable (Figure 2; Table 1). Residuals of the models for the proportion of Zoo species were mostly spatially unstructured (Figure S4).

Seed density increased with number of patches for both dispersal modes (Figure 3; Table 1; Table S3). Although forest cover alone had a weak effect, its interaction with the number of patches strongly influenced seed density of Zoo species. In other words, this response variable increased in sites with a high forest cover percentage, but mainly in highly fragmented landscapes (i.e. with more patches). Although a few distance classes showed significant Moran's *I* values, the residual correlogram for Zoo species exhibited highly irregular oscillations around zero, without a consistent spatial trend (Figure S5). For Non-Zoo species, seed density tended to decrease with forest cover, being slightly higher in more deforested sites (Figure 3; Table 1; Table S3). Latitude also influenced seed density of Non-Zoo species, which showed higher values towards southern (cooler) patches (Figure 3; Table 1). In contrast, no spatial autocorrelation was detected for the model fitted to Non-Zoo species, indicating that residuals were spatially independent (Figure S5).

Both forest cover and precipitation appeared in the best model explaining species richness (Figure 4; Table 2; Table S4). Basically, species richness increased with higher forest cover and higher precipitation levels. Each predictor individually influenced species richness, whereas their interaction was weak (Figure 4; Table 2). Likewise, species richness increased towards southern patches (more negative latitudes; Figure 4; Table 2).

Spatial turnover increased in patches with higher forest cover, influenced by the interaction between forest cover and precipitation (Figure 5; Table 2; Table S4). Lower turnover values were found in drier sites under low forest cover percentages. Latitude had little to no effect on turnover patterns (Figure 5; Table 2). Residuals of the models were mostly spatially unstructured for both species richness and spatial turnover (Figures S6 and S7).

4 | DISCUSSION

On a broad scale, our study shows how landscape and climate features drive seed rain patterns across the Atlantic Forest, a highly fragmented biodiversity hotspot. Water resource availability strongly influenced the proportion of Zoo species, most likely due to a higher production of fleshy fruits in sites with higher precipitation levels. Such ecological relationships of climatic factors with dispersal mode have been previously identified for vertebrate-mediated dispersal syndromes in standing communities of tropical forests (Almeida-Neto et al., 2008; Correa et al., 2015, 2023). In particular, Almeida-Neto et al. (2008) found that the relative frequency of endozoochory in the Atlantic Forest decreases with increasing distance to the coast, since precipitation declines towards the continent's interior, which is consistent with our findings. Across biomes, the increased presence of Zoo species follows a clear pattern along a dry-to-moist gradient, from semi-arid woodlands (the Brazilian Caatinga) to Atlantic Forest patches (Tabarelli et al., 2003). Such increase is likely associated with the presence of myrtaceous species and other fleshy-fruited families dominant in moist environments

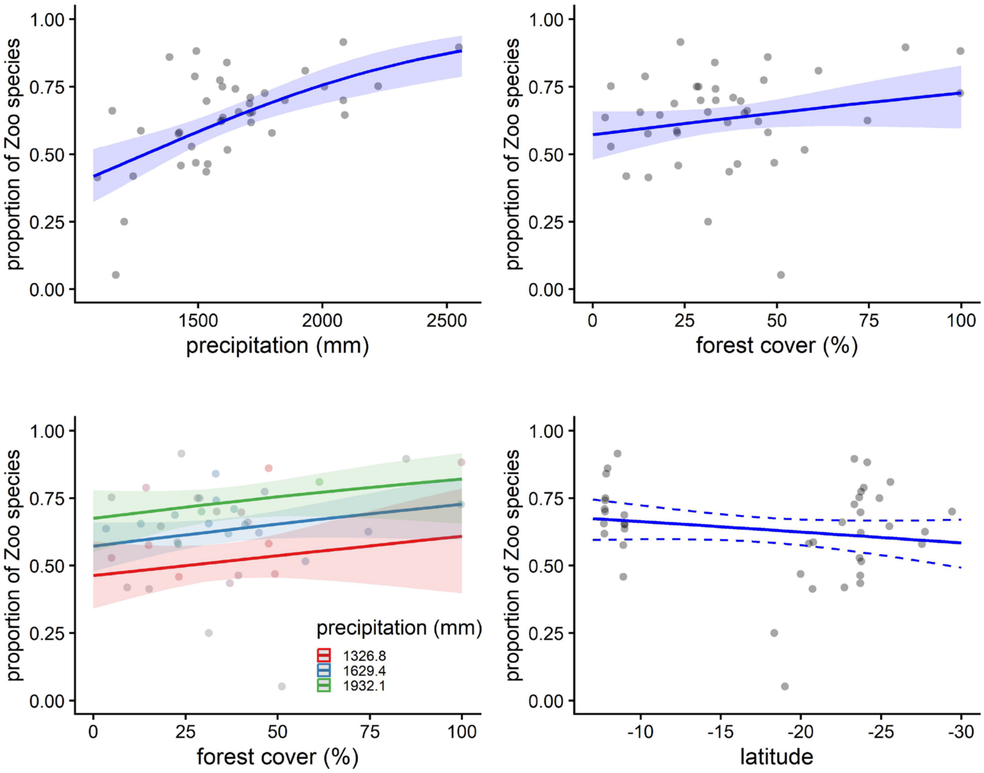

FIGURE 2 Predictions from the best (selected) models for the proportion of zoochorous (Zoo) species, using an ordbeta distribution, across Atlantic Forest patches. Statistical coefficients are detailed in Table 1. For a list of all models and their AIC ranking, see Table S3.

TABLE 1 Statistical coefficients for the best models (ΔAIC <2) predicting the proportion of zoochorous (Zoo) species and seed density per dispersal mode as response variables in GLM models across Atlantic Forest patches.

Response variables	Model ΔAIC	Weight	R^2	Model predictors	Estimate	SE
Proportion of Zoo spp.	0.0	0.565	0.356	Intercept	0.848	0.256
				Precipitation	0.481	0.109
				Latitude	0.017	0.013
	1.6	0.252	0.389	Intercept	0.961	0.258
				Forest cover	0.158	0.103
				Precipitation	0.476	0.108
				Latitude	0.023	0.013
				Forest cover × precipitation	0.023	0.104
Seed density (Zoo)	0.0	0.772	0.299	Intercept	4.130	0.635
				Forest cover	0.337	0.280
				Number of patches	0.958	0.313
				Latitude	0.039	0.033
				Forest cover × number of patches	1.198	0.331
Seed density (Non-Zoo)	0.0	0.242	0.157	Intercept	1.272	0.613
				Number of patches	0.461	0.244
				Latitude	−0.041	0.032
	0.5	0.186	0.146	Intercept	0.761	0.594
				Forest cover	−0.407	0.235
				Latitude	−0.069	0.031
	1.4	0.119	0.083	Intercept	0.916	0.608
				Latitude	−0.060	0.031
	1.6	0.107	0.204	Intercept	0.992	0.626
				Forest cover	−0.283	0.240
				Number of patches	0.343	0.251
				Latitude	−0.058	0.034
				Forest cover × number of patches	0.265	0.384

Note: Zoo = zoochorous dispersal (animal-dispersed species); Non-Zoo = non-zoochorous dispersal (wind- + self-dispersed species). For AIC rankings of all tested models, see Table S3.

(Galetti et al., 2011; Gressler et al., 2006; Pizo, 2002; Smith-Ramírez et al., 1998; Staggemeier et al., 2017).

Given the great extension of the Atlantic Forest, latitude had an effect on seed density of Non-Zoo species, which increased under lower temperatures. For instance, Jesus et al. (2012) registered a greater abundance of anemochorous seeds in small and isolated patches compared to larger forest fragments in southeastern Brazil, where cooler and drier conditions prevail from April to August. This aligns with patterns observed for an increased presence of Non-Zoo species along altitudinal gradients, where higher altitudes are mostly cooler (Acosta-Rojas et al., 2023; Buitrón-Jurado & Ramírez, 2014; Chapman et al., 2016). Seed density of Non-Zoo species also decreased with forest cover, tending to be higher in the more deforested sites. Higher levels of anemochory have been found in open Brazilian savannas compared to woody sites (Escobar et al., 2021), showing that vegetation structure plays a role on seed dispersal.

Seed density increased with fragmentation for both dispersal modes, a pattern likely driven by the dominance of generalist trees along forest borders, typically producing large amounts of seeds that proliferate in fragmented sites (Lôbo et al., 2011; Tabarelli et al., 2010). Besides anemochory, many small-seeded pioneers found in the seed rain in Atlantic Forest patches can be zoochorous (Knörr & Gottsberger, 2012). These fleshy-fruited species that produce many seeds, such as *Ficus* and *Miconia*, act like key resources for frugivores (Messeder et al., 2020), enhancing dispersal rates in fragmented landscapes. However, we show that not only fragmentation drives seed density of Zoo species, but also the combination of a high number of patches with high forest cover. This supports the idea that fragmentation can be a positive factor affecting ecological processes at the landscape level, mainly by increasing connectivity compared to non-fragmented sites with the same amounts of habitat (Fahrig, 2013; Fahrig et al., 2019; Watling et al., 2020). Higher seed densities have been observed along edges of mature forest patches (>40 years old), decreasing into the core patch in relation to the distance from the border (Piotto et al., 2019). Some important pollinators, mostly bees, can be associated with forest

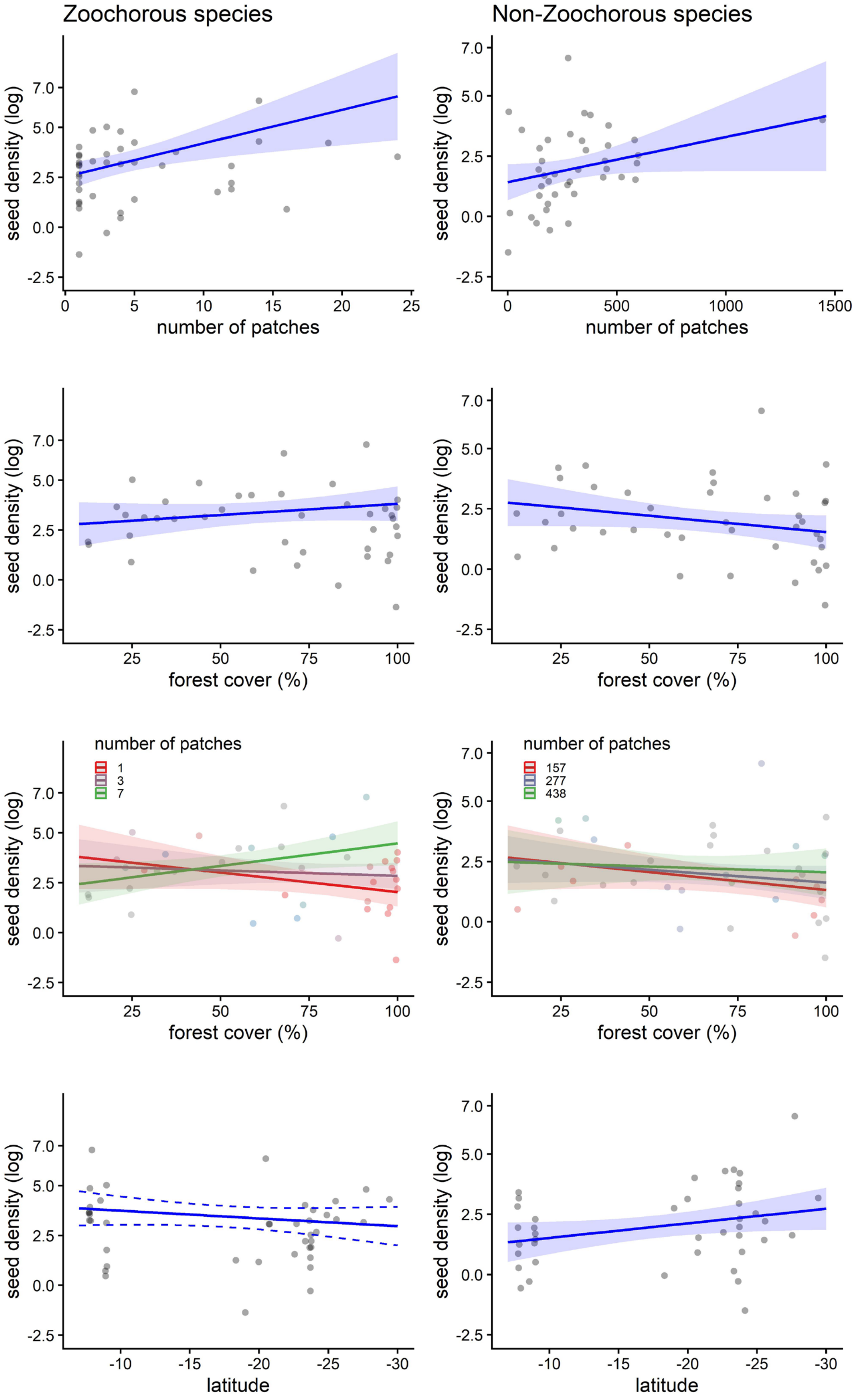

FIGURE 3 Predictions from the best (selected) models for the log of seed density (N_{seeds} m^{-2} $month^{-1}$) per dispersal mode (Zoo and Non-Zoo), using a Gaussian distribution, across Atlantic Forest patches. Statistical coefficients are detailed in Table 1. For a list of all models and their AIC ranking, see Table S3.

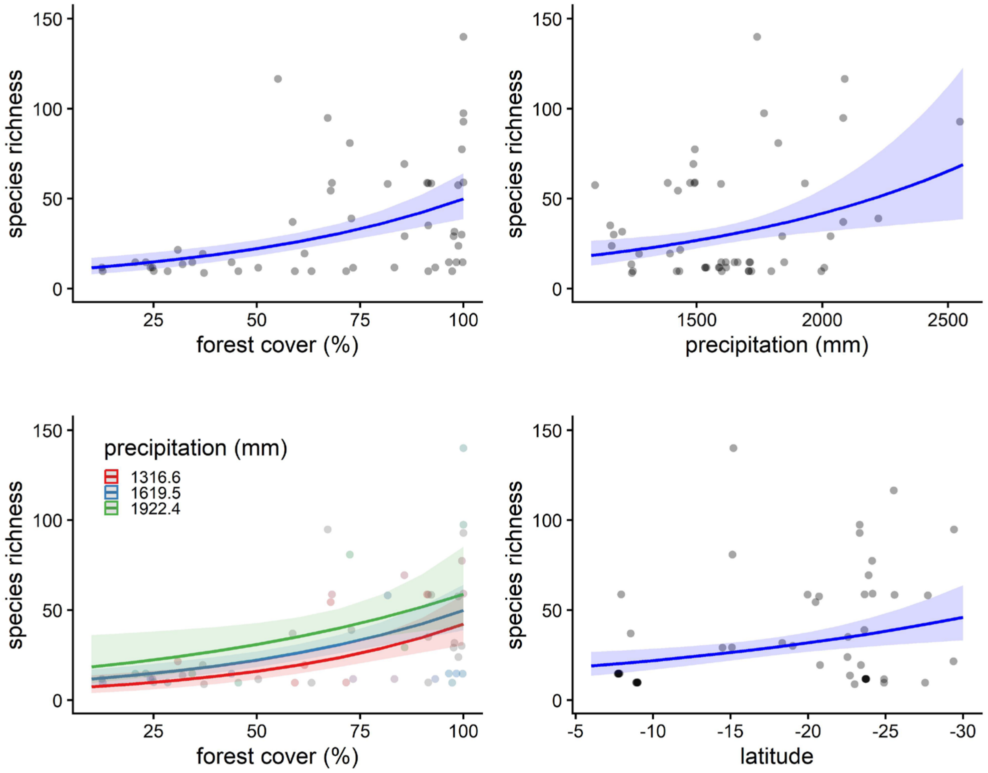

FIGURE 4 Predictions from the best (selected) models for species richness, using a Gamma distribution with log link function, across Atlantic Forest patches. Predicted values are presented on the original response scale (i.e. after applying the inverse of the log link). Statistical coefficients are detailed in Table 2. For a list of all models and their AIC ranking, see Table S4.

TABLE 2 Statistical coefficients for the best models (ΔAIC <2) predicting species richness and spatial turnover as response variables in GLM models across Atlantic Forest patches.

Response variables	Model ΔAIC	Weight	R^2	Model predictors	Estimate	SE
Species richness	0.0	0.831	0.550	Intercept	2.722	0.242
				Forest cover	0.468	0.088
				Precipitation	0.269	0.092
				Latitude	−0.037	0.012
				Forest cover × precipitation	−0.095	0.110
Spatial turnover	0.0	0.821	0.439	Intercept	1.759	0.219
				Forest cover	0.451	0.080
				Precipitation	0.182	0.077
				Latitude	0.003	0.011
				Forest cover × precipitation	−0.125	0.076

Note: For AIC rankings of all tested models, see Table S4.

edges (Gutiérrez-Chacón et al., 2018), contributing to enhanced seed production. Increased light availability has also been related to higher amounts of fruits of some tropical species (Alberti & Morellato, 2008, 2010).

For species richness, we found no increase towards warmer sites closer to the Equator; instead, it tended to increase towards the southern portions of the biome. Because latitude was modelled as a linear predictor, we did not test for a unimodal (hump-shaped) pattern such as that reported for tree species richness by Zwiener et al. (2020). Therefore, comparisons with that large-scale richness pattern should be interpreted cautiously. Nevertheless, it is noteworthy that the central-southern parts of the Atlantic Forest harbour a high tree diversity, partly due to floristic influences from adjacent biomes, including seasonal forests and savannas (Oliveira-Filho et al., 2015), which may contribute to the latitudinal trend observed in our dataset. Although more humid and warmer tropical areas show higher biodiversity at large extensions, the spatial distribution and isolation of similar climatic conditions (the geography of climate) enhances species diversity,

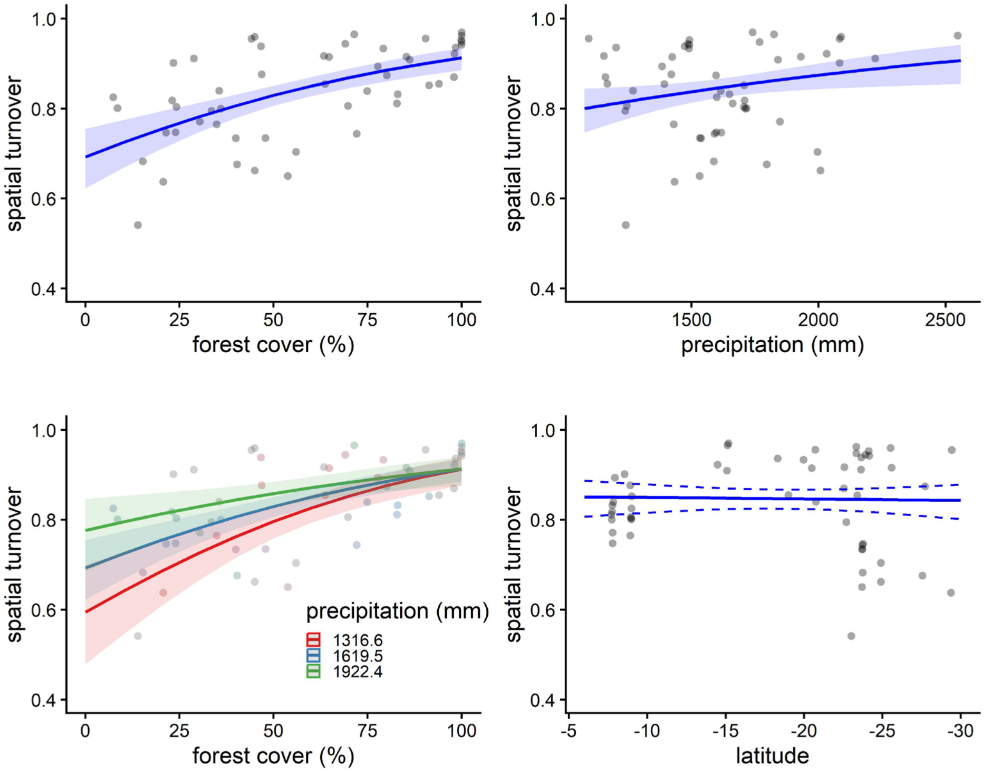

FIGURE 5 Predictions from the best (selected) models for spatial turnover, using an ordbeta distribution, across Atlantic Forest patches. Statistical coefficients are detailed in Table 2. For a list of all models and their AIC ranking, see Table S4.

as shown for tetrapods (Coelho et al., 2023). Land-use history can also have shaped biodiversity patterns across the Atlantic Forest. This region is the most populous region in Brazil, and has undergone a range of human activities, including sugarcane cultivation in the northeast, coffee plantations in the central and timber extraction in the southern region (Carlucci et al., 2021; Lins-e-Silva et al., 2021).

In Brazilian northeast, that corresponds to the northern portion of the Atlantic Forest, historical aspects of high deforestation and fragmentation rates have caused a pronounced bias in the seed rain in Atlantic Forest areas, mainly by excluding large-seeded species (Costa et al., 2012; Melo et al., 2006), which contributes to both functional and taxonomic impoverishment of the local flora (da Silva & Tabarelli, 2000; Oliveira et al., 2008; Santos et al., 2008; Tabarelli et al., 2004). In general, such impact leads remnant patches to display early successional features (Pütz et al., 2011; Tabarelli et al., 2008, 2010). Atlantic Forest patches with less than 40% of forest cover are more susceptible to degradation effects, such as biodiversity loss, biomass reduction and decreased carbon stocks (Rocha-Santos et al., 2016).

Both species richness and turnover increased with forest cover and precipitation. Forest cover is a key metric for evaluating landscape composition (habitat amount) and primarily influences seed rain parameters in tropical forests at the landscape scale (San-José et al., 2020). In our study, forest patches with lower forest cover, mostly in drier sites, likely displayed a floristic homogenization (lower spatial turnover), possibly driven by the dominance of a limited set of pioneer species (Arroyo-Rodríguez et al., 2013; Lôbo et al., 2011). This low spatial turnover pattern contrasts with the high temporal turnover dynamics observed over time at forest edges (Laurance et al., 2006), where species replacement is greater due to disturbance and drought effects. In sites with greater forest cover, the higher levels of spatial turnover among seed traps may reflect a higher diversity of parent plants producing seeds, most of them potentially falling directly from parent plants, causing a patchy pattern of the seed rain. High turnover values indicate that seed dispersal agents may not be effectively mixing (homogenizing) the seed rain community among traps (Wandrag et al., 2017). Therefore, dispersal limitation can be a critical bottleneck constraining beta diversity in such hyper-diverse communities (Muller-Landau et al., 2002; Nathan & Muller-Landau, 2000).

In deforested and fragmented forests, effective seed dispersers, such as large-bodied frugivores (e.g. primates and birds), are often the first animals to become locally extinct due to habitat loss and hunting pressure (Bello et al., 2015; Fuzessy et al., 2022; Marjakangas et al., 2020; Rogers et al., 2021). Quality of the habitat also influences the presence and behaviour of most dispersers; for example, forest specialist birds are less likely to fly across unsuitable habitat matrices and are usually found foraging in the core areas of connected fragments, or mostly flying parallel to the edges (Levey et al., 2005). Fahrig (2013) proposed that total habitat amount in the surrounding landscape is more important than patch size for maintaining species richness of standing communities, suggesting that different effects of fragmentation can be observed on biodiversity patterns at patch versus landscape levels (Fahrig, 2024; Riva & Fahrig, 2023).

We argue that, at landscape level, both forest composition and configuration influence ecological interactions related to seed dispersal across a fragmented biome (see also San-José et al., 2020). At patch level, the size of forest fragments per se was not necessarily the best feature to explain seed rain patterns. For instance, a patch can be large in size (hectares) but be inserted in a poor matrix, with low forest cover and no other patches around. In the Amazon, maintaining secondary forests nearby old-growth patches seems to reduce fragmentation and edge exposure, forming a landscape mosaic of adjacent patches that mitigates the problems of building strip-shaped corridors (Smith et al., 2023), which may be extrapolated to Atlantic Forest patches.

Our large-scale approach provides a synthesis of how landscape features impact dispersal across fragmented forests, offering valuable insights for the conservation of plant diversity and biological interactions. In summary: (1) precipitation is an important abiotic resource driving the proportions of Zoo species; (2) seed density increases with fragmentation, depending on forest cover; (3) habitat amount drives alpha and beta diversity patterns in the seed rain, alongside precipitation, being more important than patch size itself. Although fragmentation may enhance dispersal rates, a suitable surrounding environment for dispersal must include increased amounts of habitat, promoting connectivity among patches, and conserving most ecological interactions and ecosystem functions. By understanding seed rain patterns across the landscape, we can better guide conservation strategies towards more connected ecosystems and enhance our ability to predict how tropical forest communities will assemble and function in a rapidly changing world.

AUTHOR CONTRIBUTIONS

Luís Felipe Daibes, Marco Aurélio Pizo, Haldre S. Rogers, Rafael Barbizan Sühs, Fulbert J. K. Gnonlonfoun, Renato Augusto Ferreira de Lima, Daniella Vinha and Débora Cristina Rother conceived the ideas and designed methodology; Luís Fábio Silveira and Marco Aurélio Pizo were responsible for funding acquisition and project administration; Haldre S. Rogers, Luís Fábio Silveira and Marco Aurélio Pizo supervised the study; Luís Felipe Daibes, Fulbert J. K. Gnonlonfoun and Talita Zupo conducted data analyses; Paulo Alves Almeida Junior, Angela Luciana de Avila, José Marcos Barbosa, Romualdo Morelatto Begnini, Antonio Jorge Tourinho Braga, Marcos Vinicius Wincker Caldeira, Elivane Salete Capellesso, Andre Targa Cavassani, Eliana Cazetta, Ricardo Gomes Cesar, Marilena Menezes Silva Conde, Cléber Covre, Henrique Machado Dias, Pavel Dodonov, Rinaldo Luiz Caraciolo Ferreira, Cintia Gomes Freitas, Milena Gama, Gerhard Gottsberger, Flavia Moraes de Jesus, Carlos Alfredo Joly, Ute Christiane Knörr, Sustanis Horn Kunz, Vinícius Londe, Ana Lícia Patriota Feliciano Marangon, Luiz Carlos Marangon, Fabiana Maraschin-Silva, Marcia C. M. Marques, Adriana M. Z. Martini, Valéria Forni Martins, Larissa Lopes Mellinger, Luís Fernando Tavares de Menezes, Sandra Bos Mikich, Luiz Fernando Duarte de Moraes, Marcelo Trindade Nascimento, Marcelo Augusto Meratti de Oliveira, Monique Perini, Julia Fleming Pimentel, Daniel Piotto, Rita de Cássia Quitete Portela, Janaine Isabela da Silva Rocha, Ricardo Ribeiro Rodrigues, Débora Cristina Rother, Jerônimo Boelsums Barreto Sansevero, Amanda Souza dos Santos, Flavio Antonio Maës dos Santos, Jaqueline Pêgo Quintino Santos, Nelson Augusto Santos Junior, Tanise Luisa Sausen, Carlos Rodrigues da Silva, Joselane Príscila Gomes da Silva, Jorge Yoshio Tamashiro, Daniella Vinha, Luiz Roberto Zamith, Leticia Bolian Zimback, Raquel Fernandes Zorzanelli and Victor Pereira Zwiener collected the data and provided the raw datasets used in the analyses; Luís Felipe Daibes led the writing of the original draft. All authors contributed to manuscript revision and approved the final version of the study.

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CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

R scripts and datasets are available at https://doi.org/10.5281/zenodo.19597741 (Daibes, 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Information of data owners and location of the study sites included in the seed rain database across the Atlantic Forest patches. Study locality = local names of study sites (and Brazilian state where the study was conducted); N traps = number of traps used; trap area = area of the traps (m^2); Months = sampling duration in months.

Table S2. Delta and weight values of model selection ranking based on Akaike Information Criterion (AIC) using different buffer sizes for forest cover and number of patches (at 500 m, 1 km, 2 km and 5 km radius) as predictors for all response variables. ΔAIC = delta AIC values; Weight = AIC weight values.

Table S3. Model selection ranking based on Akaike Information Criterion (AIC) for the proportion of zoochorous (Zoo) species and seed density per dispersal mode (Zoo and Non-Zoo) as response variables in the GLM models. ΔAIC = delta AIC values (best models, with ΔAIC <2, highlighted in bold); df = degrees of freedom; Weight = AIC weight values.

Table S4. Model selection ranking based on Akaike Information Criterion (AIC) for species richness and spatial turnover as response variables in the GLM models. ΔAIC = delta AIC values (best models, with ΔAIC <2, highlighted in bold); df = degrees of freedom; Weight = AIC weight values.

Figure S1. Proportions of identified (ID) and unidentified (Undet) taxa to at least the family level across study patches (top panel), and species proportions per dispersal mode (bottom panel); only study patches with ≥50% of species identified were included, and final proportional values were adjusted by the number of identified taxa in each patch. Non-Zoo = non-zoochorous dispersal (wind-+self-dispersed species), Undet = undetermined dispersal mode and Zoo = zoochorous dispersal (animal-dispersed species). Dispersal mode data obtained from the TreeCo database and complemented by an additional literature survey.

Figure S2. Species proportions per growth form of identified species across study patches; only patches with ≥50% of species identified were included, and final proportional values were adjusted by the number of identified taxa with growth form data available in each patch. Growth form data obtained from the TreeCo database.

Figure S3. Spearman's correlation coefficients between patch- and landscape-level metrics (latitude, patch size, forest cover, number of patches and edge density) and climatic variables (mean annual temperature and total annual precipitation). Landscape-level metrics (forest cover, number of patches and edge density) were calculated within different buffer sizes (500 m, 1 km, 2 km and 5 km radius).

Figure S4. Spatial correlograms of Moran's *I* values in relation to distance classes for residuals of the best (selected) models for the proportion of Zoo species as response variable. Black points indicate distance classes with significant spatial autocorrelation, whereas white points represent non-significant classes.

Figure S5. Spatial correlograms of Moran's *I* values in relation to distance classes for residuals of the best (selected) models for seed density per dispersal mode (Zoo and Non-Zoo) as response variables. Black points indicate distance classes with significant spatial autocorrelation, whereas white points represent non-significant classes.

Figure S6. Spatial correlograms of Moran's *I* values in relation to distance classes for residuals of the best (selected) model for species richness as response variable. Black points indicate distance classes with significant spatial autocorrelation, whereas white points represent non-significant classes.

Figure S7. Spatial correlograms of Moran's *I* values in relation to distance classes for residuals of the best (selected) model for spatial turnover as response variable. Black points indicate distance classes with significant spatial autocorrelation, whereas white points represent non-significant classes.

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