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Seed rain variation across a tropical humid forest chronosequence

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Abstract

Chronosequences provide space-for-time substitutions to study ecological succession and guide restoration efforts. We evaluated seed rain dynamics across a tropical forest chronosequence in the lowland mountain landscape of Caquetá, Colombia, using monthly seed trap data collected from September 2017 to August 2018 in 18 plots (50 × 50 m) classified into early-secondary, intermediate-secondary, and old-growth forest. Seed morphospecies richness and mean seed mass increased with stand age, while total seed abundance declined, suggesting a transition from small-seeded pioneer species to larger-seeded, late-successional species. Despite differences in richness and abundance, species composition did not differ among stand age groups, likely due to the limitations of morphospecies identification. Seed rain positively correlated with precipitation with a lag time of 3 months, suggesting that heavy rainfall is a prerequisite for fruit production. Seed rain peaks were dominated by *Eugenia* sp. and *Piptocoma discolor*, the latter contributing most seeds in early- and intermediate-secondary forests. Correlations between morphospecies richness and seed abundance with basal area (m^2/ha), species richness, and species diversity are likely explained by resources associated with structural variables (e.g., fruit abundance, canopy cover, and microhabitat diversity) that influence seed disperser behavior. Additionally, successional stage may play a role, as older or more structurally complex forests tend to support more plant species that may contribute to higher seed rain diversity and abundance. Early-secondary forests in this landscape are unlikely to be dispersal-limited, indicating potential for unassisted restoration, though isolated patches may require connectivity interventions such as plantings or living fences to overcome seed input constraints. Further studies are required to evaluate disperser movements across the fragmented landscape as well as plant recruitment, prior to making recommendations on ecological intervention strategies.

Keywords Early successional · Fragmented landscapes · Seed dispersal · Tropical restoration ecology

Introduction

During ecological succession of forests, the quality and quantity of seed rain play a key role in shaping plant communities (de la Peña-Domene and Martínez-Garza 2018; van Breugel et al. 2019). Low seed input from species characteristic of mature forests can lead secondary growth to alternative stable states, sometimes dominated by exotic species, altering successional pathways and associated ecosystem services (Cramer et al. 2008; Wolfe et al. 2019). For tropical forests, dispersal limitation often results from lack of seed dispersers, as biotic dispersal is predominant across the tropics, except in recently abandoned clearings (Howe and Smallwood 1982; Chazdon 2003; McConkey et al. 2012). Dispersal-limited species, often large-seeded, not only suffer density-dependent mortality near parent trees, but also have comparatively lower capacity to colonize new areas, thereby constraining their potential as sources of new recruits (Comita et al. 2014). In the context of ecological restoration, determining whether dispersal limitation is present and how to address it is of paramount importance for designing proper intervention strategies.

Regenerating forest patches with dispersal limitation will receive fewer and less diverse seeds than they would from

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nearby seed sources. Regions with highly fragmented forests such as Caquetá, Colombia (Murad and Pearse 2018) are particularly susceptible to dispersal limitation due to how animal dispersers are affected. Fragmented forest landscapes support fewer large fauna, some of which provide high quality and quantity seed dispersal (e.g., keel-billed toucans), and those remaining will vary in their proclivity to cross from one patch to another (Şekercioğlu et al. 2002; Prevedello and Vieira 2009; Canale et al. 2012; Beltrán and Howe 2020). Some dispersers will only cross between forest patches when there is a compelling reason to do so, such as seeking shade, fruit, or territory (Guevara et al. 1986; Janzen 1988). As ecological succession occurs and more resources become available at developing patches, animal visitations and seed rain are expected to increase (del Castillo and Ríos 2008; Martínez-Garza et al. 2009; Zhang et al. 2015). As biotic dispersal becomes more prevalent, average seed size should also increase, given that wind-dispersed species typically produce smaller seeds (see Khurana et al. 2006; Ibarra-Manríquez et al. 2015). A forest patch undergoing succession can be described through biodiversity and forest structure metrics, such as stem density, basal area, species richness, and species diversity, relative to reference values from a primary forest (Chazdon 2003; Gann et al. 2019). If seed rain quality and quantity remain unchanged over time, it could indicate that current resources are insufficient to alleviate dispersal limitation, justifying assisted intervention techniques.

A humid tropical forest chronosequence experiment in Caquetá, Colombia allowed us to investigate how seed rain quality and quantity change over time in response to biodiversity and forest structure. Established in 2017, this experiment uses a space-for-time substitution to study ecological succession (Rodríguez and Cuéllar 2020). As in most Neotropical countries, Colombia's fragmented forest landscapes are largely a result of cattle pasture expansion (De Sy et al. 2019). While assisted interventions, such as fenced tree planting, can enhance succession, natural regeneration can also yield favorable outcomes with fewer resources, provided dispersal and seedling establishment are not limited (Gann et al. 2019; Beltrán et al. 2022). Here, we assess whether seed dispersal quantity and quality (richness and diversity) vary over ecological succession using chronosequence plots in the lowland mountains of Caquetá. We predicted that seed abundance, morphospecies richness, and individual seed mass would be highest in older plots and positively correlate with forest structure and floristics. Additionally, given that dispersal modes shift over succession, we expected seed morphospecies composition to differ among stand age groups. We also predicted differences in seed rain peaks across stand age groups, as dominant seed species are likely to vary in their phenological triggers (Günter et al. 2008). Since precipitation is a likely driver, we examined how seed rain correlated with precipitation lags (0 to −3 months) both across the landscape and within stand age groups.

Methods

Study area

This study area was located in the Andean-Amazonian transition of Caquetá, Colombia that includes the municipalities of Morelia, Florencia, San José del Fragua, and Belén de los Andaquies. This region comprises five physiographic landscapes, with rolling hills covering the largest portion (67.9% of the territory), followed by mountains (11.7%), massifs (10%), alluvial valleys (9.7%), and piedmont (0.7%) (IGAC 2014). The plots selected for this study are located in small valleys that form part of the lowlands of the mountains. Forests in these areas belong to the humid tropical forest life zone (Holdridge 1967; Monsalve 2019). Average temperature is 25.3 °C, relative air humidity 84%, and precipitation 3,307 mm. Caquetá's seasons include a high rainy season from April to June, and a mild rainy season from September to November. The dry months are December to March and July to August (Guzmán et al. 2014). Soils are characterized as oxisols and ultisols of mild acidity (pH < 6) and clayey textures (IGAC 2014).

Chronosequence plots

In 2015 and 2016, the Amazonian Scientific Research Institute (SINCHI) established 52 plots (50 × 50 m) across sites in Caquetá with different times since pasture abandonment to evaluate ecological succession along a chronosequence. A buffer of approximately 25 m around each plot offers some protection from edge effects—for example, limiting the influx of disturbance-adapted plants and mitigating higher vapor pressure deficits. For this study, 18 plots in the lower altitudinal ranges of the mountain physiographic landscape were sampled (300–700 masl). Plots have been categorized into three groups based on years since abandonment: early-secondary forests have largely fragmented vegetation between 5 and 20 years old, intermediate-secondary forests between 20 and 40 years, and old-growth forests at least 40 years. A table including information on the selected plots, including their estimated age, coordinates, altitude, forest structure, and floristics is provided in Online Resource 1. Maps illustrating the specific locations of the chronosequence plots are provided in Fig. 1 and were created using the "sf" R package (Pebesma 2018; Pebesma and Bivand 2023). Categorizing into stand age groups for

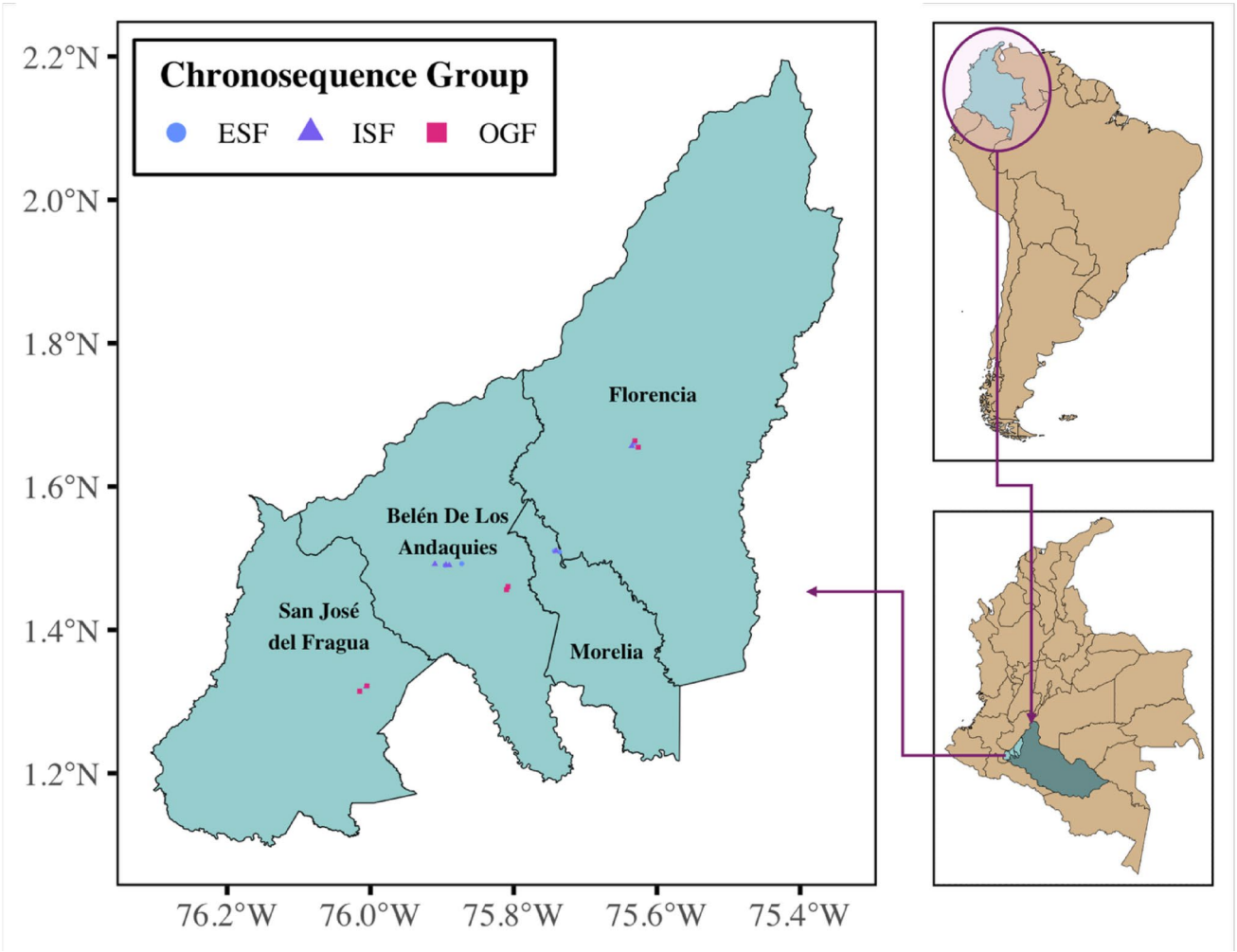

Fig. 1 Study area: the 18 lowland mountain plots selected for this study are located in the four northernmost municipalities of Caquetá, Colombia: Florencia, Belén de los Andaquies, San José del Fragua, and Morelia. Chronosequence stand-age groups are classified as follows: ESF (early-secondary forest), ISF (intermediate-secondary forest), and OGF (old-growth forest)

analysis through ANOVA is a commonly used approach in chronosequence studies (Rocha-Ortega and García-Martínez 2018; Abbas et al. 2019; Martínez-Ramos et al. 2021). Stand age was estimated using satellite imagery dating back to 1984 as well as from local expert knowledge. All plots have been structurally and floristically characterized (all individual trees ≥ 10 cm DBH) by the Amazonian Herbarium of SINCHI to obtain a variety of forest structure and floristic variables characterizing each plot, including: basal area (m^2/ha), stem density (ha^{-1}), species richness, and species diversity (Shannon's H'). Dominant tree species by stand age group include *Henriettea fascicularis* (Sw.) M. Gómez (Melastomataceae) and *Miconia minutiflora* (Bonpl.) DC. (Melastomataceae) in early-secondary forest, *Graffenrieda conostegioides* Triana (Melastomataceae) and *Casearia arborea* (Rich.) Urb. (Salicaceae) in intermediate-secondary forest, and *Pseudosenefeldera inclinata* (Müll. Arg.) Esser and *Wettinia praemorsa* (Willd.) Wess. Boer (Arecaceae) in old-growth forest. Climatic data consisting of monthly precipitation (mm) for each plot of the study was obtained from the global-scale platform for earth science data, Climate Hazards Group InfraRed Precipitation with Station Data (see Rodell et al. 2004; Funk et al. 2015).

Data collection

Seed rain data were collected from seed traps placed in a 3 × 3 formation, 20 m apart from each other, in each of the 18 selected plots monthly from September 2017 to August 2018. Polyvinyl chloride (PVC) pipes were used to construct the four 1 m posts that held a square frame (1 × 1 m), also of PVC, which held 1 mm nylon netting in a conic shape with a depth of 50 cm. In each plot, the contents of the nine seed traps were pooled monthly to generate a single composite sample per plot. The organic material collected in the seed traps was transported to the SINCHI Seed Laboratory of the

University of Amazonia for processing on a monthly basis. Following the procedure outlined by Shen et al. (2014), the samples were washed through a 4 mm mesh sieve to exclude thick materials and afterwards through a 0.21 mm mesh sieve to remove finer material. The leftover material was placed in a desiccating oven at a temperature of 103 °C for 48 h. Once dry, seeds were counted, weighed, and characterized to morphotypes. In some cases, seeds were successfully identified to genus or species; however, the lack of a comprehensive identification guide for the region limited the extent of taxonomic resolution.

Statistical analysis

All statistical tests were performed in R (R Core Team 2024). Differences in morphospecies richness across the three stand age groups were evaluated using a Type I Analysis of Variance (ANOVA) applied to a linear model. Total seed abundance (9 m^2) was analyzed using a generalized linear model with a negative binomial distribution, implemented via the glm.nb function from the MASS package (Venables and Ripley 2002). Pairwise comparisons were conducted using the emmeans function with Tukey's adjustment method from the emmeans package (Lenth 2024). For mean seed mass (g), attempts to apply transformations and fit generalized linear models with various distributions and link functions failed to satisfy model assumptions. Consequently, differences among groups were assessed using the non-parametric Kruskal-Wallis test using the kruskal.test function from the stats package (R Core Team 2024) and the Conover post-hoc test using the conover.test function from the conover.test package (Dinno 2024).

To compare morphospecies composition among stand age groups, an Analysis of Similarities (ANOSIM) and Permutational Analysis of Variance (PERMANOVA) were conducted using an abundance-based Chao-Jaccard dissimilarity matrix (Oksanen et al. 2022). The Chao-Jaccard dissimilarity is a statistical modification of the classic Jaccard index, designed to account for unseen or rare species while correcting for bias due to unseen or rare species. This correction was achieved by estimating the contribution of shared but undetected species based on the frequencies of rare species (e.g., singletons and doubletons) in the samples (Chao et al. 2005). A beta dispersion test was also conducted using the permutest and betadisper functions, also from vegan (Oksanen et al. 2022). Morphospecies composition was illustrated using Non-Metric Multidimensional Scaling (NMDS) with the forest structure and floristic variables depicted as loading arrows representing the direction and strength of their correlations with the ordination axes.

To evaluate whether stand age groups differed in forest structure and floristics, a series of linear models were created and analyzed using ANOVA. Statistically significant results were followed by pairwise comparisons with Tukey's adjustment using the emmeans function (Lenth 2024). To evaluate monthly variation of seed rain in relation to precipitation, Spearman's rank correlation analyses were performed between seed rain and synchronous precipitation, as well as 1-month lag, 2-month lag, and 3-month lag precipitation. Lagging precipitation analyses were conducted as the impacts of precipitation or its absence on seed rain may not be immediate. All figures were created using the R package ggplot2 (Wickham 2016).

Table 1 Statistical test results comparing morphospecies richness (ANOVA on a linear model), total seed abundance (ANOVA on a negative binomial generalized linear model), and mean dry seed mass (Kruskal-Wallis) among stand age groups (ESF = early-secondary forest, ISF = intermediate-secondary forest, OGF = old-growth forest)

Response Variable	ANOVA or Kruskal-Wallis	ESF vs. ISF	ESF vs. OGF	ISF vs. OGF
Morphospecies Richness	$F_{2,15} = 5.49$ $p = 0.016$	$t = -1.96$ $p = 0.156$	$t = -3.29$ $p = 0.013$	$t = -1.33$ $p = 0.4$
Total Seed Abundance	$F_{2,15} = 8.3$ $p = 0.016$	$z = -1.04$ $p = 0.55$	$z = 1.89$ $p = 0.141$	$z = 2.93$ $p = 0.009$
Mean Dry Seed Mass	$X^2 = 6040.58$ $p < 0.001$	$t = 39.22$ $p < 0.001$	$t = -48.07$ $p < 0.001$	$t = -82.69$ $p < 0.001$

Pairwise comparisons were conducted using tukey's adjustment method for ANOVA models and a Conover post-hoc test for the Kruskal-Wallis test

Results

Seed morphospecies richness differed among the three stand age groups (Table 1; Fig. 2a). Old-growth forest had 1.6 times more morphotypes than early-secondary forest and similar morphospecies richness as intermediate-secondary forest. Early- and intermediate-secondary forest had similar morphospecies richness. Total seed abundance also differed among the stand age groups (Fig. 2b). Intermediate secondary forest had 2.6 times more seeds than old-growth forest and similar seed abundance as early-secondary forest. Early-secondary and old-growth forests did not differ in seed abundance. Mean dry seed mass also differed among stand age groups (Fig. 2c). All pairwise comparisons were statistically significant, with old-growth forest having the heaviest seeds and early-secondary forest the lightest.

The sample-size-based curve (Fig. 3) showed that seeds in the old-growth forest were distributed across a greater number of morphotypes, resulting in a higher sampling effort required to saturate morphospecies richness compared to younger chronosequence groups, despite the lower number of seeds collected. Conversely, the early-secondary forest, characterized by high seed abundance but low

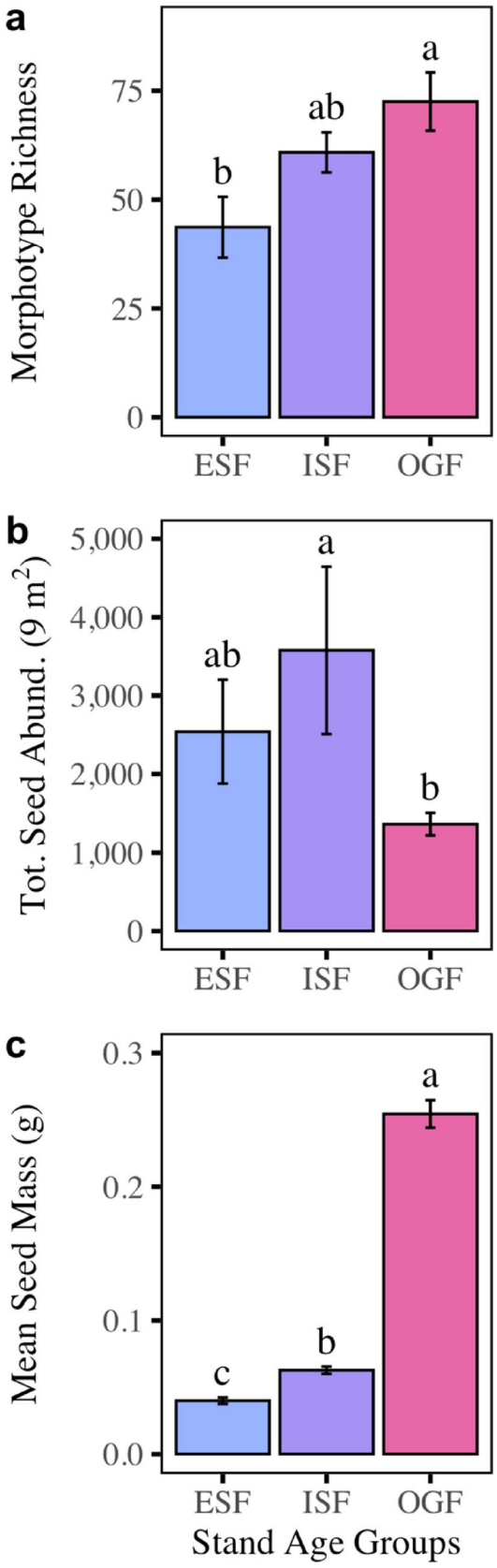

Fig. 2 Mean (**a**) morphotype richness, (**b**), total seed abundance (9 m^2), and (**c**) mean dry seed mass by stand age group (ESF = early-secondary forest, ISF = intermediate-secondary forest, OGF = old-growth forest). Error bars represent standard error. Letters above bars indicate statistical groupings; bars that share the same letter do not differ significantly ($p > 0.05$). For the statistical test results, see Table 1

morphospecies richness, required the least sampling effort to saturate morphospecies richness.

Seed morphospecies composition showed no statistically significant differentiation among stand age groups (Fig. 4; ANOSIM: $R = -0.029$, $p = 0.619$). Similarly the PERMANOVA showed that chronosequence group explained only 10.97% of the variation in community composition, and this effect was not statistically significant ($F_{2,15} = 0.924$, $p = 0.533$). The beta dispersion test indicates that there are no significant differences in multivariate dispersion among the habitat groups ($F_{2,15} = 0.045$, $p = 0.953$). This suggests that the PERMANOVA and ANOSIM results are not confounded by unequal group variances or dispersion.

Linear models showed that stand age groups differed in basal area, species richness, and species diversity, but not stem density (Fig. 5). Pairwise comparisons showed that old-growth forest had significantly higher richness, diversity, and basal area than the early-secondary forest ($p < 0.05$). Compared to intermediate-secondary, old-growth forests had marginally higher basal area ($t = 2.436$, $p = 0.068$) and richness ($t = 2.55$, $p = 0.095$) and similar diversity levels. The early-secondary forest showed significantly lower richness and diversity, as well as marginally lower basal area than the intermediate-secondary forest ($t = 2.410$, $p = 0.071$). Spearman Rank correlations between the seed rain variables and forest structure and floristic variables (Fig. 6) showed that both, morphotype richness and seed mass, correlated positively with basal area, species richness, and species diversity. Total seed abundance correlated negatively although marginally with basal area (rho = −0.44, $p = 0.07$).

Monthly variation in seed rain

Seed rain in the early-secondary forest and old-growth forest peaked in September (3783 and 1583 seeds respectively) while the intermediate-secondary forest peaked in October (5872 seeds) (Fig. 7). The peak in early-secondary forest seed rain was mainly driven by two seed morphotypes identified as a *Eugenia* sp. (42.98%) and *Piptocoma discolor* (41.48%); the most frequently collected morphotype over the 12-month sampling period was an unidentified morphotype labeled M2 (20.85%), followed by *P. discolor* (15.71%) and *Eugenia* sp. (15.22%). The October peak in intermediate-secondary forest was 88.88% *P. discolor*, and in September, most seed rain was also *P. discolor* (80.44%); over the sampling period, the most frequently collected morphotype

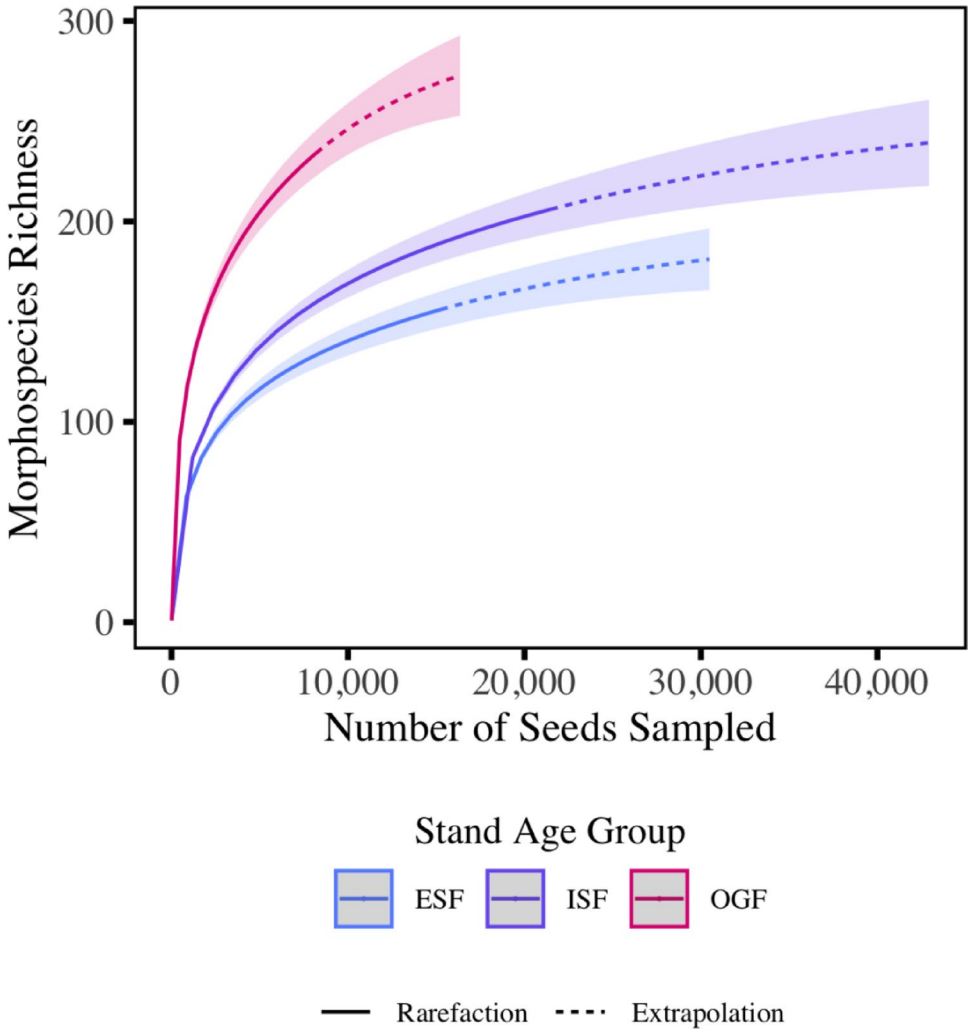

Fig. 3 Rarefaction and extrapolation curves for morphospecies richness across chronosequence stand age groups (ESF = early-secondary forest, ISF = intermediate-secondary forest, OGF = old-growth forest) as a function of the number of seeds sampled. Solid lines represent interpolated data, and dashed lines indicate extrapolated estimates. Shaded area around lines represent 95% confidence intervals

was *P. discolor* (46.65%) followed by an unidentified morphotype labeled M309 (8.9%). In the old-growth forest, the September peak was 31.46% *Eugenia* sp. and 9.54% *P. discolor*; the most frequently collected morphotypes over the sampling period were *Eugenia* sp. (13.85%), M2 (10.1%), and *P. discolor* (8.24%).

Seed rain peaks occurred during a period of moderate rainfall following the rainy season months. Seed rain in the landscape correlated significantly and positively with rainfall when the latter was set to a 3-month lag (Spearman: $p < 0.001$, rho = 0.276). Correlations with synchronous precipitation or 1-month lag were not significant. When separated by stand age groups, the intermediate-secondary and old-growth forest groups showed a significant, positive correlation with 3-month lag precipitation ($p < 0.001$, rho = 0.276 and $p < 0.001$, rho = 0.377, respectively). All correlation scores are provided in Online Resource 3.

Discussion

Seed rain quantity and quality varied across stand age groups, with younger stands receiving a higher volume of predominantly light seeds, while old-growth forests had fewer but larger seeds. Seed morphospecies richness and mass increased with stand age, whereas total seed abundance declined. Increases in seed richness and seed mass are expected as succession occurs, but a decline in seed abundance is unusual (del Castillo and Ríos 2008; Martínez-Garza et al. 2009; Zhang et al. 2015) although not unprecedented (Young et al. 1987). As seed dispersal is predominantly biotic in the tropics (Howe and Smallwood 1982), seed dynamics in ecological succession reflect species turnover of plants as well as of animals. This is especially true with increasing seed size, as large-seeded tree species more often lack redundant dispersal assemblages (Cramer et al. 2007). In this chronosequence, there is a clear turnover away from small-seeded, pioneer species with superior seed production, towards larger seeds that are more likely to

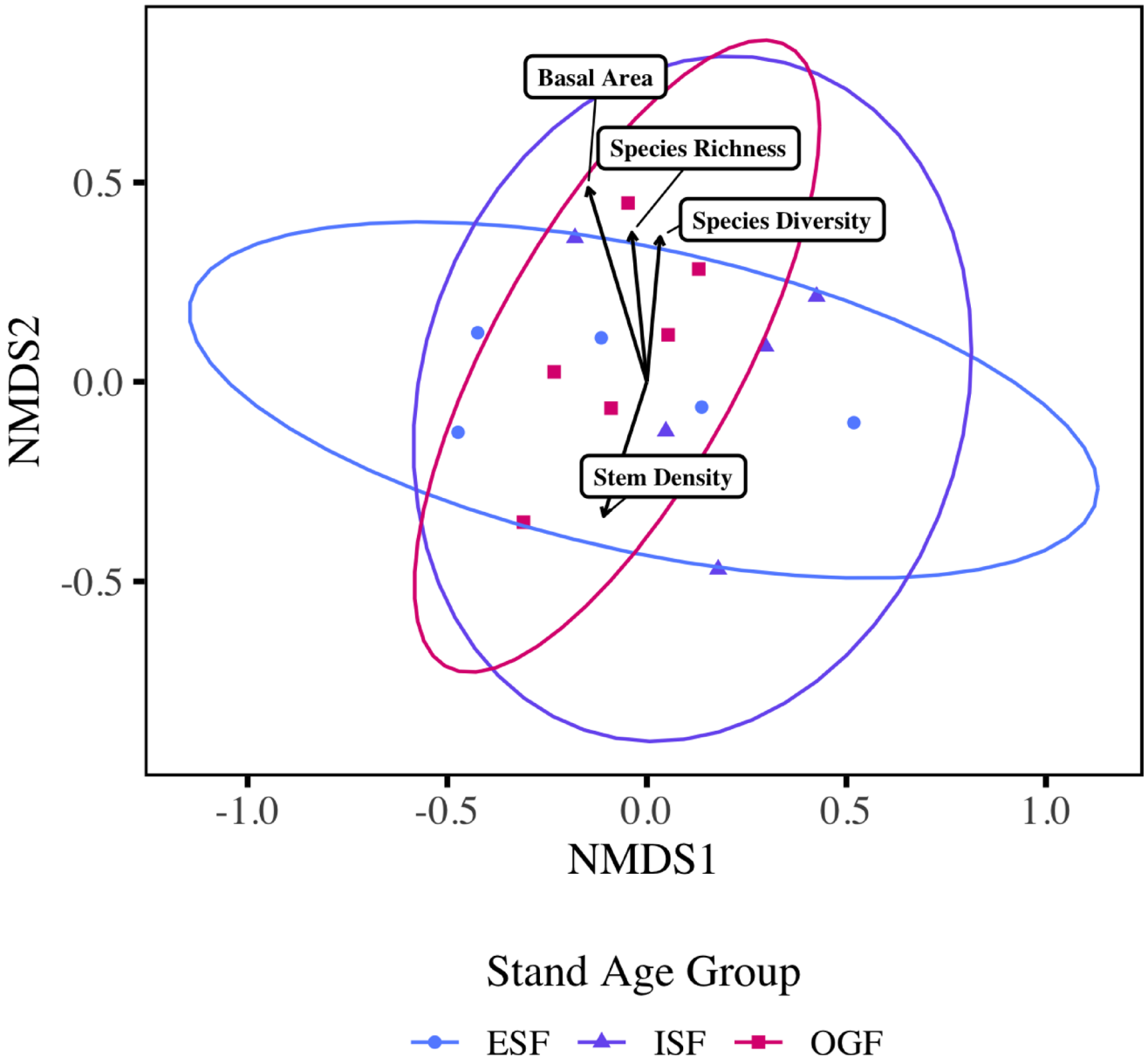

Fig. 4 Non-Metric Multidimensional Scaling (NMDS) comparing morphospecies composition by chronosequence stand age groups: ESF = early-secondary forest, ISF = intermediate-secondary forest, and OGF = old-growth forest. Ovals represent the 95% confidence intervals around for each stand age group. Loading arrows represent the direction and strength of the correlations between the ordination axes (NMDS1 and NMDS2) and forest structure and floristic variables, including stem density (ha^{-1}), species richness, tree species, Shannon-Wiener diversity index (H'), and basal area ($m^2\ ha^{-1}$)

be shade-tolerant, animal-dispersed, and late-successional (Smith and Fretwell 1974; Moles et al. 2004; Chazdon et al. 2007; Martínez-Garza et al. 2009). The origin of seeds is nonetheless uncertain and possibly local for younger plots, as tree species common in early- and mid-succession often fruit early and abundantly, are wind-dispersed, and are abundant themselves, making it possible for them to be the producers of a great proportion of seeds captured by seed traps (Young et al. 1987; Holl 1999). Since effective wind dispersal requires light seeds, it is reasonable to assume that the heavier seeds in this study were biotically dispersed.

The sample-size-based rarefaction curve demonstrates that old-growth forests require greater sampling effort to fully represent morphospecies richness, likely due to their higher species diversity and the presence of rare taxa. It is important to note that seed rain is only one stage of plant recruitment and may not necessarily reflect seedling establishment patterns (Schupp and Fuentes 1995).

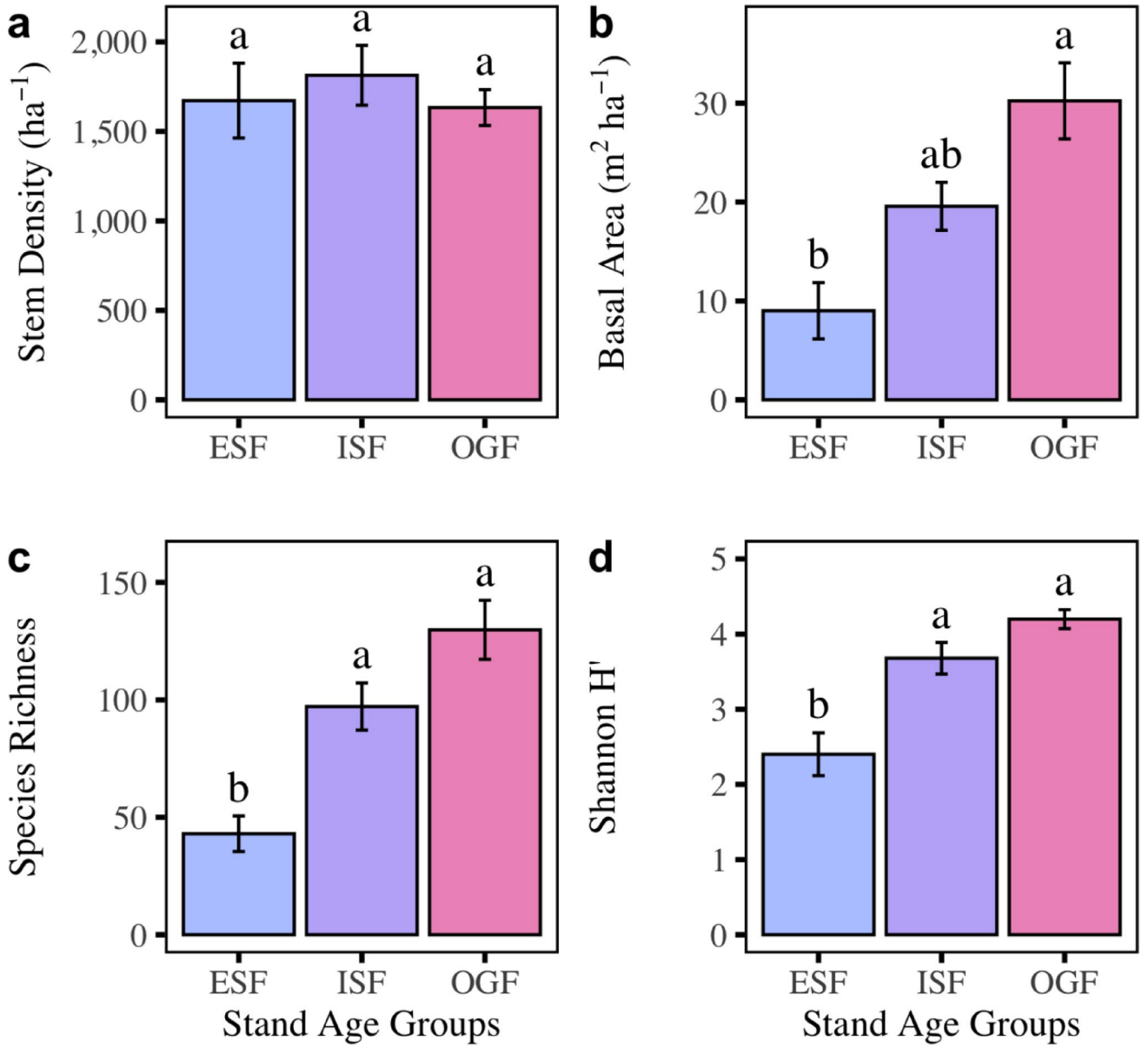

Fig. 5 Mean (**a**) stem density, (**b**) basal area, (**c**) species richness, and (**d**) species diversity by stand age group (ESF = early-secondary forest, ISF = intermediate-secondary forest, OGF = old-growth forest). Error bars represent standard error. Letters above bars indicate statistical groupings; bars that share the same letter do not differ significantly ($p > 0.05$). For the statistical test results and descriptive statistics, see Online Resource 2

The strong positive correlations between seed mass and morphotype richness with basal area, tree species richness, and tree species diversity suggest that seed rain quality and quantity are not solely functions of stand age but also reflect increasing structural and floristic complexity. These attributes, in turn, are indicative of greater habitat heterogeneity and resource availability—such as fleshy fruit abundance, but also including canopy cover and microhabitat diversity—that attract fauna including seed dispersers. This aligns with findings from a restoration experiment in southern Mexico, where fruit-eating birds were 3.1 times more likely to visit stands dominated by animal-dispersed species than naturally regenerating stands of the same age (Howe 2017). Moreover, animal-dispersed stands received a richer seed rain than their naturally regenerating counterparts (Popoca-Ortega 2016), reinforcing the role of disperser-mediated processes in shaping seed dynamics. Increasing seed mass over ecological succession is encouraging, as large-seeded species—typically characteristic of old-growth tropical forests—are rarely dispersed across fragmented landscapes without incentives such as fleshy fruits or a developed canopy (Janzen 1988; McConkey et al. 2012; Howe 2017). This

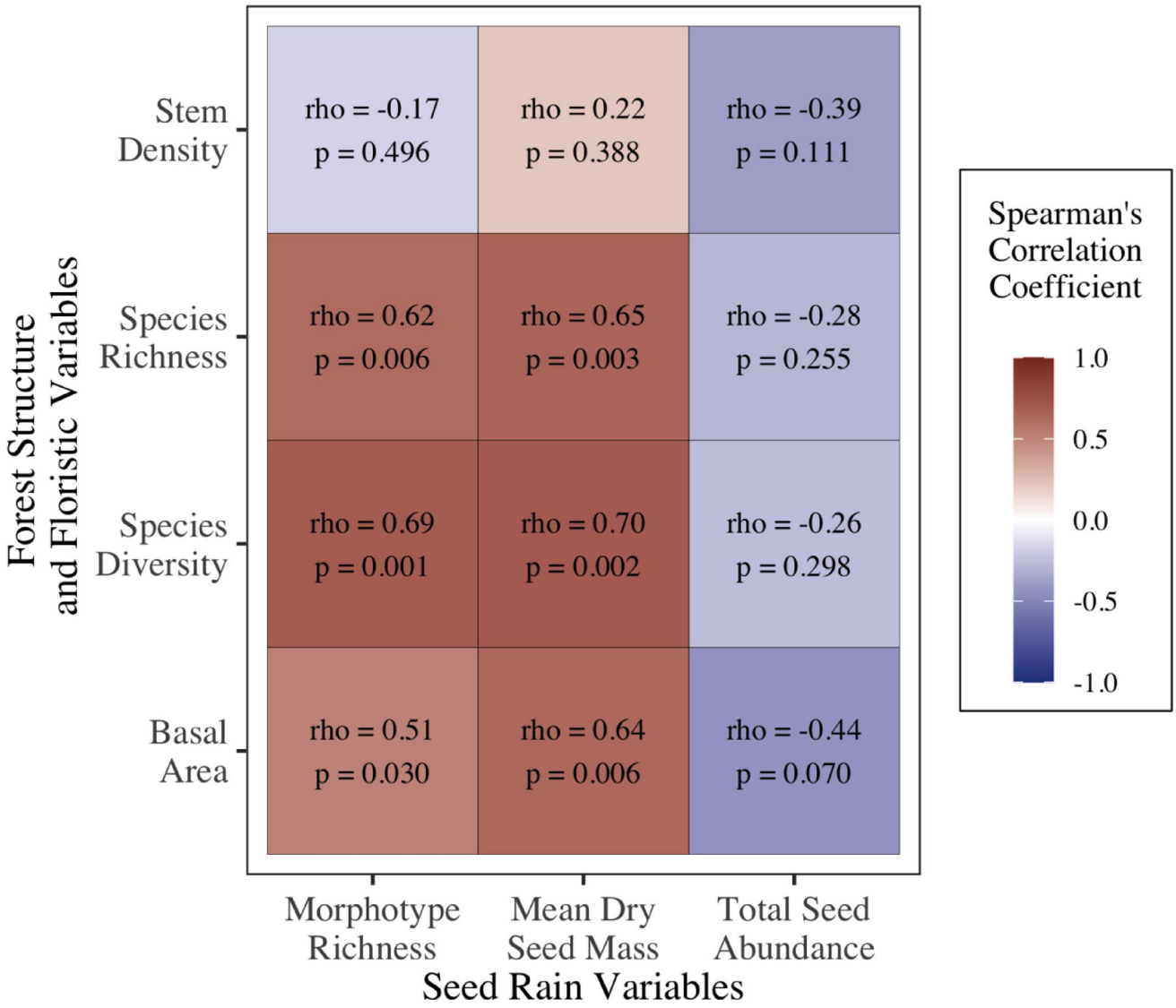

Fig. 6 Heatmap of Spearman's Rank Correlation between seed rain variables and forest structure and floristic variables. Colors represent the strength and direction of correlations, with blue indicating negative correlations, red indicating positive correlations, and white representing near-zero relationships. Correlation coefficients and their associated p-values are displayed within each tile

suggests that developing forest patches provide key incentives that help maintain landscape connectivity. Successional stage may also contribute to these patterns, as older or more structurally complex forests support a richer and more diverse plant community that can drive higher seed rain quantity and quality. Regarding seed abundance, only its correlation with basal area was marginally significant, yet all four variables displayed a negative relationship with forest structure and floristic attributes. This pattern likely reflects the suppression of early-successional species as succession advances and the canopy closes, reducing light availability. Since many early-successional trees and shrubs are prolific seed producers and shade-intolerant species (e.g., Greig 1993), their decline results in lower overall seed abundance in later successional stages.

Seed morphospecies composition did not differ among stand age groups, as indicated by the lack of differentiation in community composition and the absence of confounding effects from differences in group dispersion. These findings contrast with the observed differences in seed morphospecies richness and seed mass, suggesting that finer-scale taxonomic resolution might be necessary to detect differences in seed rain community composition among stand age groups, as observed in other studies (del Castillo and Ríos 2008; Martínez-Garza et al. 2009). More detailed characterization could also reveal whether stand age groups differ in the proportion of wind-dispersed to animal-dispersed seeds, as well as their likely dispersers. Unfortunately, the lack of a seed identification guide for Caquetá limited the ability to achieve this during seed processing.

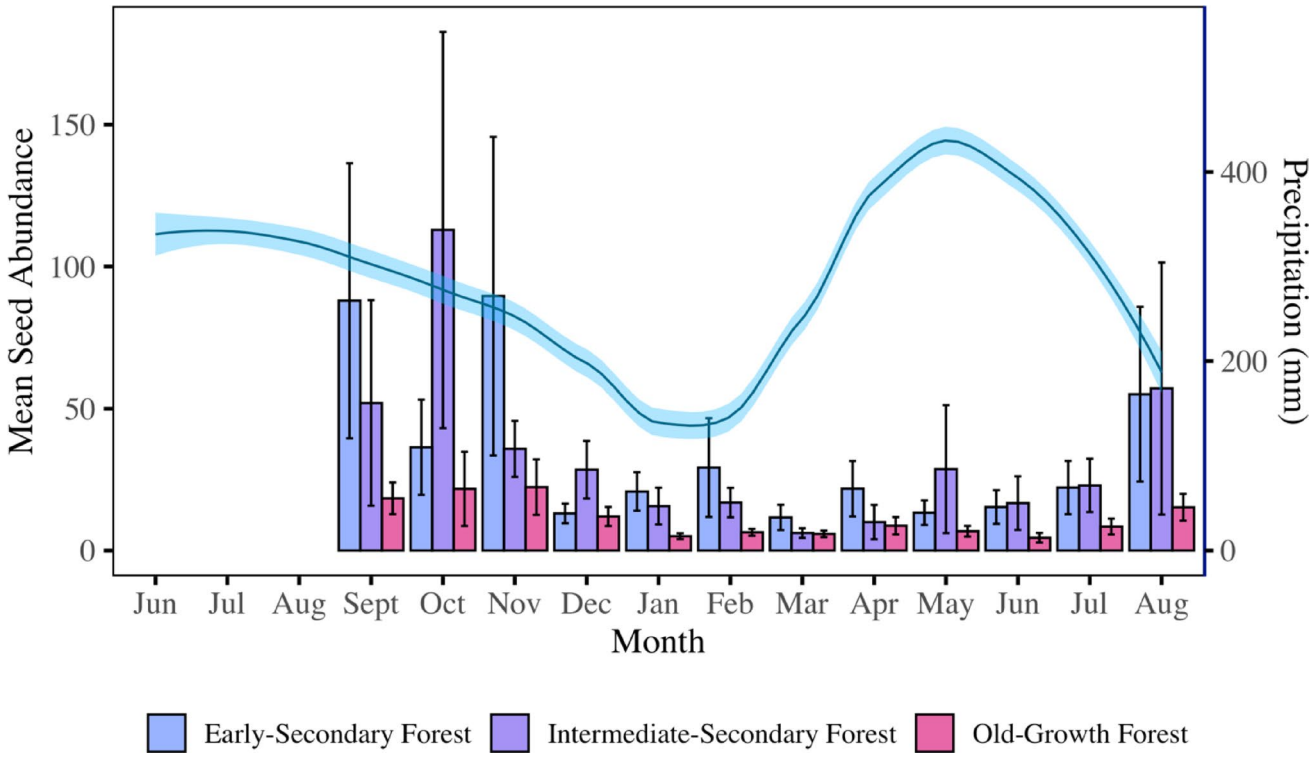

Fig. 7 Total seed abundance by month and chronosequence stand age groups in the lowland mountain physiographic landscape from September 2017 to August 2018. Blue lines represent monthly precipitation from June 2017 onward, plotted against the secondary y-axis. Precipitation is modeled using a LOESS-smoothed curve, and the shaded ribbon represents the 95% confidence interval around the fit

Despite this limiting factor, notable exceptions were identified, including *Eugenia* sp., a genus characterized by biotic dispersal, and *P. discolor* a pioneer, wind-dispersed species (Foster and Janson 1985; Homeier et al. 2013). As expected for a pioneer species, *P. discolor* characterized most of the seed rain collected from early- and intermediate secondary forests. *Eugenia* comprises a diverse array of early-fruiting species, including both pioneers and non-pioneers, which may explain why even in old-growth forest this morphotype characterizes nearly a third of seed rain during the September peak. Moreover, in the Neotropics, *Eugenia* is dispersed by a variety of avian species, including tanagers, flycatchers, thrushes, toucans, and bellbirds (Cortes et al. 2009; Jones et al. 2023), aiding its spread across sites in different successional stages. *Eugenia* holds both cultural and economic significance in Caquetá, with its most common species, *E. stipitata*, commonly known as "arazá" playing a key role in local gastronomy. As its agro-industrial potential is developed in the region (Nastur et al. 2016), the prevalence of *Eugenia* in forests of varying stand age could encourage agroforestry practices that protect secondary forest patches.

Seed rain is linked to the timing of fruiting and seed production by different plant species, which is influenced by abiotic factors such as rainfall (Günter et al. 2008). In our study, seed rain was highest from August through November during the mild rainy season. A positive correlation with time-lagged precipitation by 3 months suggests that high rainy season precipitation (April to June) is a prerequisite for fruit production. The lack of correlation between precipitation and seed rain in early-secondary forests may be explained by the dominance of species like morphotype M2, which was present across multiple months but showed a modest peak in November (2033 seeds), rather than during the main September peak in overall seed rain. This more diffuse temporal distribution likely reduced the strength of any correlation with seasonal rainfall. Seed rain peaks in the landscape were driven by a small subset of morphospecies, mainly *Eugenia* sp. and *P. discolor*, the latter of which is known for consistent fruiting peaks in less humid months (Bendix et al. 2006; Günter et al. 2008). Other abiotically-dispersed species tend to produce fruits during the dry season (Knowles and Parrotta 1995; Stevenson 2004). A seed rain peak in February, the driest month, is likely composed of wind-dispersed species, but compared to the peaks from August through November, this contribution is small.

Conclusions and future research

Our results show that the quality and quantity of seed rain varies among stand age groups, with richness and mean seed mass increasing over ecological succession. These findings

suggest that, despite the fragmented nature of the lowland mountain landscapes of Caquetá (Murad and Pearse 2018), forest patches do not appear to be dispersal limited. The decline in seed abundance with succession likely reflects species turnover, as early-successional species that reproduce quickly and abundantly are gradually replaced by large-seeded, late-successional trees. Seed rain peaks during the rainy season, along with increasing seed size in older stands, suggest that animal dispersal is the dominant seed input across sites. While this suggests that dispersers are moving between forest fragments, a landscape connectivity analysis is still needed to evaluate how fragmentation affects different dispersal agents (Beltrán and Howe 2020). Moreover, patches farther away from external seed sources are more vulnerable to dispersal limitation (Jacquemyn et al. 2003), but these have yet to be identified. Enhancing connectivity to these isolated patches through plantings or living fences could facilitate succession and promote forest recovery (de la Peña-Domene et al. 2013; Beltrán et al. 2022).

In our study, characterization of seeds to morphospecies provided useful but limited information on seed rain changes over ecological succession. Regional guides such as that of Ibarra-Manríquez et al. (2015) for the seeds of Los Tuxtlas, Veracruz, Mexico, are crucial. Developing a guide for Caquetá, Colombia would enhance accessibility to the field and improve the quality of research, thereby facilitating forest management and restoration efforts.

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Author contributions Conceptualization of the study and its design were carried out by (A) M. P.-V., who was also in charge of material preparation and initial investigation. She was supervised by L. L. R.-F. as part of her Master's thesis. C. H. R.-L. provided resources and funding. L. C. (B) then performed additional analyses, provided new graphs, and wrote the original draft of the manuscript. L. L. R.-F. aided, reviewing and editing the manuscript to its final form.

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Data availability No datasets were generated or analysed during the current study. The datasets analyzed during the current study and corresponding code are available in a GitHub repository [https://github.com/Luisca92/PolancoSeedRain.git].

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article
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