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RESEARCH ARTICLE

Spatio-temporal variability in seed production of tree species: implications for restoration in the Cerrado–Amazonia transition zone

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The use of propagules collected in ecotonal regions for restoration purposes is challenging because of the mix of species from different vegetation types and reproductive phenological variability. We used a database of the Xingu Seed Network in Brazil, which contains data on 139 native tree species for 8 years (2011–2018) in the Cerrado–Amazonia transition zone, to answer three questions: (1) What is the spatio-temporal variability in the seed dispersal of tree species, and how does it relate to the species' preferential habitat? (2) Is there a relationship between the seed dispersal period and climate variables? (3) Is the frequency of tree species with different dispersal syndromes equally distributed among biomes and seed-size classes? Independent of their preferred ecosystem (Amazonia or Cerrado), some species showed substantial spatio asynchrony in fruit dispersal, extending the dispersal period at a regional scale. The seed dispersal period was strongly correlated ($r_s > 0.6$) with precipitation and minimum or maximum air temperature in 41% ($n = 57$) of the studied species. We showed that three-quarters of the species ($n = 105$) dispersed seeds in the late dry and early rainy periods, with little variation among dispersal syndromes. Our findings will enhance the effectiveness of restoration initiatives by increasing the accuracy of predictions of the location and time for collecting seeds in the extensive Cerrado–Amazonia transition zone.

Key words: diaspores, ecosystem recovery, fruit ripening, savanna, seed collection, tropical forest

Implications for Practice

- Tropical tree species may exhibit high asynchrony in seed production, which could enhance the long-term planning of seed collector associations and help in meeting the demand for restoration projects.
- Tree species with seed production strongly linked to climate may be more affected by ongoing climate change and impact seed production and resilience of areas being restored.
- Species with extended fruiting periods and reproductive phenology less sensitive to climate variations can enhance resource availability for fauna and increase the resilience of restoration areas.

Introduction

Plant diaspore production (seeds and fruits) is one of the main ecological processes that regulates forest dynamics (Norden et al. 2007; Török et al. 2020), and the primary input in restoration initiatives (Marchand et al. 2020). Studies on spatio-temporal seed dispersal of native species in natural environments have improved our understanding of the conservation status of native vegetation (Marchand et al. 2020) and have fostered seed harvesting initiatives and restoration supply chains (Santos et al. 2012; Pedrini et al. 2020). However, studies conducted in neotropical regions have focused on the seed dispersal period of local populations, which normally does not last longer than a year (Lenza & Klink 2006; da Silva & Scariot 2013). Thus, the lack of spatio-temporal replication makes it difficult to predict when and where it is viable to collect seeds to meet restoration demand.

Thus, there is a sense of urgency to increase the number of studies on the spatio-temporal variation of fruit and seed dispersal of trees in the tropics, a region that still harbors high species richness but is losing native remnants at a fast pace

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(Marimon et al. 2014; Esquivel-Muelbert et al. 2019). Most tropical regions have experienced severe land use changes such as agriculture, cattle ranching, logging, and forest fires (Maracahipes-Santos et al. 2020; Marques et al. 2020), as is the case in the transitional region between the Cerrado (Brazilian savanna) and Amazonia. In this region, the recognition of plant reproductive phenological patterns is even more important, particularly because there is a growing demand for seeds of native species as input for restoration projects (Schmidt et al. 2019). This region coincides with Brazil's "*arc of deforestation*" (Marques et al. 2020), where many degraded areas must be restored to meet the Brazilian federal law for native vegetation protection (Brasil 2012; Soares-Filho et al. 2014). In this region, there are also large indigenous reserves, such as the *Xingu* Indigenous Territory, which have undergone intense conversion of native vegetation to pastures and crops in adjacent areas, as well as an intensification of fire regimes (Silvério et al. 2015, 2022), increasing, even more, the restoration demand. Thus, despite the current scenario of deforestation and native vegetation degradation, there is still a lack of information regarding when seeds of native species are available, compromising the supply chain for restoration initiatives (Cross et al. 2020; León-Lobos et al. 2020).

Information regarding life history is of significant importance in selecting species for restoration efforts in ecotone zones. For example, information such as the preferential habitat, dispersal syndrome, size of fruits and seeds, and how phenology is coupled to climate could help define species combinations suitable for restoration actions in different ecosystems or in the same type of ecosystem, but in different locations. Additionally, this ecological information is essential for optimizing the field collection, storage, and processing of seeds and the efficiency of seedling nurseries (Primack & Rodrigues 2001; Pedrini et al. 2020).

Successful ecological restoration depends on accurately assessing the degree of degradation and clearly defining the reference ecosystem, which guides the selection of appropriate species for planting as seedlings or for direct seeding. The restoration process is particularly complex in the Cerrado–Amazonia transitional zone because of its ecological diversity and rapid climatic changes (Duffy et al. 2015). This region is characterized by a diverse mosaic of savanna, semi-deciduous, and evergreen forests (Ivanauskas et al. 2008; Torello-Raventos et al. 2013; Marques et al. 2020), which makes species selection critical. Moreover, seed collection, a vital component of restoration efforts, relies heavily on local seed collectors widespread over different vegetation types (Sanches & Futemma 2019), which may be related to the lower establishment success for a large number of tree species used in direct seed restoration projects (Rodrigues et al. 2019). Thus, a deeper understanding of plant reproductive cycles and their ecological requirements is essential to enhance the restoration outcomes in this dynamic and diverse region.

To improve the knowledge about seed production of tree species used in restoration projects in the Cerrado–Amazonia transition zone, we investigated the period of seed dispersal for 139 tree species collected by 24 seed harvesting groups of the *Xingu* Seed Network (XSN) between 2011 and 2018. We sought to answer three questions related to the demands for initiatives to recover degraded areas: (1) what is the spatio-temporal variability in seed dispersal of tree species and how does it relate to the species' preferential habitat? The answer to this question could provide direction for seed collection efforts in other parts of the Cerrado and the Amazonia; (2) is there a relationship between seed dispersal periods and climate variables? If that is the case, it will help to anticipate the consequences of global warming for social and ecological restoration initiatives; (3) is the frequency of tree species with different dispersal syndromes equally distributed among biomes and seed-size classes? When compared with the proportions already registered for Amazonia and Cerrado in the literature, the bias in the collected species related to dispersal and seed size helps to predict the possible ecological vulnerability of communities restored by these seeds.

Methods

Study Area

Our study was conducted in the northeastern region of Mato Grosso State, Brazil (Fig. 1), which coincides with the transitional region between the Cerrado and Amazonia biomes (IBGE 2019; Marques et al. 2020). The study area encompasses the *Chapada dos Parecis*, *Cuiabana* Depression, *Araguaia Tocantins*, *Paraná Guimarães*, and *Bananal* ecoregions (Sano et al. 2019) and extends over a 600 km long latitudinal gradient. In the northern portion, there is a predominance of semi-deciduous seasonal transition forests, whereas in the southern portion, savannas are predominant (Ratter et al. 1973). This broad Cerrado–Amazonia transition belt presents a high heterogeneity of vegetation types and includes patches of dense forests and savannas in a matrix of lower, open transition forests (Ratter et al. 1973; Ackerly et al. 1989; Torello-Raventos et al. 2013). Additionally, evergreen tropical forests (locally known as perennial seasonal forests) occur in the upper Xingu River region (Ivanauskas et al. 2008).

The climate of the region is Tropical Rainy Savanna (Aw) according to the Köppen classification, with two well-defined seasons: one dry (April to September) and another rainy and warm (October to March). The annual precipitation ranges from 1400 to 2000 mm and an average temperature range between 22 and 24°C (Alvares et al. 2013). The maximum temperatures are higher in the south (Nova Xavantina), and the minimum temperatures and rainfall are higher in the north (São José do Xingu) (Figs. 1 & S1).

Data Collection

We used the database of the XSN in Brazil, which contains seeds and ripe fruits harvesting data for 139 native tree species for 8 years (2011–2018; see Fig. S3). XSN is an organization created in 2011 and formalized as a non-profit association in 2014. The organization was created because of the seed demand for the *Y Ikatu Xingu* campaign, which started in 2004 and aimed to restore riparian forests on private land across the Xingu basin

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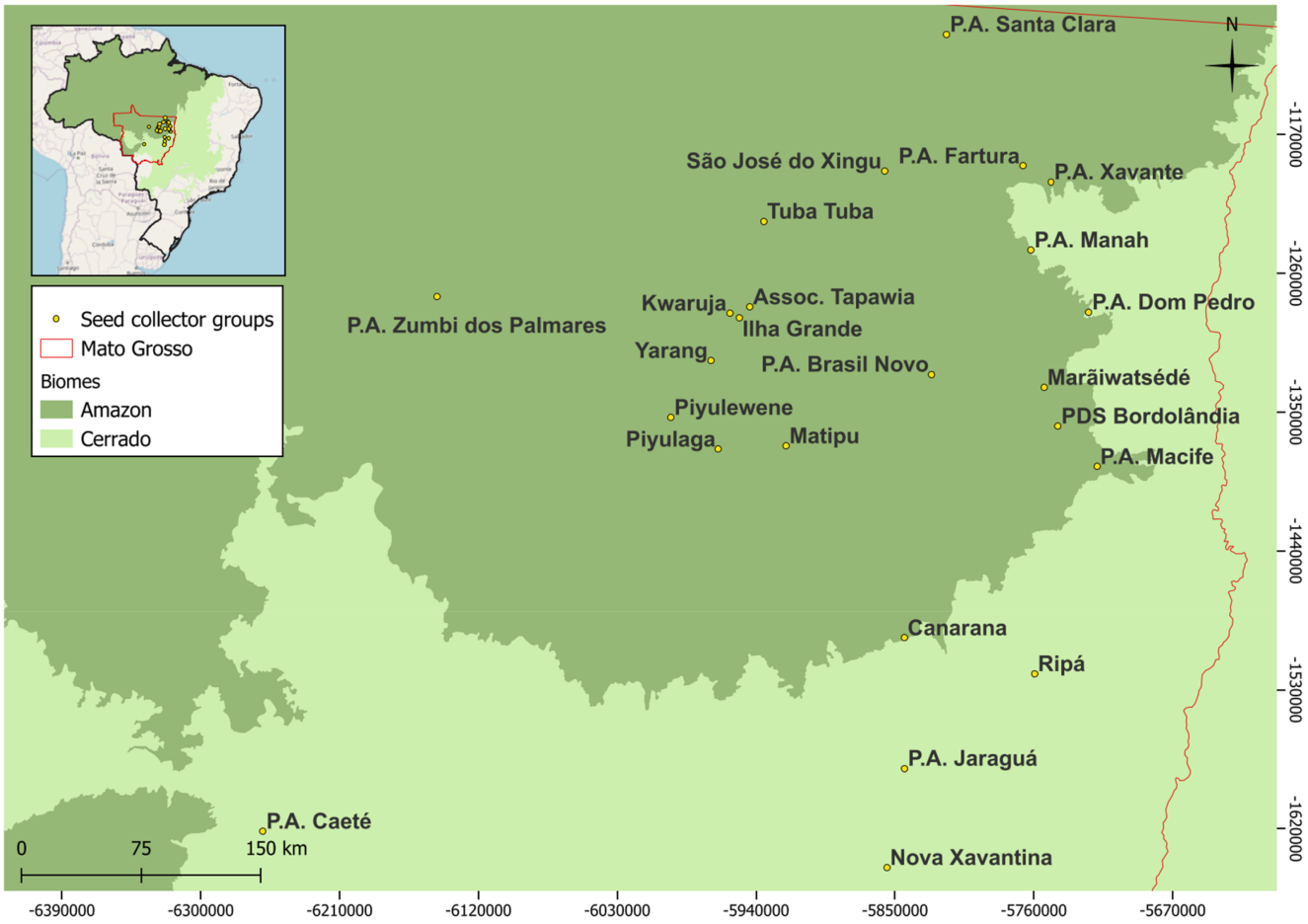


Figure 1. Location of the study area and the 24 groups of native seed harvesting in natural environments of the Xingu Seed Network (XSN) in the Cerrado–Amazonia transition zone, Mato Grosso state, Brazil. Sources: Indigenous land boundaries based on FUNAI (2016); collector groups in XSN (2021).

(Durigan et al. 2013). Today the XSN has more than 500 seed collectors belonging to 24 different groups (Sanches & Futemma 2019). XSN harvester record the exact location and day of seed harvesting in the field and are trained to harvest only ripe fruits, mature, or recently dispersed seeds. Our database included all dispersal units of angiosperms (i.e. fruits and seeds), but for simplicity, we called them "seeds." Among all collected species, we selected only tree species classified as native to the Cerrado and/or Amazonia biomes according to the Flora do Brasil platform (Reflora 2020). We used the same platform to verify scientific spellings, update taxon names, and define botanical families. We selected only the tree species collected in XSN (139 species belonging to 41 botanical families; Table S1), which are composed mostly of species with orthodox seeds that tolerate a longer time between harvest, transport, handling, and storage (Rodrigues et al. 2019). The XSN prioritizes non-recalcitrant seeds owing to logistical constraints (Rodrigues et al. 2019); this might inadvertently impose a functional diversity filter, potentially excluding valuable species with less flexible dispersal strategies or longer dormancy periods.

Species identification followed a standardized protocol, with annual training of the collectors by botanists and checking by XSN experts upon receipt of the seeds. In addition to annual training, the seed network was developed and distributed to collector identification manuals to assist in field identification (Campos-Filho 2007, 2009, 2013). Despite this, uncertainties remained about the differentiation of species in the genera *Byrsonima* (Malpighiaceae) and *Terminalia* (Combretaceae). Considering the extensive empirical knowledge of the collectors and the great representativeness of the species of these genera for ecological restoration in the region, we chose to retain them in our database, identifying them with the abbreviation "check—cf." in the worksheet in Table S1.

Ecological Data of the Species

We described three ecological traits for each of the 139 tree species studied: (1) dispersal syndromes, following the criteria proposed by Hansson et al. (1992): zoochoric (animals dispersed), anemochoric (wind dispersed), and autochoric (explosive dispersal). For this, we considered the morphological characteristics of the dispersal units and performed an extensive search of the scientific literature; (2) the biome of occurrence of the species, following the classification proposed in the REFLORA

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platform (Reflora 2020): typical species of the Cerrado, the Amazonia, or both biomes; (3) the size classes of seeds, following the method adapted from Tabarelli and Peres (2002), which takes into account the length of the seeds: very small (1–3 mm), small (3.1–6 mm), medium (6.1–15 mm), large (15.1–30 mm), and very large (>30 mm). Information regarding seed size was compiled based on different studies in the literature (Lorenzi 1998, 2020, 2021; da Silva-Júnior & da Silva Pereira 2009; da Silva-Júnior 2012; Kuhlmann 2012; Martins et al. 2016).

Spatio-Temporal Patterns of Seed Dispersal

We used circular statistics to calculate the mean angle of fruit production and test for circular uniformity using the Rayleigh test. This test evaluates whether fruit production has a nonrandom distribution throughout the year. First, we calculated the Julian day of the year using data on seed collection in the field, transformed the Julian day in degrees, and finally created a circular object and conducted the statistical analysis. Rayleigh tests were implemented in the R package "circular" and function "rayleigh.test" (Agostinelli & Lund 2023).

To analyze the spatio-temporal seed dispersal periods, we assessed differences in the duration of the local (each group alone) and regional (all groups) dispersal periods by employing the following four steps: (1) the duration of the local seed dispersal period for each species by counting the number of days between the first and the last collection date in that year within each group; (2) the duration of the regional seed dispersal period as the number of days between the first and the last collection date in the year for each species, considering the species information from all seed collector groups together; (3) the difference in the number of days between the local and regional seed dispersal periods, calculated as exemplified in the previous steps; and (4) we calculated a linear regression between this temporal difference in dispersal period (resulting from the previous step) and the total number of months in which the species dispersed seeds on a regional scale. Thus, positive and significant relationships suggest that the species with longer regional dispersal time is associated with greater spatio variability during the fruit dispersal period.

Relationship Between Climate and Dispersal Periods

We employed Spearman correlation analysis to assess the relationship between climate variables (minimum and maximum temperatures and precipitation) and total seed mass collected every month. We extracted monthly climate data for the period between 2011 and 2018 from the WorldClim database (WorldClim 2021), with 1 km spatio resolution, for the 24 locations indicated by geographic coordinates (Fig. 1). We calculated the average of seed mass for each species collected each month for the 24 sites for the entire period (2011–2018) using the dates of field collection and seed mass information. The total seed mass for each species in each month was correlated with the monthly average of precipitation (mm) and the maximum and minimum temperatures (°C). To ensure an adequate correlation analysis, we excluded species collected just one year (Fig. S3) or from less than four groups ($n < 4$) and applied the modified false discovery rate (FDR) correction that corrects for the probability of type I error (Narum 2006). Spearman correlation is a nonparametric analysis where the values are ranked, which helps mitigate the potential impact of differences in total seed mass variability between different months of the year.

Association Between Dispersal Syndromes and Other Ecological Traits of the Species

To evaluate possible associations between the plant functional traits and species dispersal syndromes (dispersal syndrome, seed size, and biome of occurrence), we employed mosaic analysis and illustrative graphs. We built two contingency tables: (1) the number of species per dispersion syndrome against species in each biome of occurrence and (2) the number of species per dispersion syndrome against species in each biome of occurrence. Mosaic analysis classifies data by their count in each group, and the representation is performed using rectangles where the size of the area of the rectangles is proportional to the count of the data, their positions point to associations between the data presented, and the filled colors indicate the expected frequency at random with a 95% significance degree (Hartigan & Kleiner 1984). We performed all the above analyses using R Environment (R Core Team 2021).

Results

Spatio-Temporal Variation in Seed Dispersal

Over the 8 years, most species dispersed seeds at the end of the dry season and the beginning of the rainy season (Figs. 2 & 3). The mean angle for fruit production was 239° (September first), and the Rayleigh test indicated that seed production for most species is concentrated around this average ($z = 0.644$; $p < 0.001$). Species that concentrated seed production exclusively between August and November (drought period) comprised 18% (25) of the total studied. Considering only seed production registered in the same month for 2 or more years, the concentration of dispersion in the same period was registered by an additional 42 species (30%). The seed production peak (i.e. the period in which most species are dispersing seeds) of anemochoric and autochoric species occurred at the peak of the dry season (August and September), while for zoochoric species, the peak occurred at the transition between the dry and rainy seasons (September and October) (Fig. 3). A group of 18 species (13%) (e.g. *Xylopia sericea*, *Sterculia apetala*, and *Protium heptaphillum*) dispersed seeds in only 1 month. During the entire period, 19 species (13.7%) registered seed production for nine or more months of the year (e.g. *Byrsonima crispa*, *Cecropia pachystachya*, and *Senna macranthera*) (Fig. 2).

At the regional scale (i.e. all sites), the seed dispersal periods recorded for several species were longer than the average dispersal duration at the local scale (i.e. each site), indicating asynchrony in the dispersal period for the different sites evaluated (Fig. 4A & 4B). Thus, many species had long periods of dispersal regionally, even though the local dispersal period was short. For example, for

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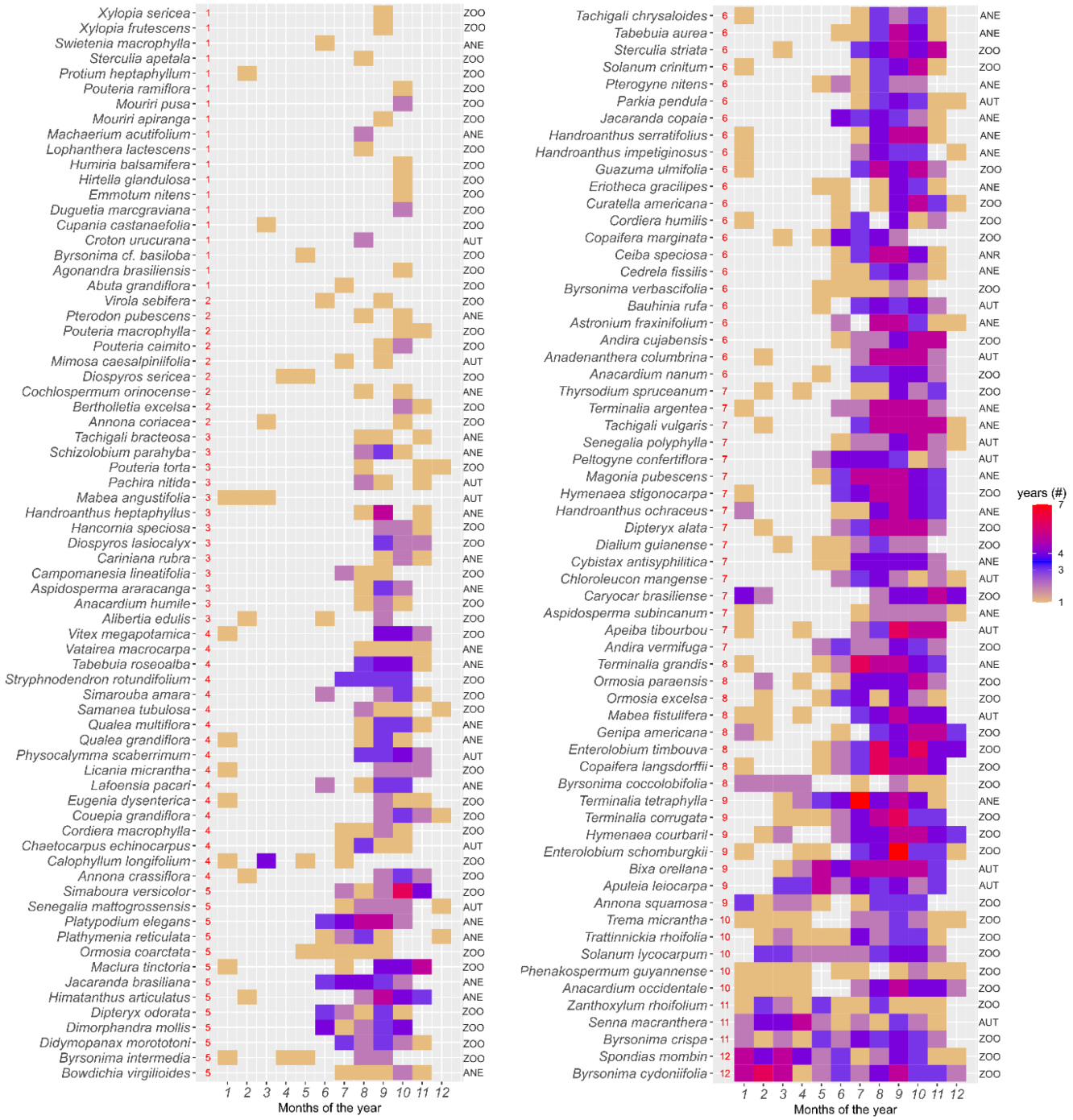


Figure 2. Months for which seed dispersal of 139 native tree species were recorded between 2011 and 2018 in a region encompassing 24 seed harvesting groups in the Cerrado–Amazonia transition zone. Species listed according to the number of months of dispersal in ascending order and dispersal syndromes, where numbers in red on the left indicate the number of months that there was dispersal between 2011 and 2018; the colors of the cells indicate the number of years of dispersal of the species in the respective month, according to the color legend shown. ANE, anemochoric; AUT, autochoric; ZOO, zoochoric.

the same species, the number of days in which seed dispersal was recorded at the regional scale was positively related to time asynchrony among the local sites where this species was collected (Fig. 4B; $F = 68.73$; $p < 0.05$; $r^2 = 0.46$). Although the number of sites at which a species had its seeds collected ranged from one to 24 sites, only 22 species (15.8%) were collected from less than three sites and removed from this analysis (Figs. 4A & S2). Additionally, the regional duration of seed production for a specific species did not correlate with the number of sites where it was registered (Fig. 4A).

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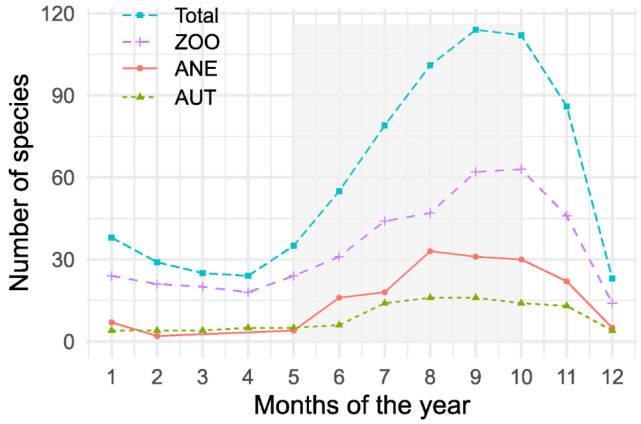


Figure 3. Number of species producing seeds for the different dispersal syndromes along the year. The gray area indicates the dry period. ANE, anemochoric; AUT, autochoric; ZOO, zoochoric.

Relationship Between Dispersal Period and Climate

The dispersal period of 61% of the species (57 of the 94 species in the analyses) was significantly correlated with at least one of the climatic variables evaluated (Fig. 5). In the case of precipitation, the seed dispersal period of 34 species showed a correlation higher than 0.6 ($r_s > 0.6$) (with one positive and 33 negative); with the application of the FDR correction, the number total of significant correlations was 15. For maximum air temperature, 49 species showed a correlation higher than 0.6, and with FDR correction, there remain 41 significant correlation (Fig. 5). In the case of minimum air temperature, we observed a correlation higher than 0.6 for six species (four positive and two negative) and no significant correlation with FDR correction. Furthermore, the dispersal of 35 species was significantly related to only one of the climate variables: 11 with two, and none with three (Fig. 5).

Relationship Between Dispersal Syndromes, Seed-Size Class, and the Biome of Occurrence

For each dispersal syndrome, the species studied was evenly distributed among the biome of occurrence and for most classes of seed size (Fig. 6). Most species ($n = 86$; 62%) occur in both biomes, while 22 (16% of the total) occur only in the Cerrado, and 31 species (22%) are exclusive to Amazonia (Table S1). Of the 139 species analyzed, 61% are zoochoric, 26% anemochoric, and 13% autochoric (Table S1; Fig. 6). The proportion of zoochoric species in the XSN is comparable to that observed in tree communities in Cerrado (approximately 60%) but is lower than that observed for tree communities in Amazonia (70%; Fig. S4). Species with different dispersal syndromes are evenly distributed among the biomes (Fig. 6A). The frequency of the dispersal syndrome for each seed size indicated that a higher proportion of very large seeds are anemochoric species (Fig. 6C), whereas a large fraction of the species with small seeds was autochoric (Fig. 6D).

Discussion

This study presents evidence of high spatial variability in seed production of tree species in the Cerrado–Amazonia transition zone, but with concentration at the end of the dry season (August to October). There was a strong correlation between the seed production period and monthly variability in the

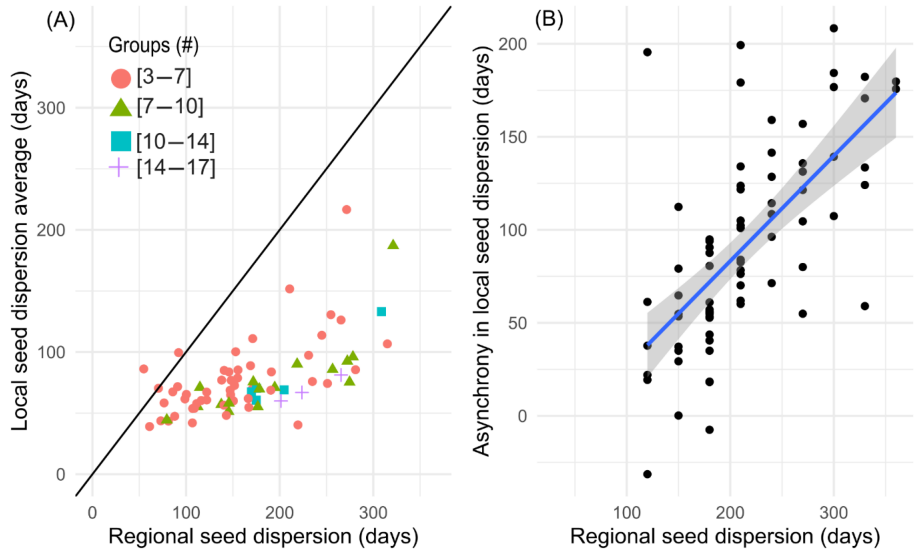


Figure 4. Regional variation in seed dispersal time of 139 tree species between 2011 and 2018 in a region covering 24 seed harvesting groups in the Cerrado–Amazonia transition zone. (A) Relationship between the mean time of seed dispersal within collector groups (local dispersal) as a function of the mean number of days of dispersal considering the 24 groups (regional dispersal). (B) Regression between the difference in mean dispersal time (in days) within each year and the meantime (in months) of dispersal in each collector group ($F = 68.73$; $p < 0.05$; $r^2 = 0.46$). The bracketed values indicated in "Groups (#)" in the panel "(A)" indicate the number of collector groups where seed harvesting occurred.

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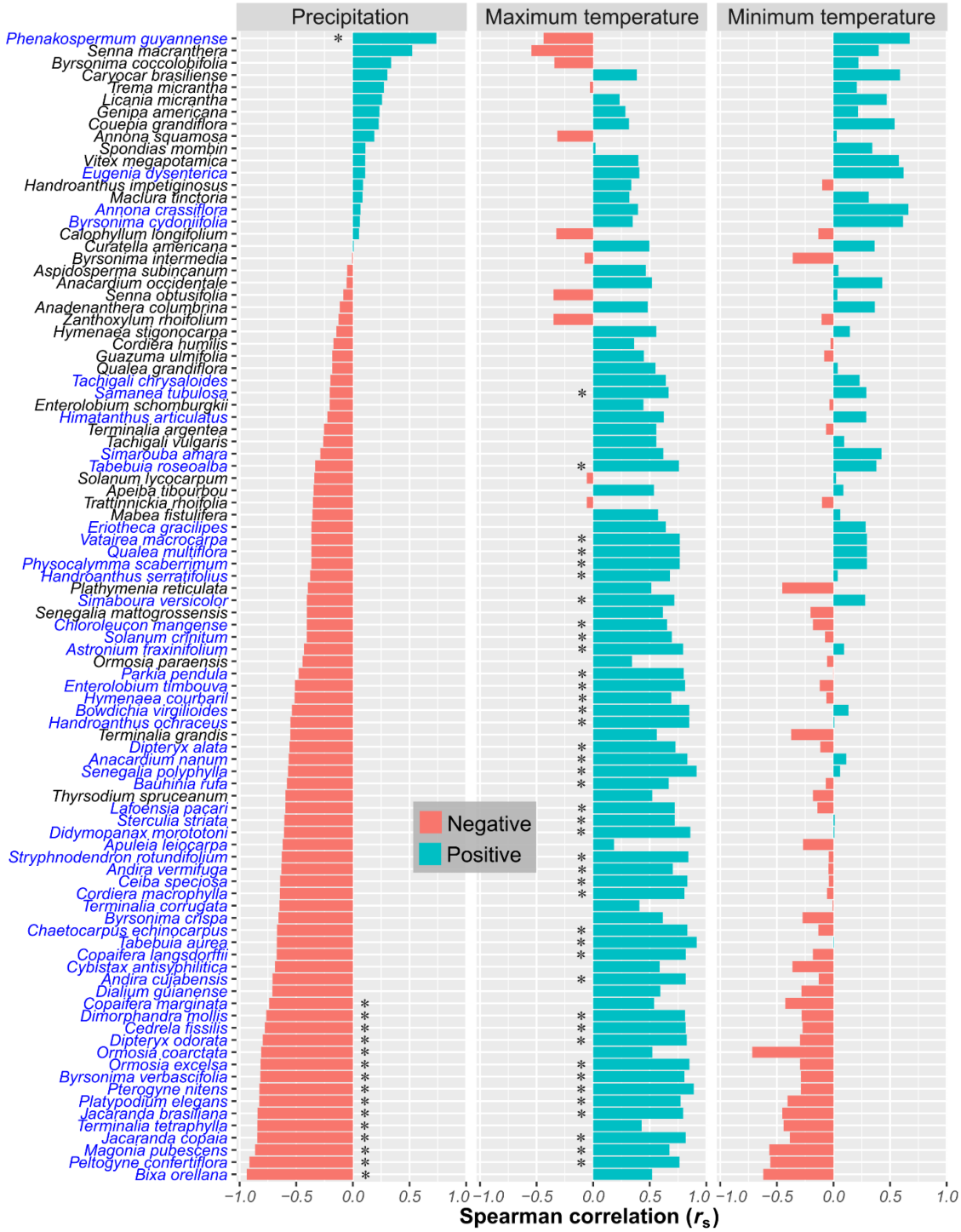


Figure 5. Correlation between mean seed mass (g) of 94 native species collected by 24 groups of collectors and precipitation (mm) and maximum and minimum temperatures (°C) between 2011 and 2018 in the Cerrado–Amazonia transition zone, Mato Grosso state, Brazil. Light blue and red bars represent positive and negative correlations, respectively. Species names spelled in blue indicate those in which the correlation was greater than 0.6 for at least one of the three climate variables. The symbol "*" indicates that p value with the FDR correction is lower than the significance level ($\alpha = 0.05$).

precipitation and the minimum and maximum air temperatures for nearly two-thirds of the studied species, indicating that these species may be more sensitive to the ongoing climate change. In contrast, we observed unexpectedly high spatio asynchrony in the seed dispersal period, which extended the regional dispersal period for many species. Overall, our results contribute

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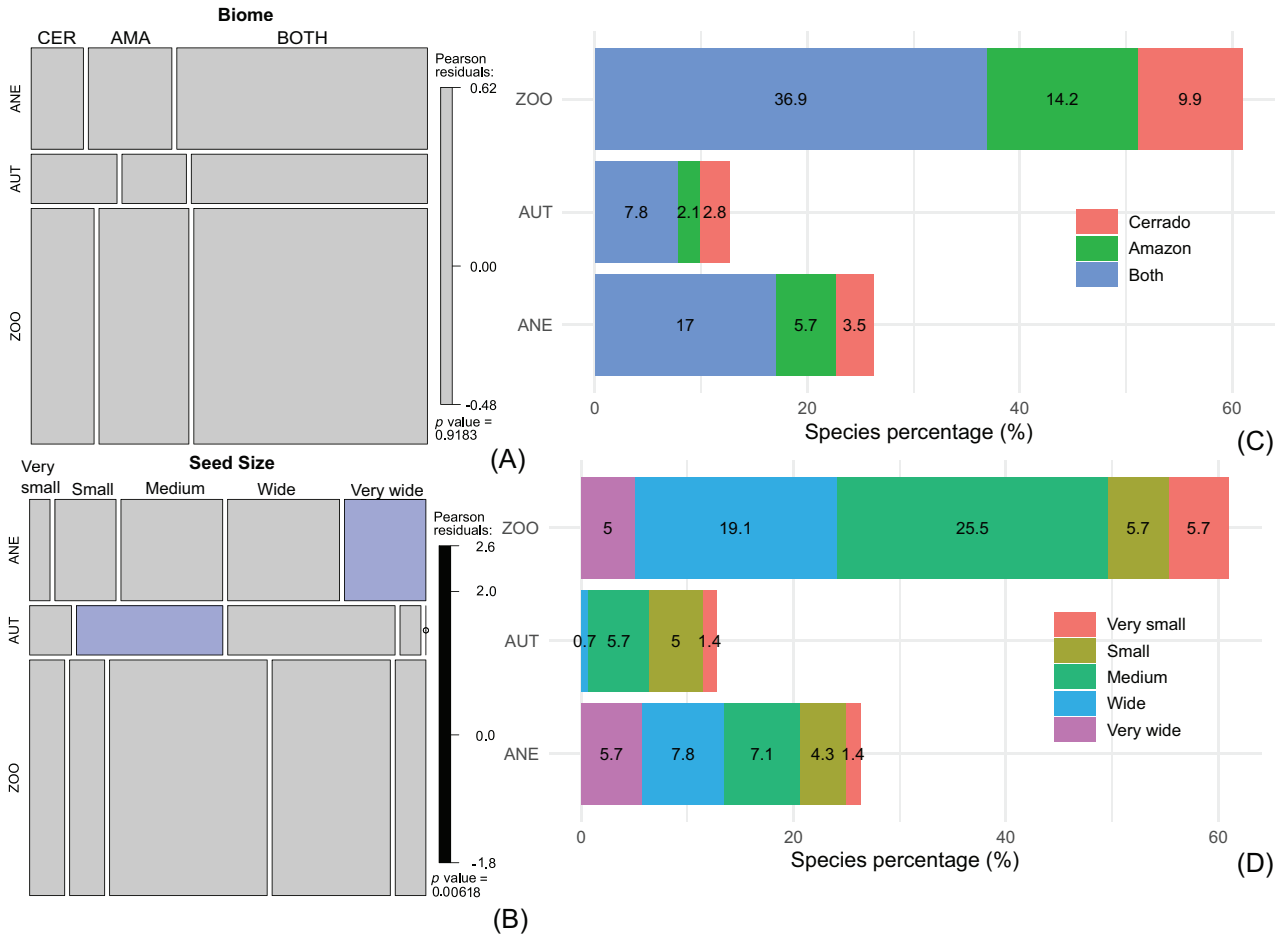


Figure 6. Percentage of the 139 species evaluated between 2011 and 2018 in the Cerrado–Amazonia transition zone. The species dispersal syndromes (ANE, anemochoric; AUT, autochoric; ZOO, zoochoric) are grouped according to their (A) biome of occurrence (AMA, Amazonia; CER, Cerrado; and BOTH), (B) size of their seeds, adapted from Tabarelli and Peres (2002) (M, medium; S, small; W, wide; VS, very small; VW, very wide). Extended mosaics showing the percentage of species: (C) present in the CER, AMA, and BOTH biomes; (D) within each seed-size class with dispersal syndromes ZOO, AUT, or ANE. Blue blocks indicate frequencies of cells greater than expected at random.

substantially to advancing our understanding of the reproductive phenology of these species by offering valuable insights into both spatio-temporal variability. These findings are also important for enhancing the intraspecific variability of seeds used in tropical forest restoration initiatives and for guiding the selection of species combinations that boost the resilience of restoration projects in this region.

Spatio-Temporal Variation in Seed Dispersal

The seed production for a large number of tree species was concentrated at the end of the dry season. The reproductive cycles of woody plants in Brazilian savannas are highly seasonal (Lenza & Klink 2006; Silvério & Lenza 2010), whereas those of plants in tropical rainforests are less seasonal (Nakagawa et al. 2019). Given that our study area lies in the Cerrado–Amazonia transition zone, dispersal concentrated in the transition between dry and rainy seasons seems to be an adaptive adjustment of the transitional tree assemblage to the seasonal climate that predominates in the region. For example, fruit dispersal at the end of the dry season for Cerrado species is an adaptive strategy that ensures seed germination and the initial establishment of seedlings throughout the rainy period following dispersal (Oliveira 2008). In addition, it is associated with an adjustment to favorable environmental conditions (i.e. adequate humidity levels, wind velocity, and temperature) for seed dispersal (Oliveira 1994). This seems to be the case not only in savannas but also in the transitional forests of the region (Ivanauskas et al. 2008; Torello-Raventos et al. 2013; Marimon et al. 2014).

In economic and social terms, the prolonged regional availability of seeds throughout the year guarantees a continuous source of income for the collector groups. It allows for a continuous supply of seeds for commercial nurseries and restoration actions (Broadhurst et al. 2008; Jalonen et al. 2018; Pedrini & Dixon 2020). In addition, introducing seeds from individuals within species with slightly different dispersal times implies introducing intraspecific variation in phenological patterns to an area under restoration. This intraspecific variation in flower and fruit production can result in a constant supply of resources

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for pollinators and seed-dispersing animals. Furthermore, asynchrony reduces intraspecific and interspecific competition for pollinators and dispersal agents (Rathcke & Lacey 1985). Usually, the phenology of plant species and the origin of seeds are not considered in the process of species selection for restoration projects (Buisson et al. 2017; Rodrigues et al. 2019). However, this can have strong implications for the success of species establishment, as well as resilience to climate oscillations, considering the restored community as a whole.

Just like the XSN prioritizes non-recalcitrant seeds owing to logistical constraints, the finding of substantial spatio asynchrony in seed dispersal among species in this study presents an intriguing counterpoint. Introducing phenotypic plasticity can enhance restoration efforts by ensuring that species are better adapted to future site conditions. For instance, early dispersers may escape drought stress, whereas late dispersers may benefit from increased moisture availability. Understanding these patterns alongside predicted climate changes is crucial for matching species and provenances to restoration sites and maximizing establishment and fitness (Thomas et al. 2014). While previous studies (e.g. Garwood 1983) have emphasized germination timing as the main driver of dormancy length, our finding of a higher concentration of seed production at the end of the dry season regarding seed dispersal syndromes requires further investigation. Perhaps the recalcitrance of the excluded species leads to shorter dormancy periods and may be normally dispersed during the rainy season. Examining dormancy data from XSN alongside dispersal syndromes and climatic variables could shed light on these complex interactions. Our study highlights the potential tension between logistical constraints and functional diversity considerations within the XSN, while spatio asynchrony in seed dispersal offers promising avenues for incorporating ecological resilience (Thomas et al. 2014). Integrating such knowledge into restoration strategies is essential for maximizing the success and long-term sustainability of restoration efforts in the Cerrado–Amazonia transition zone.

Relationship Between Dispersal Syndromes and Climate

The regional asynchrony in the fruit dispersal period for the same species observed in this study seems to be associated with an adjustment to the climate variability observed in the studied region (Heydel & Tackenberg 2017; Cortés-Flores et al. 2019; Johnson et al. 2019). Indeed, our analyses assessing the correlation between the fruit dispersal period and climatic variables showed a strong correlation for 46 species (45% of the species included in this analysis). However, among the 19 species with the greatest regional asynchrony in the dispersal period, only four (*Enterolobium schomburgkii*, *Phenakospermum guyannense*, *Solanum lycocarpum*, and *Byrsonima crispa*) showed a significant relationship with precipitation or minimum and maximum air temperatures. The lack of a relationship between the fruit dispersal period and climate variables for a fraction of the studied species (55%) may be linked to three other factors not evaluated here: (1) the adjustment of fruit dispersal may be related to other local environmental conditions, such as soil chemical or physical properties and soil water availability; (2) intraspecific variability related to changes in the composition or activity of seed dispersers; and (3) variability in the fruit maturation time, as a result of genetic variability in the different populations. Further investigations to test these hypotheses may help better understand the reproductive phenology of the studied tree species.

In addition to the dispersal concentration at the beginning of the rainy season, we did not observe significant variation among dispersal syndromes, revealing a certain discrepancy in the pattern observed in other studies. The reduced number of zoochoric species dispersing fruits during periods of higher precipitation in our study does not fully agree with the literature, which shows a higher concentration during the rainy season (Ragusa-Netto & Silva 2007; Jara-Guerrero et al. 2020). This apparent discrepancy may also be related to the fact that we did not evaluate the entire zoochoric assemblage; instead, we evaluated a subset of the species over a large region. Most species studied here have orthodox seeds that tolerate longer storage times and have higher commercial value for restoration. Also, Garwood (1983) indicates that species with a longer seed dormancy period tend to disperse seeds during the rainy season, while species dispersing seeds at the end of the dry season tend to present a short period of dormancy. These results may indicate differences in the dispersion period of zoochoric species with orthodox or recalcitrant seeds (desiccation-sensitive), and should be further investigated.

Relationship Between Dispersal Syndromes and Species Ecological Characteristics

By evaluating the seeds collected and marketed by the XSN, we observed a higher frequency of medium-to-large-sized seeds. This is likely because the size of these seeds provides them greater resistance to desiccation, making them more suitable for restoration projects with direct seeding (Camargo et al. 2002; Hooper et al. 2002; Passaretti et al. 2020). Seed size is also directly related to nutrient storage capacity (Westoby et al. 1996), so large seeds tend to have greater resistance to desiccation and the ability to survive for long periods (Westoby et al. 1996; Dalling & Hubbell 2002; Moles & Westoby 2002). These are important characteristics when choosing species to compose a heterogeneous seed set for direct seeding that is susceptible to desiccation stress until the propagule is established (Doust et al. 2006; Palma & Laurance 2015). However, some species with small seeds have a good on-field establishment rate after direct seeding (Rodrigues et al. 2019) and should not be excluded from restoration projects (e.g. *Astronium* spp., *Bixa orellana*, *Guazuma ulmifolia*, and *Handroanthus* spp., *Senna* spp., *Psidium* spp., *Solanum crinitum*, *Apeiba* spp., *Maclura tinctoria*).

The results of this study contribute to a better delineation of restoration actions in the Cerrado–Amazonia transition, from seed harvesting planning to strategies to increase the diversity and quality of commercial seeds. We showed that most of the tree species used in the restoration action in this region disperse fruits at the end of the dry season and the beginning of the rainy season, and that this does not seem to be related to the dispersal

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syndrome of species. The spatio-temporal variation in seed dispersion is strongly associated with the climate along the Cerrado–Amazonia transition for nearly two-thirds of species, especially considering precipitation and maximum air temperatures. Ultimately, our findings are useful for guiding collection efforts, optimizing the time and resources required for this task, and consequently increasing the effectiveness of ecological restoration projects using seeds.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Climatogram for Nova Xavantina and São José do Xingu.
Figure S2. Species in which seeds were collected in the field between 10 and 23 collection sites.
Figure S3. Years for which there was seed collection in the field for 139 species evaluated between 2011 and 2018 in a region covering 11 municipalities in the Mato Grosso state, Brazil.
Figure S4. Relationship between the proportion of species in the community with zoochoric dispersal for the Cerrado ($n = 34$) and Amazon ($n = 143$) biomes.
Table S1. List of 139 tree species whose seeds were collected between 2011 and 2018 by collector populations in the Cerrado–Amazonia transition region.

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