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RESEARCH ARTICLE

Plant and frugivore species characteristics drive frugivore contributions to seed dispersal effectiveness in a hyperdiverse community

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Abstract

1. Seed dispersal by frugivores is a crucial step of the life cycle of most plants, influencing plant population and community dynamics. Although very important for most ecosystems, we are just beginning to understand which are the mechanisms driving frugivore-mediated seed dispersal. Most studies identifying the drivers of seed dispersal use interaction frequency as a proxy for estimating seed dispersal success, rather than looking at the functional outcomes of those interactions (e.g., contributions to successful seed germination). A valuable tool to link plant–frugivore interactions to seed dispersal success is the seed dispersal effectiveness (SDE) framework, which accounts for the quantity and quality components of seed dispersal.
2. We evaluated which mechanisms, including morphological traits, trait matching and phenological overlap of interacting species, as well as degree of frugivory and feeding behaviour of frugivores, influenced the quantity (interaction frequency and number of seeds dispersed per visit) and quality (seed germination after gut passage) components of SDE. To this end, we combined three methods (focal observations, mist-netting and camera traps) to sample interactions between plants, birds and mammals in a species-rich community of Cerrado in southeastern Brazil.
3. We recorded 590 pairwise interactions between 34 plants and 49 frugivores. We found that phenological overlap among interacting species explained most of the variation in interaction frequencies. Trait matching affected the number of seeds dispersed per visit more for gulpers than mashers and peckers, and frugivore body mass and seed sizes positively affected seed germination. Finally, interaction frequencies had a stronger contribution to SDE, compared with the number of seeds dispersed per visit and seed germination, indicating an indirect effect of phenological overlap on SDE.
4. *Synthesis*. We found that highly abundant plant–frugivore species with the most overlap in their phenologies also yield the highest values of SDE, suggesting that phenological overlap was the most important driver of SDE in this hyperdiverse

community. However, the number of seeds dispersed per visit also influenced SDE and seed germination was species-specific, suggesting that estimating SDE at the community level is necessary to understand how communities work, and the current and future challenges they face.

KEYWORDS
body mass, Cerrado, interaction frequency, phenological overlap, plant-frugivore interactions, seed germination, trait matching

1 | INTRODUCTION

Frugivorous animals play key roles in ecosystems by dispersing seeds and, consequently, influencing the distribution, abundance and genetics of plant populations and communities (Christian, 2001; Jordano et al., 2007; Wang & Smith, 2002). Although crucial for the life cycle of most plant species, we still struggle to link interactions between frugivores and fleshy-fruited plants with their functional outcomes in ecosystems (e.g. successful plant recruitment; Nevo et al., 2023; Simmons et al., 2018). A valuable tool to link plant–frugivore interactions with their actual contributions to plant recruitment is the *seed dispersal effectiveness* framework (hereafter 'SDE'; Schupp, 1993; Schupp et al., 2010). This framework proposes that SDE is formed by a *quantity component*, determined by the frequency of interactions and the number of seeds dispersed per visit to a fruiting plant, and a *quality component*, representing the probability of a particular seed being recruited to the plant population (Figure S1). The SDE quality component is influenced by the mouth and gut treatment provided by a frugivore (e.g. the probability of seed germination after gut passage) and the environmental conditions of the site where seeds are deposited (Schupp, 1993; Schupp et al., 2010). Although useful for the quantification of frugivore contributions to plant recruitment, the SDE framework has been mostly used in studies focussing on communities with low-to-moderate species richness, often oceanic islands (González-Castro, Calvino-Cancela, et al., 2015; Nogales et al., 2017). Consequently, our understanding of the SDE framework in species-rich systems, such as those occurring in the mainland Neotropics, remains limited (Nevo et al., 2023).

Besides linking plant–frugivore interactions to its functional outcomes, the SDE framework may allow us to better understand the relative contribution of different seed dispersal drivers within communities (Gómez et al., 2022). For instance, although multiple drivers of plant–frugivore interactions may also affect seed dispersal success (Quintero et al., 2024), unravelling their relative contribution remains a challenge (Donoso et al., 2017; Pizo et al., 2022; Vázquez et al., 2022). Therefore, linking SDE estimates with plant–frugivore interactions may help us understand the relative contributions of the mechanisms behind each SDE component, and consequently, allow us to predict successful seed dispersal events.

Studies assessing the mechanisms behind plant–frugivore interactions indicate that interactions are influenced by neutral and niche processes (Bender et al., 2018; Dehling et al., 2014; Morán-López et al., 2020; Peña et al., 2023; Pizo et al., 2022; Vitorino et al., 2022). Neutral theory states that plant–frugivore interactions are mostly a product of random encounters between individuals and, therefore, species abundances increase the chances of species encountering and interacting with each other (Peña et al., 2023; Pizo et al., 2022; Vitorino et al., 2022). Because species abundances often vary in space and time, combining the concurrent abundance patterns of interacting species with the timing of their biological events (such as fruit production), provides a useful measure of how much plant–frugivore phenologies overlap (i.e. phenological overlap; Pleasants, 1990). For instance, a plant species that reaches its fruiting peak at the same time a bird species reaches its maximum abundance will have a high phenological overlap, possibly leading to high interaction frequency between those partners (González-Castro, Yang, et al., 2015). Therefore, plant and frugivore species' phenological overlap may better explain variations in interaction frequency and SDE, compared to simply using species abundances (Figure 1a). While the phenological overlap metric that incorporates species abundances has proven useful in pollination (Aizen & Vázquez, 2006) and invasive species studies (Mazzolari et al., 2020), it has not yet been used in frugivory and seed dispersal studies.

Plant–frugivore interactions are also shaped by biological factors (i.e. niche processes), such as morphology and behaviour (Bender et al., 2018; Dehling et al., 2014; Morán-López et al., 2020). For example, a frugivore may interact more frequently with a plant species with matching traits (e.g. gape width and fruit diameter, Figure 1b; Bender et al., 2018; Dehling et al., 2014), provided this alignment of traits facilitates food acquisition (Martins et al., 2024). Nevertheless, the effect of trait matching on plant-frugivore interactions may depend on frugivore feeding behaviour. While gulpers (i.e. frugivores that swallow whole fruits) can only interact with fruits of a specific range size due to gape width limitations, mashers (i.e. frugivores that crush fruits before ingesting them) and peckers (i.e. frugivores that only take pieces of fruit pulp) can interact with a wider range of fruit sizes (Levey, 1987; Moermond & Denslow, 1985). Consequently, gulpers may interact more frequently with fruits that best match their traits, whereas trait matching may not be as important to determine interactions between mashers/peckers and fruits. Furthermore, animal degree of frugivory can also influence plant–frugivore interactions, and

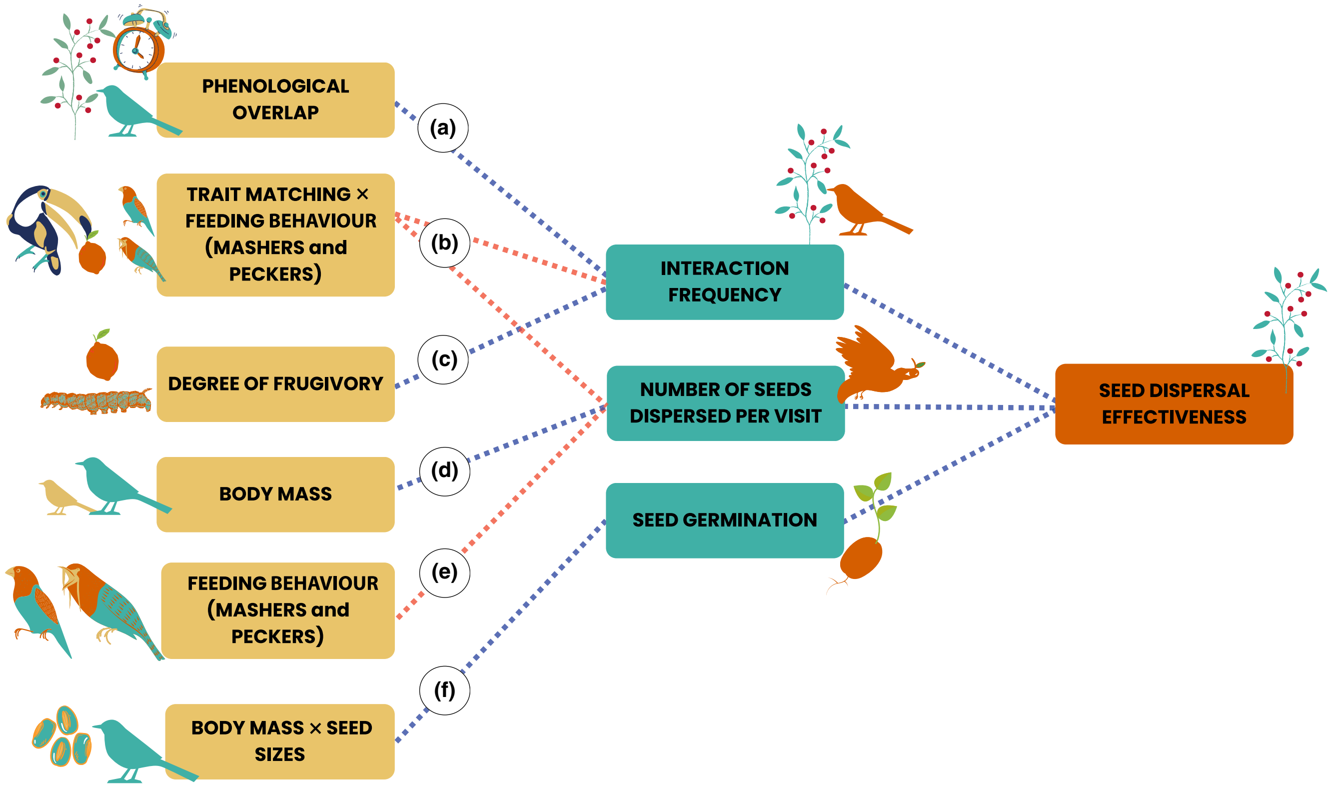

FIGURE 1 Schematic representation of the expected relationships between species characteristics and the subcomponents of seed dispersal effectiveness (SDE). Boxes on the left represent characteristics of frugivores and plants that may affect the subcomponents of SDE: Interaction frequency, number of seeds dispersed per visit and seed germination. Dotted blue and red lines represent the expected positive and negative effects, respectively. Interactions between predictors are depicted with ×. We expect that: (a) plant and frugivore species co-occurring at high abundances, i.e., with high phenological overlap, will interact more frequently compared to species with lower phenological overlap (González-Castro, Yang, et al., 2015); (b) frugivores whose traits better match plant traits will be more frequent partners to plants (Dehling et al., 2014) and disperse more seeds per visit (Peña et al., 2023) compared to frugivores with low trait matching, and this relationship should be stronger for gulpers compared to mashers and peckers (Guerra et al., 2018); (c) highly frugivorous animals will be more frequent partners to plants compared to animals with lower degree of frugivory (Pizo et al., 2021); (d) large frugivores will disperse more seeds per visit compared to small frugivores (Godínez-Alvarez et al., 2020); (e) mashers and peckers will disperse less seeds per visit compared to gulpers (Guerra et al., 2018); and (f) larger seeds will benefit more from passing through the guts of large frugivores, compared to small seeds (Verdú & Traveset, 2004).

animals that depend strongly on fruits may interact more frequently with fruiting plants, compared with animals whose overall diets include a lower percentage of fruits (Pizo et al., 2021; Figure 1c). Estimating the relative contribution of species characteristics governing plant–frugivore interactions is key to understanding their currently unknown impact on SDE.

Species characteristics may also influence the number of seeds dispersed per frugivore visit, consequently impacting SDE. For instance, while large-bodied frugivores may be infrequent visitors to plants due to their lower abundances (McGill, 2008), they also consume a large amount of fruits at once (Jordano, 2000; Figure 1d), ultimately dispersing as many seeds as smaller-bodied frugivores visiting plants more frequently (Godínez-Alvarez et al., 2020). Furthermore, larger frugivores may provide long-distance seed dispersal and transport large seeds that smaller frugivores fail to disperse (Donoso et al., 2020; Jordano et al., 2007). The match between plant and frugivore traits, as well as frugivore feeding behaviour, may also affect the number of seeds dispersed per visit (Guerra et al., 2018; Peña et al., 2023). For example, gulpers interacting with fruits matching their gape width may be more prone to swallow and disperse seeds away from the parental plant than those with a poor matching (e.g. a small gape compared to fruit diameter; Levey, 1986, 1987; Moermond & Denslow, 1985). Conversely, mashers and peckers interacting with fruits that match their gape width may sometimes swallow entire fruits, but often remove pieces of fruit pulp on their beaks during manipulation, increasing the chances of seeds being ejected and dropped beneath the parental plant, or not even being removed from the fruit (Figure 1e; Guerra et al., 2018; Levey, 1986, 1987; Moermond & Denslow, 1985). Although dropped seeds may be rescued by secondary seed dispersers (Christianini & Oliveira, 2009, 2010), most seeds dropped pulp-free beneath parental plants have a low recruitment probability due to interaction with seed predators (Guerra et al., 2018) and negative density-dependent effects on seed and seedling survival (Comita et al., 2014). Therefore, understanding what influences the number of seeds a frugivore disperse per visit is crucial to predict seed dispersal success within communities.

Seed dispersal effectiveness also depends on the gut treatment given to the seed by frugivores with different characteristics, affecting seed germination probabilities (Fuzessy et al., 2016). For example, larger frugivores have longer guts and seed retention times than smaller frugivores, which could result in prolonged seed scarification, either benefiting seed germination or not, depending on seed characteristics (Traveset & Verdú, 2002; Verdú & Traveset, 2004). Specifically, large seeds are more prone to benefit from gut passage compared to small- and medium-sized seeds, because smaller seeds retained for long periods in frugivore guts often suffer from excessive abrasion, decreasing seed germination (Figure 1f; Traveset & Verdú, 2002; Verdú & Traveset, 2004). Therefore, the outcomes of seed germination are species-specific and can hardly be transposed between different plant–frugivore interactions. Although key to SDE, frugivore gut treatment and its effect on seed germination are often neglected in community-level studies (but see Fricke et al., 2019; González-Castro, Calviño-Cancela, et al., 2015; Nogales et al., 2017 for examples in oceanic islands).

Several studies have assessed the drivers behind plant–frugivore interactions (Bender et al., 2018; Dehling et al., 2014; Morán-López et al., 2020; Peña et al., 2023; Pizo et al., 2022; Vitorino et al., 2022). However, understanding the relative importance of such drivers for SDE remains a challenge, especially in species-rich ecosystems. Therefore, we assessed whether plant and frugivore species characteristics influence frugivore contributions to seed dispersal success in a species-rich community of the Cerrado savanna in Brazil. Specifically, we evaluated the effects of plant and frugivore morphological traits (i.e. body mass and seed size), phenological overlap and trait matching of interacting species, as well as animal degree of frugivory and feeding behaviour, on interaction frequencies, the number of seeds dispersed per visit (SDE quantity component) and seed germination (SDE quality component; Figure 1), identifying which drivers explained most variation in frugivore contributions to SDE.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted the study from January 2021 to August 2022 in Estação Ecológica e Experimental de Itirapina (22°12′ S, 47°51′ W), a ca. 5512 ha protected state park in southeast Brazil. This area is covered by Cerrado, a species-rich fire-prone tropical savanna growing on sandy soils, and a biodiversity hotspot with over 4800 endemic plant and vertebrate species (Strassburg et al., 2017). The study area has a wet season concentrated from October to March, with average rainfall of 1090 mm and temperature of 26.3°C, and a pronounced dry season from April to September, with average rainfall of 327.8 mm and temperature of 21.7°C (data from 2014 to 2019 from the park's climatological station). We sampled plant–frugivore interactions on six sites haphazardly established, covering a gradient of increasing tree cover, to sample the natural variation in vegetation density often found in Cerrado (Figure S2). Sites were on average 4.1 km ± 2.8 km from each other, with a minimum of 521 m between the closest sites (Table S1). Permission to work in the area was granted by COTEC—Instituto Florestal, n° 006242/2020-02. SISBIO granted us permission for this scientific research (n° 75907-1) and CEMAVE allowed us to capture birds using mist nets (n° 4560/1).

2.2 | Sampling plant–frugivore interactions

To increase sample coverage of plant–frugivore interactions, we combined different methods. Specifically, we sampled plant–frugivore interactions monthly through focal observations, faecal samples from birds captured with mist nets, and videos from camera traps (see Appendix S1). At each site, we established a 100 m × 10 m plot that was visited every month. Because in Cerrado plant species have patchy distributions and only a few species fruit in winter, from June to September some plots had fewer sampling hours compared with others. Furthermore, in August 2021, there was a wildfire in our study area that suppressed the vegetation of one of our sites. This incident precluded the sampling of interactions within the site for about 5 months, until vegetation was partially recovered, allowing plant–frugivore interactions to be recorded again.

To sample plant–frugivore interactions, we performed monthly focal observations by walking along each plot searching for plants bearing fruits and recording plant–frugivore interactions. During our walk, we stopped every time we observed interactions between animals and fruiting plants, recording them before continuing with our plot walk. The total sampling effort of focal observations ranged from 41.50 to 95.35 h per plot. Additionally, we installed mist nets in four of our plots, sampling each of those once per month, as logistics allowed (see Appendix S2). We used five mist nets at each time, three measuring 3 m tall and 7 m long (mesh 16 mm), and two measuring 2.5 m tall × 7 m long (mesh 20 mm). Nets were opened 2–3 days and checked every 30 min from dawn to dusk, with a pause from 11:30 until 14:30 due to heat peaks during summer. Birds captured in the nets were kept in cotton bags for about 20–30 min or until they defecated. We then checked the bags for seeds that were later identified, allowing us to record plant-frugivore interactions. We considered one interaction event when we found seeds of a specific plant species in a bird faecal sample. To increase sampling completeness (e.g. trying to record shy, nocturnal or less abundant frugivore species), we also installed camera traps on plots with fruiting plants available. Because we only had four cameras, we rotated the cameras across the plots. Specifically, we set one camera per plot in front of a fruiting plant wherever possible, alternating the cameras monthly between plant species and plots to encompass all sites. We chose the plant individuals of each plant species that had the highest number of ripe fruits and hence were potentially most attractive to frugivores. Cameras were set to record videos of 30 s, in intervals of 2 min, during an average of 2662.54 h per plot.

We considered an interaction event when seeds were found in frugivore faeces (based on captured birds) and every time a frugivore visited a plant and interacted with fruits and/or seeds (based on focal observations and camera trap records), even if the outcome was not seed dispersal away from the parental plant. For instance, frugivores that only pecked fruit pulp or dropped fruits or seeds beneath the canopy were recorded as visitors, although the number of seeds they dispersed per visit were set to zero. We included those interactions because we also wanted to understand which plant-frugivore characteristics affected interaction frequency, regardless of the result of interactions for plant regeneration. Carrying fruits to a more suitable perch and sequentially eating the pulp and dropping seeds are common behaviours for some bird species known as mashers and were considered seed dispersal events (i.e. stomatochory; McConkey et al., 2024). During frugivore visits, we recorded how many fruits were swallowed, dropped or carried, and the frugivore feeding behaviour (i.e. gulpers, mashers or peckers, see Section 2.6).

Because we recorded plant–frugivore interactions using three different sampling methods (focal observations, captures with mist nets and camera traps), we first built one species interaction network for each sampling method, compiling the information collected per method across all sites. Combining information across sites allowed us to better estimate the range of interaction partners across the Cerrado. After checking for sampling completeness of each of the three interaction networks (see Appendix S3; Figure S4), we merged the data from different sampling methods using the grand total standardization method (Quintero et al., 2022). Briefly, the grand total standardization approach transforms the interaction frequencies of each sampling method into the probability that a certain pairwise interaction will occur among all interactions sampled. To calculate it, we first weighted the number of interactions (i.e. visits) by dividing them by the corresponding effort in hours used to sample interactions for each method. Specifically, for focal observations and captures with mist nets, we divided interactions by the total amount of hours sampled across all sites, while for camera traps we divided interactions by the total amount of hours sampled per plant species. Second, the values of each interaction frequency matrix were weighted by the total sum of interactions per hour recorded under each specific sampling method. Third, each interaction matrix was weighted by the sampling completeness corresponding to the specific sampling method. Once all matrices were weighted, we combined them to obtain a matrix representing species-interaction frequencies by calculating the average value for each pairwise interaction.

The total sampling effort put into focal observations varied from 41.5 to 95.35 h per plot, whereas the effort of captures with mist nets varied from 302.75 to 453.69 h across plots and sampling with camera traps varied from 141.07 to 2938.37 h per plant species (see Appendix S2). Therefore, the total sampling effort merging all methods was 22,870.34 h.

2.3 | Quantity component of SDE

We used interaction frequency and number of seeds dispersed per visit to estimate the SDE quantity component (Figure S1). As interaction frequency estimates, we used the matrix resulting from the grand total standardization method. To estimate the number of seeds dispersed per visit for interactions recorded from focal observations and camera traps, we multiplied the number of fruits ingested or carried away per visit by the average number of seeds contained inside fruits of each plant species (see Section 2.6). For interactions recorded with mist nets, we used the number of seeds encountered in the faeces of bird individuals as an estimate of the number of seeds dispersed. Then, we calculated the average number of seeds ingested/carried per visit for each pairwise interaction across the different sampling methods.

2.4 | Quality component of SDE

We used the probability of seed germination after treatment in the mouth and gut (hereafter seed germination), to estimate the SDE quality component (Figure S1). To assess whether frugivores influenced seed germination probability, we did germination experiments with gut-passed seeds, manually depulped seeds and whole fruits. Gut-passed seeds were obtained during bird captures with mist nets or collected from easily identifiable frugivore species' faeces in the field, that is when we saw the frugivore defecating or when faeces were very characteristic of a certain animal species. To increase sampling coverage, we also offered fruits from 11 plant species to captive individuals of Pale-breasted Trush *Turdus leucomelas* (all plant species were recorded interacting with this bird species in the wild), which were part of a parallel study (SISBIO n° 78615-1, Comitê de Ética no Uso de Animal—CEUA UNESP n° 1329). All seeds and fruits were identified at the species level and cleaned with a 5% hypochlorite solution before germination experiments to avoid excessive fungal proliferation.

For the germination experiment, seeds and fruits were distributed in Petri dishes (9 cm diameter each) according to treatment (gut-passed, manually depulped and whole fruits). The number of seeds and fruits in each Petri dish depended on their sizes. For small seeds (<2 mm long), we included up to 300 seeds in each Petri dish, whereas for large seeds (>2 mm long), we included from 10 to 30 seeds per Petri dish. For fruits, we followed the same logic, including from 5 to 20 fruits per Petri dish, depending on fruit sizes. Petri dishes were stored in germination chambers set at 27°C and 12–12 dark–light hours and watered every 2–3 days. We considered a germination event when a seed showed the protrusion of the radicle. Seeds and fruits remained in germination chambers until seeds germinated or for a maximum of 6 months.

Despite our large sampling effort on mist netting and additional experiments with captive birds, we were not able to estimate seed germination for all plant–frugivore interactions recorded. Nevertheless, germination experiments allowed us to obtain gut-passed seed germination data from 47% of plant species whose seeds passed through the guts of 33% of frugivore species, and 22% of unique plant–frugivore interactions. We used this subset of interactions to build a quality component SDE matrix containing average values of seed germination.

2.5 | Seed dispersal effectiveness

To estimate SDE, we used a subset of the plant–frugivore interactions for which we had values of seed germination after gut passage. We multiplied interaction frequencies by the average number of seeds dispersed away from the parental plant by seed germination for each unique interaction. We did not estimate the contribution of the quality of seed deposition to SDE (Figure S1) due to the logistical difficulties of identifying and monitoring seedling emergence and survival at the community level. Therefore, our SDE estimate should be interpreted as the contribution of frugivores to SDE prior to seed deposition.

2.6 | Plant and frugivore traits

To assess the influence of plant and frugivore traits on SDE, we selected traits that were likely to affect fruit and seed consumption by frugivores (Bender et al., 2018; Peña et al., 2023; Pizo et al., 2021). For plants, we measured fruit and seed length, diameter and height (Pérez-Harguindeguy et al., 2013), and counted the average number of seeds within 2–20 fruits from 1 to 5 plant individuals (depending on their availability) of each species. We then calculated the average value of each trait for each plant species. Because different measurements of seed dimensions were highly correlated and one dimension was enough to estimate seed sizes, we used only the largest dimension of seeds for each plant species (hereafter seed size). For birds, we measured body mass, gape width and beak length, whereas for mammals we measured body mass and gullet size. Gullet size was measured as the distance between the final teeth of the upper jaw, obtained from mammal skulls (Fuzessy et al., 2022). All birds captured in mist nets were weighed and measured, whereas for bird species that were not captured but observed interacting with fruits, we obtained trait values from databases (Bello et al., 2017; Tobias et al., 2022; Wilman et al., 2014) complemented with gape width and beak length measurements taken from museum specimens (6–10 individuals per species) at the USP Zoological Museum (MZUSP). For mammals, we collected body mass data from databases (Bello et al., 2017; Souza et al., 2019) and measured gullet sizes from specimens (3–10 individuals per species) at the MZUSP. When bird and mammal traits were available from more than one source, we calculated average values considering all sources.

We used the percentages of fruits in frugivore diets as an indicator of the degree of frugivory. We extracted the percentages of fruits in frugivore diets from Wilman et al. (2014) for birds and, when available, from diet reports for mammals (Bueno & Motta-Junior, 2004; Gayot et al., 2004; Pedrosa et al., 2019; Rodrigues da Silva et al., 2014). In addition, frugivore feeding behaviour was determined based on the most common behaviour observed during interaction sampling. Specifically, for each plant–frugivore interaction, the frugivore was classified as a gulper when most of its feeding behaviour towards the plant species consisted of swallowing entire fruits, as a masher when most fruits were crushed and mandibulated before ingestion, sometimes resulting in seeds being dropped beneath the canopy, and as a pecker when the frugivore only pecked the fruit pulp without removing the seed (Levey, 1987; Moermond & Denslow, 1985). Seed predators were also classified as gulpers or mashers, depending on how they fed on fruits.

Using morphological plant and frugivore traits known to affect animal frugivory (gape/gullet size × fruit diameter, and fruit length × beak length, the last available only for birds, Dehling et al., 2014), we quantified trait matching of interacting partners using a multivariate trait congruence approach (Peralta et al., 2020), which accounts for the correlation between traits within species. To accomplish this, we first built a similarity matrix of morphological traits for plants and a similarity matrix of morphological traits for frugivore species using the Gower similarity coefficient (Gower, 1971) and the ‘vegdist’ function from the vegan R package (Oksanen et al., 2022). We used Gower's distance as it allows combining multiple traits scaling differences from single traits on a common scale. Then, using the plant and frugivore trait similarity matrices and a binary species interaction matrix, we ran a Parafit test (Legendre et al., 2002) with the ‘parafit’ function from the ape R package (Paradis et al., 2004). The Parafit test allowed us to assess whether frugivore species interact more frequently with plant species with similar traits, compared to a scenario where species interact randomly.

2.7 | Fruit and frugivore abundance and phenological overlap

To assess the influence of fruit and frugivore abundances and phenological overlap on seed dispersal, we monthly recorded the number of ripe fruits available from all plant species in the sampled plots. Because all plots had the same area, we did not weight fruit abundance per m^2. To estimate fruit abundances, we walked through each plot, identified fruiting species and counted the number of ripe fruits available. We only considered plant individuals that had their main stem originating inside the plot. For shrub and tree species with lower canopies and small crops (<100 ripe fruits), we counted all ripe fruit. For plant species with large crops (>100 ripe fruits), or trees that were too high to allow proper counting, we counted the ripe fruits in subunits of the crop (usually with binoculars) and then made extrapolations for the whole fruit crop (Chapman et al., 1992) or estimated fruit crop size based on plant sizes (see Appendix S4).

To estimate bird abundances, we established two point counts on each plot, 50 m apart from each other. Those point counts were visited once or twice a month, at dawn and dusk (2–4 point counts per plot per month). For each point count, we recorded bird species that were within a 50 m radius for 10 min. Then, we weighted bird abundances by dividing the number of records of each species by the effort in hours applied in point counts for each plot in each month. To estimate mammal abundances, we recorded the number of times mammal individuals passed by the camera traps, originally installed to capture interactions within plots. We also recorded the number of encounters we had with mammal individuals during our focal observations. We then weighted the number of records of each mammal species by the total sampling effort put into focal observations and camera traps per month. To make fruit and frugivore abundance comparable, we estimated relative abundances by dividing the abundance of each species on each month by the total abundance of all recorded species in that specific group (i.e. plants or frugivores). Then, we calculated the degree of temporal overlap between plant and frugivore species based on the abundance of interacting species co-occurring in the same month (i.e. phenological overlap; Mazzolari et al., 2020). Specifically, for each pair of plant–frugivore species we selected the minimum relative abundance of the interacting pair each month. Then, we summed all minimum relative abundances across all months for each pair of species (Pleasants, 1990). Therefore, our measure of phenological overlap accounts for the probability of two species encountering each other over months based on the abundance of fruits and frugivores, and the number of months when both species were present.

2.8 | Replication statement

To understand how plant and frugivore characteristics affect SDE, we used species interaction frequencies, the number of seeds dispersed per visit and seed germination as response variables, and plant-frugivore species characteristics as predictor variables. Data on interaction frequencies and number of seeds dispersed per visit were available for 171 unique plant-frugivore interactions between 49 frugivore and 34 plant species, and data on seed germination were available for 38 unique plant-frugivore interactions between 16 frugivore and 16 plant species. The scale of inference is at the species-interaction level. Variables of interest at the interaction-level are trait matching (continuous) and phenological overlap (continuous) of interacting species and feeding behaviour (factor) of frugivore species. Variables of interest at the species-level are morphological traits (body mass, seed size, and degree of frugivory, all continuous). The units of replication at each appropriate level are presented in Table 1.

2.9 | Data analysis

To determine whether species characteristics influence SDE components, we built three models. The first was a linear mixed model (LMM) with interaction frequency as response variable and degree of frugivory, phenological overlap and trait matching as predictor variables. Because trait matching effects on interaction frequencies may be different for gulpers, mashers and peckers, we added an interaction term between trait matching and feeding behaviour in the model. Also, phenological overlap is sometimes estimated as the number of months species co-occur (temporal overlap), so we performed an additional LMM with interaction frequencies as the response variable, and the temporal overlap, degree of frugivory and trait matching as predictor variables as a way to assess the importance of incorporating the relative abundance of species across time in our measure of phenological overlap (see Table S3).

The second model was a generalized linear mixed model (GLMM), with the rounded average number of seeds dispersed per visit (count variable) as response variable and body mass, feeding behaviour, number of seeds within fruits and trait matching as predictor variables, with Poisson error distribution. We rounded the average values of seeds dispersed per visit to approximate our response variable to what really happens biologically. Because trait matching effects on the number of seeds dispersed per visit may be different for gulpers, mashers and peckers, we also added an interaction term between trait matching and feeding behaviour. The third model was a GLMM with seed germination (i.e. SDE quality component) as the response variable and body mass and seed sizes as predictor variables, with binomial error distribution as the response variable was a proportion. We used our partial data set to fit this third model, and to understand whether the effect of body mass on seed germination depended on seed size, we included an interaction term between body mass and seed size.

We used the 'vif' and 'check_collinearity' functions from the car (Fox & Weisberg, 2019) and performance (Lüdecke et al., 2021) R packages to detect multicollinearity in all models. We used the lme4 (Bates et al., 2015) to build our models and included plant and frugivore species identities as random factors in all models. Continuous predictor variables were scaled using the 'scale' R function. We log-transformed the response variable of the first model to fulfil the normality and homoscedasticity assumptions. We checked for overdispersion in the second and third models using the 'testDispersion' function from the DHARMa R package (Hartig, 2016). All statistical analyses were carried out in R version 4.3.0 (R Core Team, 2023).

Furthermore, to understand the relative contribution of SDE components on total SDE, and of interaction frequencies and

TABLE 1 Scale of inference, scale at which the factor of interest is applied, and the number of replicates at each appropriate scale.

Model	Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
1, 2	Species interactions	Species interactions	171 unique pairwise interactions
1, 2	Species interactions	Species	49 frugivore and 34 plant species
3	Species interactions	Species interactions	38 unique pairwise interactions
3	Species interactions	Species	16 frugivore and 16 plant species

number of seeds dispersed per visit (subcomponents of quantity) on the SDE quantity component, we built two SDE landscapes using the effect.lndscp R package (Jordano & Rodriguez-Sanchez, 2017). The first effectiveness landscape had the quantity component (interaction frequencies multiplied by the number of seeds dispersed per visit) in the *X*-axis and the quality component in the *Y*-axis. The second effectiveness landscape had interaction frequencies in the *X*-axis and the number of seeds dispersed per visit in the *Y*-axis. Both those effectiveness landscapes were built using the partial dataset that included only the interactions in which seed germination data were available. We considered our partial dataset to be representative of our community (see Appendix S5; Table S2).

To determine the relative contributions of each component to SDE, and each subcomponent of quantity to the quantity component, we performed two spatial autocorrelation analyses using bearing correlograms (Gómez et al., 2022; Rosenberg, 2000; Valverde et al., 2016). The bearing correlogram analysis correlates a spatial distance matrix for each component of SDE (or subcomponent of quantity) with a distance matrix of SDE (or quantity component) using the Mantel test and including orientation. That is, it identifies whether the correlation between matrices is stronger or weaker in certain angles, considering that the angles represent each of the axes in the effectiveness landscape graphs. In other words, the bearing correlograms showed which components and subcomponents were driving most changes in SDE, based on how the values were distributed across the landscapes. We performed the bearing correlograms using the geosphere (Hijmans et al., 2019), aspace (Buliung & Remmel, 2008) and ecodist (Goslee & Urban, 2007) R packages.

3 | RESULTS

We recorded a total of 590 interactions, 14,544 seeds swallowed or carried away from fruiting plants and 171 unique pairwise interactions between 7 mammals, 42 birds and 34 plant species (Figure S5). Of the recorded interactions, 329 were from focal observations, 205 from camera traps and 56 from bird captures with mist nets.

We found that phenological overlap had a positive effect on plant–frugivore interaction frequencies ($t=2.92$, $p=0.004$; Table 2; Figure 2A). In addition, trait matching had a negative effect on the number of seeds dispersed per visit for interactions with mashers compared to gulpers ($z=-2.38$, $p=0.019$, Table 2; Figure 2B), and gulpers dispersed more seeds per visit compared to mashers ($z=-3.40$, $p=0.001$, Table 2; Figure 2C). Furthermore, larger seeds benefited more from passing through the gut of large animals compared with smaller seeds ($z=3.17$, $p=0.002$, Table 2; Figure 2D).

Values of SDE ranged from a minimum of 0 to a maximum of 1.97 across interacting species. There was a spatial autocorrelation of SDE along the quantity component axis, but not along the quality component axis (Table 3). This result indicates that SDE variation was strongly affected by the quantity component and suggests that our seed dispersal system was mostly quantity-driven (Mantel test$=0.320$, $p=0.001$). Conversely, there was a spatial autocorrelation of the quantity component along the interaction frequency axis and the number of seeds dispersed per visit axis, indicating both subcomponents explain variation in the SDE quantity component (Table 3; Figure 3b). However, interaction frequencies drove more changes to the SDE quantity component compared to the number of seeds dispersed per visit (Mantel test$=0.318$, $p=0.002$ vs. Mantel test$=0.238$, $p=0.019$, respectively; Figure 3b). Overall, both landscapes suggest that SDE was primarily driven by interaction frequencies, indicating an indirect effect of phenological overlap on SDE.

4 | DISCUSSION

Species abundances, morphology, phenology and behaviour are often highlighted as important mechanisms driving plant-frugivore interactions (Bender et al., 2018; González-Castro, Yang, et al., 2015; Morán-López et al., 2020; Pizo et al., 2022). Nevertheless, the relative contributions of those drivers to the functional outcomes of plant-frugivore interactions (e.g., contributions to successful plant recruitment) are yet to be unravelled. Here, we showed that although phenological, morphological and behavioural characteristics shape frugivore contributions to SDE, phenological overlap between interacting species was the most important driver of SDE provided by birds and mammals in a species-rich Cerrado community. This result indicates that highly abundant plant and frugivore species co-occurring in space and time had the highest pairwise SDE values.

Phenological overlap between interacting species affected frugivore contributions to SDE due to its influence on species interaction frequencies, the most important subcomponent of SDE. This relationship between phenological overlap and interaction frequencies was tightly linked to the inclusion of species abundances in the phenological overlap estimate, as solely the number of months species co-occur (temporal overlap) failed to explain variation in interaction frequencies (Table S4). Therefore, our results indicate that to have high SDE, interacting species not only need to overlap in time, but also to have high abundances at the same time. This finding reinforces the dominant role of species abundances as drivers of plant–frugivore interactions in our Cerrado community, as observed in other communities dominated by generalist species (Pizo et al., 2022). For instance, *Miconia rubiginosa* produces large fruit crops and has asynchronous fruit ripening among individual trees (Campagnoli & Christianini, 2022), facilitating high phenological overlap at the species level with several frugivores. Interactions involving *M. rubiginosa* encompassed five out of 10 of the highest values of SDE. Also, the fruiting time (fruiting season) can be critical for plant–frugivore interactions (Maruyama et al., 2013). For example, *Miconia minutiflora* offers large fruit crops in the dry season, when fruits from other fleshy fruited plants are scarce, representing a reliable resource for birds and ultimately receiving numerous visitors in a short period of time (Figure S5). Indeed, *Miconia* species represent key resources

TABLE 2 Coefficient table for models assessing the effects of plant–frugivore characteristics on the quantity and quality components of seed dispersal effectiveness. The results for the categorical variable 'feeding behaviour' are shown as a comparison to the reference level (gulpers). For models (1) we used a linear mixed model and t-values, while models (2) and (3) were generalized linear mixed models with Poisson and Binomial error distributions, respectively, with z-values. All models included plant and frugivore species identities as random factors. Bold values indicate significant results ($\alpha = 0.05$). Interactions between predictor variables are depicted with ×.

Response variables	Fixed effects	Estimate	Std. error	df	Test value	*p*
(1) Interaction frequencies	Intercept	−6.382	0.172	39.972	−37.167	**<0.001**
	Degree of frugivory	0.081	0.096	42.940	0.844	0.403
	Phenological overlap	0.242	0.083	148.030	2.922	**0.004**
	Trait-matching	−0.017	0.093	135.543	−0.181	0.857
	Feeding behaviour: masher	0.384	0.203	42.629	1.889	0.066
	Feeding behaviour: pecker	−0.469	0.465	145.026	−1.010	0.314
	Trait-matching × feeding behaviour: masher	0.203	0.447	156.932	0.454	0.650
	Trait-matching × feeding behaviour: pecker	−0.046	0.493	157.608	−0.094	0.925
(2) Number of seeds dispersed per visit	Intercept	2.401	0.218		10.993	**<0.001**
	Body mass	0.201	0.161		1.249	0.211
	Trait-matching	0.128	0.130		0.981	0.327
	Feeding behaviour: masher	−1.225	0.359		−3.406	**0.001**
	Feeding behaviour: pecker	−140.996	183.916		−0.767	0.443
	Number of seeds within fruits	6.411	0.479		13.382	**<0.001**
	Trait-matching × feeding behaviour: masher	−0.770	0.330		−2.337	**0.019**
	Trait-matching × feeding behaviour: pecker	−56.183	130.048		−0.432	0.666
(3) Seed germination	Intercept	−3.783	0.833		−4.541	**<0.001**
	Body mass	−11.797	3.756		−3.141	**0.002**
	Seed size	4.719	1.349		3.499	**<0.0001**
	Body mass × seed size	23.645	7.456		3.171	**0.002**

across the Neotropics due to their large crops of small- to medium-sized fruits and numerous seeds, as well as their long fruiting periods (Messeder et al., 2020, 2021). Conversely, migratory birds (such as *Elaenia mesoleuca*, *Elaenia chiriquensis*, *Tyrannus savana*, *Vireo olivaceus*; Motta-Junior et al., 2008) are present for short periods of time and bounded by forbidden links with plants not fruiting during their stopover (Olesen et al., 2011). Not surprisingly, these bird species had fewer interactions in the Cerrado community compared to resident species (such as *Turdus leucomelas*, *Tangara cayana* and *Thraupis sayaca*; Motta-Junior et al., 2008), which are present throughout the year.

Although phenological overlap explained significant variation in interaction frequencies (Figure 2A) and SDE, other mechanisms, such as negative density dependence (Carlo et al., 2024; Carlo & Morales, 2016), could be responsible for part of the unexplained variation in our models. For instance, fruit consumption by frugivores may depend not only on the encounters with individuals of a certain plant species but also on preferences and selection for certain fruits or their nutritional content (Carlo et al., 2024). Frugivore preferences for rare fruiting plants, potentially to obtain a balanced nutrition (Blendinger et al., 2022; Morán-López et al., 2018), may explain why a few plant–frugivore species interacted frequently in the Cerrado community, even under relatively low values of phenological overlap (e.g. frugivores interacting frequently with the rarer *Aegiphila verticillata*, even though that plant species produces small fruit crops lasting a short period of time during the fruiting peak of other plants in the community).

Overall, highly frugivorous animals did not interact more frequently with plants, potentially due to omnivorous generalists consuming both fruits and insects being overrepresented (see Pizo et al., 2022). In this Cerrado community, omnivorous species (i.e. <70% degree of frugivory) accounted for 87% of interactions, while highly frugivorous species (i.e. ≥70% degree of frugivory) encompassed only three bird species accounting for 13% of interactions (*Tangara cayana*, *Penelope superciliaris* and *Ramphastos toco*). Furthermore, trait matching did not affect the frequency of interactions, neither for gulpers nor mashers or peckers, as also observed in other studies (Pizo et al., 2022). Even when only considering legitimate interactions (i.e. frugivores that swallowed whole fruits), trait matching still did not affect interaction frequencies (Table S5). The absence of trait matching influence on interaction frequencies may result from a predominance of small-sized

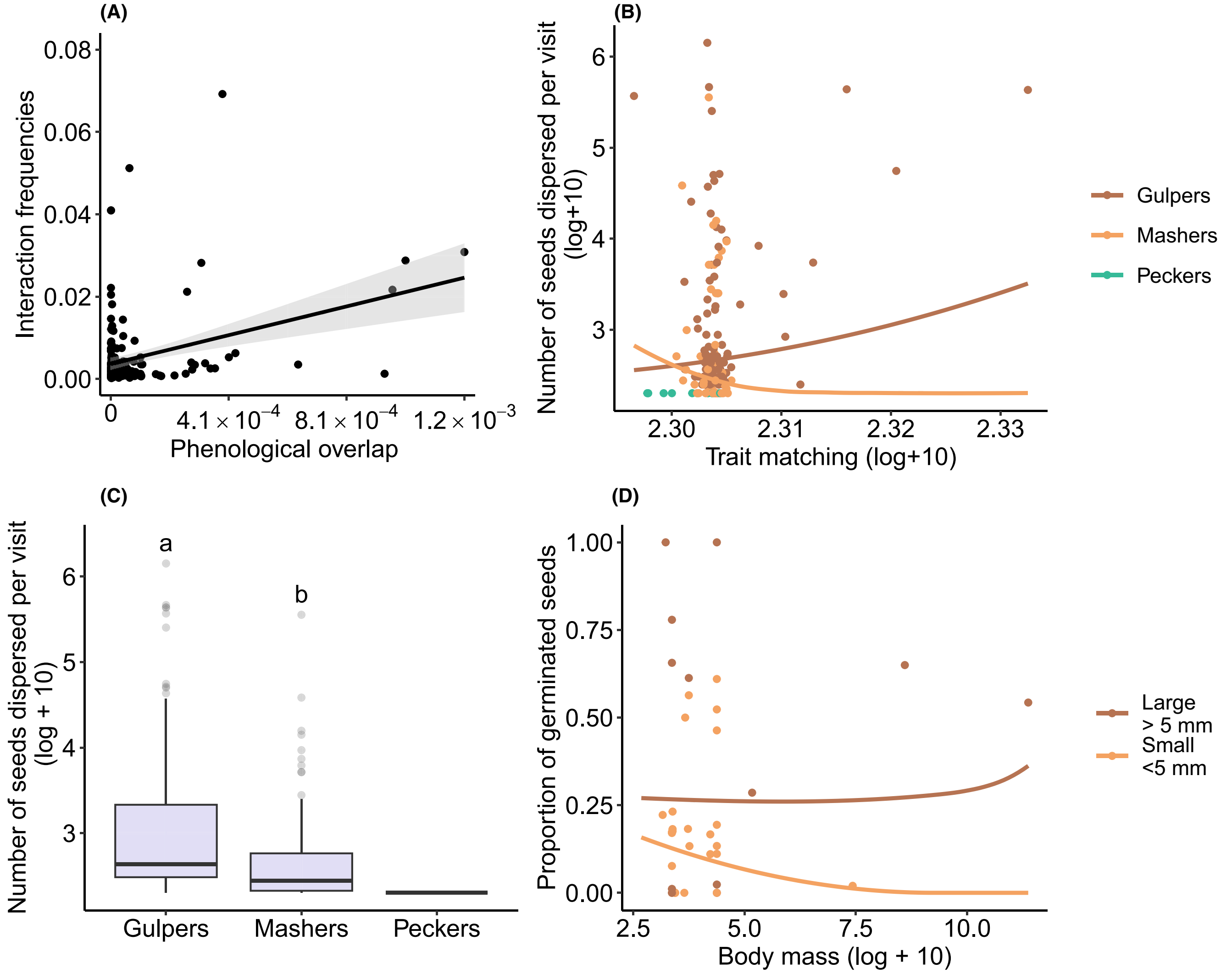

FIGURE 2 Relationship between (A) plant–frugivore interaction frequencies and phenological overlap of interacting partners; (B) the number of seeds dispersed per visit and trait matching for each feeding behaviour (gulpers, mashers and peckers); (C) the number of seeds dispersed per visit and frugivore feeding behaviour (gulpers, mashers and peckers); and (D) the proportion of germinated seeds and frugivore body mass for small and large seeds. In scatterplots, each dot represents a pairwise interaction between a plant and a frugivore species. In (A), a least-square trend line is shown to illustrate the direction of effects, while in (B, D), we used values predicted from the generalized linear mixed-effects models to build the trend lines (see Section 2). In (C), the middle line indicates the median, the bottom and top box limits represent the first and third quartiles, respectively. Whiskers indicate the most extreme points 1.5 times the interquartile range, circles indicate outliers, and different letters represent significant differences between behaviours. Because peckers never dispersed seeds, there was no variability within the pecker group to compare against the other groups and no statistically significant differences in post-hoc tests could be detected. In (D), two levels of seed size are illustrated (large and small seeds), even though seed size was used as a continuous variable in the model. Solid lines represent significant relationships and shaded areas represent the standard errors associated with model predictions. Some variables were log-transformed to improve the visibility of results in the figure.

fruits in the community (Pizo et al., 2022). However, our study system had a relatively wide range of fruit sizes, varying an order of magnitude (from 3 to 31 mm). Nevertheless, such fruit sizes did not prevent frugivores from interacting with fruits larger than their gape widths and eventually dispersing seeds, as we observed a few interactions in which birds carried relatively large fruits in their beaks (e.g. Sayaca Tanager *Thraupis sayaca* and the soft fruits of *Campomanesia pubescens* with an average of 15.6 mm diameter) or swallowed large pieces of fruit pulp with seeds immersed in it (Jays *Cyanocorax chrysops* and *C. cristatellus* interacting with fruits of the terrestrial Bromeliad *Bromelia balansae*, with an average of 27 mm diameter).

While unimportant in explaining interaction frequencies, trait matching and feeding behaviour were important to explain the number of seeds dispersed per visit, the second most important subcomponent of SDE. Specifically, trait matching mattered the most for frugivores behaving as gulpers, compared with mashers, likely because many seeds still get dropped even when mashers and fruit traits match (e.g. *Tangara cayana* with gape width 7.6 mm dropped every seed of *Myrsine guianensis* with fruit diameter 3.9 mm).

TABLE 3 Spatial autocorrelation analyses using bearing correlograms to assess the relative contributions of each seed dispersal effectiveness (SDE) component to total SDE, and of interaction frequencies and the number of seeds dispersed per visit to the total SDE quantity component. Bold values indicate significant results ($\alpha = 0.05$).

Spatial autocorrelation	Mantel *r*	*p*
Quantity component	0.3203	**0.001**
Quality component	0.0228	0.780
Interaction frequencies	0.3186	**0.002**
Number of seeds dispersed per visit	0.2381	**0.019**

Nevertheless, in Cerrado, a portion of the seeds dropped beneath parental plant crowns by mashers may escape predation and be secondarily dispersed (Christianini & Oliveira, 2010; Guerra et al., 2018). Also, we observed a few potential cases of stomatochory by mashers (i.e. events of seed dispersal without seed swallowing; McConkey et al., 2024), when birds carry fruits larger than their gape widths and latter consume the fruit pulp and drop the seeds (e.g. *Thraupis sayaca* carrying the fruits of *Campomanesia pubescens*). Drivers of the number of seeds dispersed by mashers may depend on fruit traits that were not assessed in this study (e.g. number of seeds within fruits, Rojas et al., 2021) and, hence, deserve further investigation. Furthermore, we highlight the importance of considering frugivore behaviour when investigating species roles in seed dispersal (Morán-López et al., 2020).

Frugivore body size was not related to the number of seeds dispersed per visit, even though some of the largest frugivore species had the highest values of SDE. Specifically, the introduced Wild boar *Sus scrofa* and the Crab-eating fox *Cerdocyon thous*, though infrequent visitors of *Alibertia concolor*, possibly due to their low abundance (McGill, 2008), consumed numerous fruits on each visit (Campagnoli & Christianini, 2022; Godínez-Alvarez et al., 2020). Despite detecting a few relatively large-bodied frugivores interacting with plants (e.g. the introduced *S. scrofa*, Grey brocket deer *Mazama gouazoubira*, *C. thous*, and Red-legged seriema *Cariama cristata*), other native frugivores with large body masses are already locally extinct in our sites (e.g. Greater rhea *Rhea americana*, Collared- and White-lipped peccaries *Tayassu pecari* and *Pecari tajacu*, and Tapir *Tapirus terrestris*). This defaunation process in the Cerrado may increase the importance of small frugivores for seed dispersal and plant regeneration (e.g. Béllo Carvalho et al., 2023; Fuzessy et al., 2022; Vidal et al., 2013), even though they are unlikely to provide long-distance seed dispersal (Pérez-Méndez et al., 2017; Spiegel & Nathan, 2007), plant colonization of distant sites (Jordano et al., 2007) and dispersal of large seeds (Goebel et al., 2022). Further studies assessing the contributions of large-bodied frugivores to SDE including seed deposition patterns may help clarify the role of body mass on SDE and the consequences of extinction cascades in the Cerrado (Bello et al., 2015; Fricke et al., 2022; Galetti et al., 2013).

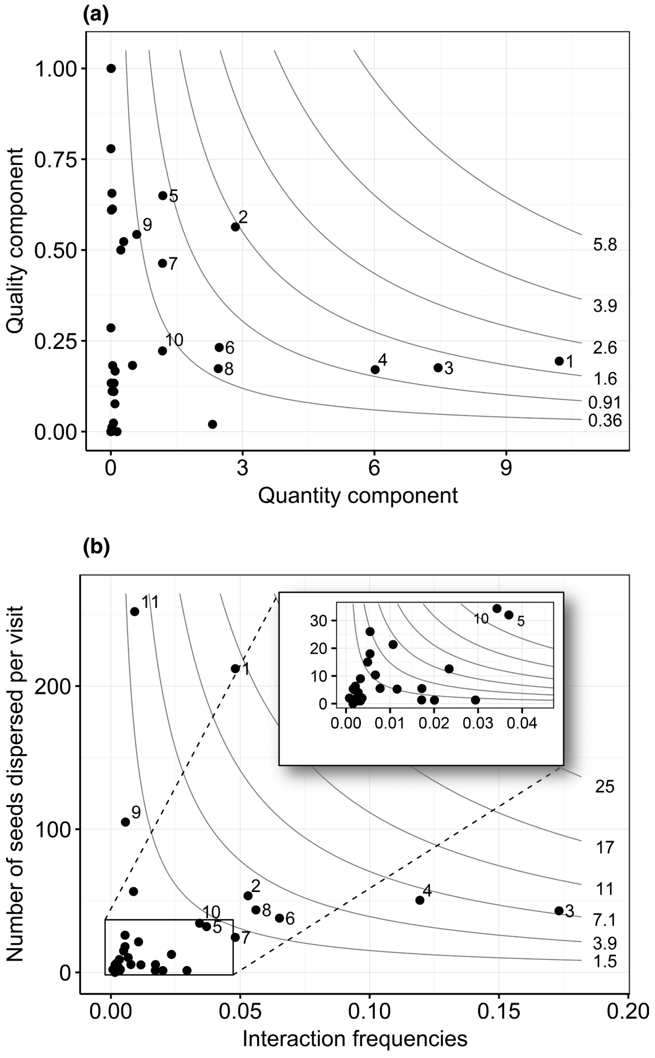

FIGURE 3 Seed dispersal effectiveness (SDE) landscapes of frugivory showing interacting species and their respective (a) SDE quality (probability of seed germination) and quantity (interaction frequency × seeds dispersed per visit) components; and (b) the two subcomponents of the SDE quantity component (interaction frequencies and number of seeds dispersed per visit). Each dot represents a pair of interacting species and isoclines represent all values of *X*- and *Y*-axes yielding the same values of (a) SDE and (b) SDE quantity component. To build the landscapes we used a subset of interactions for which we had seed germination values. The inset plot on (b) zooms the cloud of points concentrated in the low left of the graph. Numbers 1–10 represent the pairs of plant–frugivore interacting species with the highest values of SDE: 1: *Miconia minutiflora–Turdus leucomelas*, 2: *Miconia rubiginosa–Thraupis sayaca*, 3: *Miconia minutiflora–Tangara cayana*, 4: *Miconia rubiginosa–Elaenia* sp., 5: *Alibertia concolor–Cerdocyon thous*, 6: *Miconia rubiginosa–Tangara cayana*, 7: *Miconia rubiginosa–Turdus leucomelas*, 8: *Miconia minutiflora–Elaenia* sp., 9: *Alibertia concolor–Sus scrofa*, 10: *Miconia rubiginosa–Dacnis cayana*. Number 11 represents *Miconia rubiginosa–Cariama cristata*, which was quantitatively important, but not qualitatively important, appearing only in (b).

Though seed germination quality was the least important subcomponent explaining variation in SDE, different frugivores provided different outcomes for seed germination. Overall, our results agree with studies showing that frugivores improve seed germination primarily by removing the fruit pulp (i.e. deinhibition), while seed physical changes during gut passage (i.e. scarification) play a minor role (Fricke et al., 2019; Ribeiro et al., 2016; Silveira et al., 2012; Figure S6a). In addition, we found that seed germination depended on seed size and frugivore body mass. Specifically, larger seeds benefited more from passing the guts of large animals than smaller seeds, possibly due to smaller seeds being damaged by the scarification process associated with longer-gut passages (Fricke et al., 2019; Ribeiro et al., 2016; Silveira et al., 2012). For example, *Cariama cristata* strongly contributed to seed dispersal of *Miconia rubiginosa* by consuming a large amount of seeds (Figure 3b, interaction 11), despite few of the ingested seeds surviving after passing through the gut of this large bird. This reinforces the importance of evaluating the output of interactions, not only interaction frequencies (Simmons et al., 2018), including seed germination at the species- and even at the individual-level, as the probability of germination of a seed after gut passage may be species- and/or individual-specific (Campagnoli et al., 2024; Ribeiro et al., 2016; Silveira et al., 2012; Verdú & Traveset, 2004). Furthermore, gulpers and mashers provided similar seed germination probabilities after gut passage (Figure S6b), suggesting the potential relevance of mashers to seed dispersal and plant recruitment, especially for plants producing small fruits and seeds that are more easily swallowed by them (Ruggera et al., 2021).

In this Cerrado community, the SDE quantity component had a stronger influence on the contribution of frugivores to SDE compared with the SDE quality component. These results agree with studies showing the most frequent frugivore visitors are top contributors to plant recruitment success, while qualitative differences in seed treatment, and microhabitats of seed deposition frugivores provide, seem to play minor roles (Quintero et al., 2024; Rehling et al., 2023). Furthermore, our results support previous research showing that ecosystems dominated by generalist species are mostly quantity-driven (Gómez et al., 2022) and, hence, more affected by neutral rather than niche processes (Krishna et al., 2008; Pizo et al., 2022; Vázquez et al., 2022). Nevertheless, our understanding about how the relative contribution of niche and neutral processes to the seed dispersal process varies across geographically and temporally distant communities remains limited. Unravelling those patterns may enhance our ability to predict interactions across communities in different ecological contexts (Vázquez et al., 2022).

Although our results show a mostly quantity-driven community, we should acknowledge that our SDE estimate was based on a partial estimation of the quality component, considering seed germination after interaction with frugivores, but disregarding seed and seedling fate after seed deposition on the ground (Schupp, 1993; Schupp et al., 2010). Multiple factors may promote or limit seed survival and seedling establishment after seed deposition, such as secondary seed-dispersal (Christianini & Oliveira, 2010), post-dispersal seed predation (Ferreira et al., 2011), seedling competition (Harms et al., 2000), herbivory (Moles & Westoby, 2004) and/or specific microclimatic conditions (Mariano et al., 2019), affecting the SDE quality component. Given the patchy nature of plant distribution in the savanna, accounting for differences in seed deposition patterns and seedling establishment may provide new insights in understanding frugivore contributions to SDE in the Cerrado.

Because interacting species with the largest overlapping phenologies yielded the highest values of SDE, our study highlights the importance to understand not only the impacts of species extinctions, but also of population declines (i.e., declines in species abundances) on seed dispersal dynamics (Rumeu et al., 2017). Furthermore, ongoing changes in global climate and fire regimes are likely to increase phenological mismatches between plants and frugivores, altering species interactions (Pedroso et al., 2021; Pivello et al., 2021; Tylianakis et al., 2008) and SDE. Moreover, although plant-frugivore interactions play a key role in seed dispersal, estimating SDE at the community level is necessary to understand the current and future challenges these communities face and to develop adequate conservation and management strategies.

AUTHOR CONTRIBUTIONS

Mariana Campagnoli, Alexander Christianini and Guadalupe Peralta conceived the ideas and designed the methodology; Mariana Campagnoli and Alexander Christianini collected the data; Mariana Campagnoli and Guadalupe Peralta analysed the data with input from Alexander Christianini. Mariana Campagnoli led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2rbnzs7x6 (Campagnoli et al., 2024).

STATEMENT ON INCLUSION

Our study brings together authors from two different countries of South America, including two scientists based in the country where the study was carried out. We engaged with the local stakeholder and staff to provide feedback during our research by producing and distributing to them a small field guide of seed dispersers and plants commonly found in the state park, highlighting the main practical results of our work. The field guide can be accessed here: https://www.researchgate.net/publication/364354229_Guia_de_dispersores_e_frutos_comuns_do_Cerrado_do_estado_de_Sao_Paulo.

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SUPPORTING INFORMATION

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

Figure S1. Schematic representation of the seed dispersal effectiveness framework.

Figure S2. Photos of the six sampling plots.

Figure S3. Sampling completeness curves for Cerrado sensu stricto and Cerradão.

Figure S4. Sampling completeness curves for each sampling method.

Figure S5. Interaction frequency and seed dispersal effectiveness networks.

Figure S6. Boxplots showing the effects of gut passed (gulpers and mashers), depulped and whole fruit treatments on seed germination.

Table S1. Matrix showing distances between sampling plots.

Table S2. Comparison between the data contained in the complete and partial datasets.

Table S3. Results from model 1a using temporal overlap (i.e the number of month species co-occur) instead of phenological overlap.

Table S4. Results from model 1b using legitimate seed-dispersal interactions only.

Appendix S1. Sampling methods.

Appendix S2. Sampling effort across plots.

Appendix S3. Sampling completeness.

Appendix S4. Estimation of *Miconia rubiginosa* fruit abundance.

Appendix S5. Details on the partial dataset.

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