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ARTICLE
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Intrinsic and extrinsic drivers shape frugivore functional diversity within a tree population

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Abstract

In sessile organisms like plants, interactions with strong fitness implications, such as seed dispersal, are influenced by individual traits and the surrounding environmental context. Recent studies have revealed that individual variation in plant populations shapes mutualistic interactions, but the focus often remains on the taxonomic diversity of partners. We examined how intrinsic (phenotypic and phenological traits) and extrinsic (spatial context) drivers of differences in individual plants influence the multidimensional functional diversity of frugivorous birds. Our study system was a native plant population of *Schinus terebinthifolia*, a species that is invasive worldwide and whose fruits are highly attractive to birds. Despite the limited functional differentiation among the most common generalist frugivores, our findings demonstrate that plant phenotypic traits and local environmental conditions distinctly influence multiple facets and dimensions of avian alpha diversity. Tree height increased functional richness and divergence, while human infrastructure reduced both indices. Crop size had positive effects on functional divergence and regularity, and tree cover reduced functional richness. Most effects, particularly the strongest ones, were mediated by species richness, highlighting how variation in functional diversity largely stems from changes in the number of frugivorous species foraging on plants. Our results underscore the importance of moving beyond taxonomic metrics to understand diversity interaction patterns, providing insights into habitat management and restoration, and advancing our understanding of how the diversity of frugivore traits influences frugivory and seed dispersal of plant individuals.

KEYWORDS
functional divergence, functional regularity, functional richness, plant population, seed dispersal

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INTRODUCTION

Frugivory and seed dispersal by animals, particularly birds, are critical for sustaining biodiversity and maintaining ecosystem function (Bascompte & Jordano, 2007; Herrera, 2002; Kissling et al., 2009). These mutualistic interactions, involving resource and service exchange, form networks that regulate plant colonization and abundance, vegetation growth and regeneration, and support the persistence of frugivore populations (Bascompte & Jordano, 2007; Herrera, 2002; Jordano et al., 2011). Despite recent advances, research has focused mainly on community-level interactions, leaving gaps in knowledge about individual-level variation of interactions for plants, particularly beyond the taxonomic facet of the diversity of mutualist consumers (Bascompte & Jordano, 2007; Jordano et al., 2011; Vissoto et al., 2022).

Within plant populations, plant–frugivore interactions may be shaped by extrinsic drivers, including the spatial context in which individuals grow, and intrinsic drivers, such as phenotypic and phenological traits influencing disperser attraction and foraging behavior (Schupp et al., 2019; Tonos et al., 2022; Vissoto et al., 2022). Plant height, crop size, and fruiting duration are key intrinsic drivers shaping plant–frugivore interactions by affecting disperser diversity and visitation rates (Guerra et al., 2017; Miguel et al., 2018; Vissoto et al., 2022; Vizentin-Bugoni et al., 2021). Among extrinsic drivers, neighborhood effects from fruit density around plant individuals, along with the cover of surrounding vegetation and human infrastructure, play significant roles in plant–animal interactions (Cruz et al., 2013; Gleditsch et al., 2017; Herrera et al., 2011; Hopson et al., 2020; Morales & Carlo, 2006; Schneiberg et al., 2020; Vissoto et al., 2022). The relative influence of intrinsic and extrinsic drivers can enhance or reduce frugivory and seed dispersal rates, with important implications for plant and frugivore population and community dynamics (Miguel et al., 2018; Morales & Carlo, 2006; Vissoto et al., 2022).

Plant–frugivore relationships at the population level of plants have often been evaluated from a taxonomic perspective (Crestani et al., 2019; Miguel et al., 2018; Vissoto et al., 2022). Exploring these relationships from a functional viewpoint may provide novel insights, as these two facets of diversity are often complementary (Díaz & Cabido, 2001). Functional diversity refers to the distribution and range of functional traits of the organisms in a community, providing insight into how ecosystems respond to environmental changes and contribute to ecosystem processes (Díaz & Cabido, 2001). Functional traits are measurable characteristics of individual organisms relating to morphology, physiology, phenology, and behavior that reflect the role played by the species in the ecosystem and can be used to explain and compare their responses to the environment and/or their effects on ecosystem functioning (Dehling et al., 2014; Lefcheck et al., 2015).

Recently, functional diversity studies have advanced through a unified framework that defines three biologically complementary dimensions of alpha functional diversity (FDα) metrics and incorporates improvements in trait space representation (i.e., transformations or visualizations of trait matrices used to assess functional metrics; Blonder et al., 2014; Mammola et al., 2021; Mammola & Cardoso, 2020). The Pavoine–Bonsall scheme classifies FDα metrics into three core dimensions: functional richness (FRic), divergence (FDiv), and regularity (FReg), which correspond to the sum, mean, and regularity of differences among observations, respectively (Mammola et al., 2021; Pavoine & Bonsall, 2011). Combined with probabilistic hypervolumes, which model trait space as a cloud of stochastic points sampled from species traits, enabling the detection of density variation within the space, this framework offers a robust approach for evaluating how FDα responds to environmental variation (Blonder et al., 2014; Mammola et al., 2021; Mammola & Cardoso, 2020). FRic corresponds to the total volume of the hypervolume, FDiv captures trait space spread as the average distance among stochastic points or to the centroid, and FReg (or evenness) measures the regularity of trait distribution by comparing the observed hypervolume to a hypothetical one with traits and abundances evenly distributed (Mammola et al., 2021).

Within the functional facet of diversity, plant–frugivore studies have assessed three main topics: (1) the matching of functional traits between plants and frugivores, (2) the flexible response of functionally specialized dispersers to variation in fruit production, and (3) the disruption of seed dispersal via the elimination of key traits under environmental change (Bender et al., 2018; Campagnoli et al., 2024; Quitián et al., 2019; Vizentin-Bugoni et al., 2022). While these studies have advanced knowledge on frugivory and seed dispersal theory and informed restoration and conservation initiatives, they were focused primarily on the community level. The influence of individual plant variation and spatial context on frugivore functional diversity has not been adequately studied, with population-level research usually limited to emphasizing complementarity and redundancy of different functional groups in seed dispersal (e.g., Blendinger, 2017; Lavabre et al., 2016) or how variation in local conditions across plant individuals drives unequal functional contributions to seed dispersal (Isla et al., 2023). This limitation has hindered our understanding of how characteristics of individual

plants in a population influence complementary dimensions of frugivore trait diversity, which potentially impact frugivore populations, the dynamics of resource use, and the demographic consequences of seed dispersal.

Here, we assessed how intraspecific variation in a Brazilian pepper *Schinus terebinthifolia* Raddi (Anacardiaceae) population influences the diversity of functional traits of birds consuming its fruits. This abundant plant exhibits variable phenotypes, thrives in diverse habitats, and serves as the primary source of fruits during the cold season in southern Brazil (Vissoto et al., 2019, 2022). In this region, it produces a large crop of small fruits consumed by at least 19 bird species across nine families, with six generalist frugivores accounting for 80% of the fruit consumption (Vissoto et al., 2019, 2022). This plant is globally invasive (Hight et al., 2002) and understanding the mechanisms underlying its seed dispersal is essential for developing effective management strategies to limit its spread. Specifically, we examined the effect of intrinsic and extrinsic drivers of individual differences in a plant population on avian FRic, FDiv, and FReg. We expected that increases in tree height, crop size, fruiting duration, fruit density, and tree cover around individual plants would positively influence frugivore abundance and the occurrence of functionally distinct species, ultimately expanding the trait space in volume and spread (Mammola & Cardoso, 2020; Vissoto et al., 2022). Taller trees are more detectable, while larger crops and longer fruiting periods are more attractive and profitable for frugivores (Guerra et al., 2017; Miguel et al., 2018; Vissoto et al., 2022; Vizentin-Bugoni et al., 2021). High fruit density in the vicinity can attract additional frugivore species and promote frugivory through facilitation, while increased vegetation cover can enhance frugivore species richness and frugivory rates (Gleditsch et al., 2017; Herrera et al., 2011; Melo et al., 2020; Vissoto et al., 2022). Conversely, increased human infrastructure negatively impacts frugivory (Schneiberg et al., 2020; Vissoto et al., 2022). Thus, we hypothesized a negative effect of human infrastructure on FRic and FDiv and positive effects of the remaining drivers on both indices. Since the increased abundance of functionally similar species is expected to maximize trait space evenness, while the addition of functionally distinct species can offset this by filling underrepresented areas (Mammola & Cardoso, 2020; Mouchet et al., 2010), we hypothesized a positive effect of human infrastructure on FReg, while predicting a negative effect on the other drivers. We summarized the above causal assumptions in the directed acyclic graph (Figure 1). Since FDα metrics can be closely related to species richness (Mouchet et al., 2010), our estimates encompassed all direct (i.e., X → FDα) and indirect (i.e., X → species richness → FDα) effects mediated by species richness on FDα metrics of the bird community in each individual plant (Figure 1).

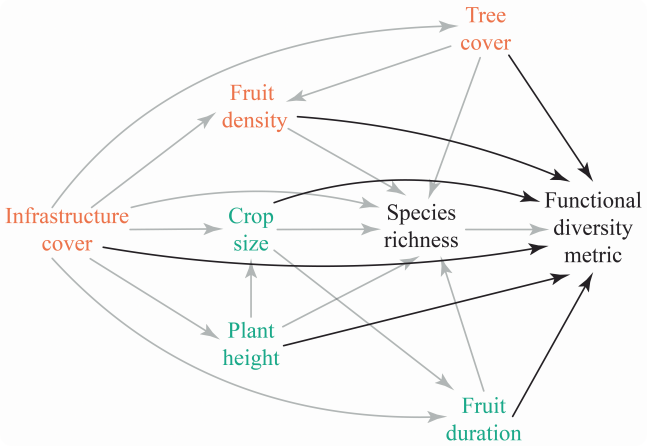


FIGURE 1 Directed acyclic graph showing the generative model explaining changes in the functional diversity metrics (i.e., functional richness [FRic], functional divergence [FDiv], and functional regularity [FReg]) of the bird community feeding on *Schinus terebinthifolia*. This causal structure assumes that intrinsic (green = plant height, fruiting duration, and crop size) and extrinsic drivers (red = fruit density in the neighborhood, tree cover, and infrastructure cover) can affect avian functional diversity directly (e.g., plant height → FRic) and indirectly through its effects on species richness (e.g., plant height → species richness → FRic). Black arrows represent the estimands in this study, and gray arrows indicate assumed dependencies between intrinsic and extrinsic predictors not evaluated here.

METHODS

Study area

The frugivory dataset is available in Vissoto et al. (2022), where additional details can be found. Data were collected from March to July 2017 across 248 ha of rural and suburban areas in and around the Capão do Leão Campus of the Universidade Federal de Pelotas, the EMBRAPA Terras Baixas Experimental Station, and adjacent private properties (31°48′–31°49′ S; 52°24′–52°26′ W) in Capão do Leão municipality, Rio Grande do Sul, Brazil. The landscape comprises a mosaic of grasslands, wetlands, *restinga* forest patches, agricultural and suburban residential areas, and academic and research facilities. The climate is humid to subhumid, with an average annual temperature of 17.8°C and precipitation of 1366.9 mm.

Frugivory sampling

Frugivory events were sampled during austral autumn and winter (March–July 2017), coinciding with the peak fruiting season of *S. terebinthifolia* (Vissoto et al., 2019, 2022). Observations were conducted on 29 individual plants representing key spatial and phenotypic contexts in the study region. Bird visits, defined as events where a bird consumed at least one fruit (Saracco et al., 2004), were recorded using focal observations (Altmann, 1974) over five 2-h periods per plant, totaling 290 h of sampling effort (Vissoto et al., 2022). As interaction rates are not biased by the time of day in this system, observations were conducted throughout daylight hours (07:00–18:00), but avoided days with strong winds or heavy rain (Vissoto et al., 2019, 2022).

Intrinsic drivers included plant height, estimated from base to tip; crop size, extrapolated from counts of fruits in 10 sampled infructescences; and fruiting duration, measured as the interval from first ripening to fruit removal or inactivity, with fortnightly monitoring. Extrinsic factors included interspecific fruit density within a 15-m radius, as well as tree cover and human infrastructure cover within 100 m, quantified using satellite imagery.

Avian functional traits

We used a limited set of traits that capture complementary functional aspects of birds (i.e., body size and the feeding, perching and flying apparatuses) aiming to minimize dimensionality, mitigate hypervolume boundary effects, and ensure robust estimates of FDα indices: (1) body mass, which relates to metabolic rate, foraging behavior, longevity, and home-range size; (2) bill height/width ratio, indicative of the size of fruits that birds can manipulate and ingest; (3) tarsometatarsus length, related to foraging behavior such as perching or hanging abilities; and (4) wing length, linked to movement capacity, indicating seed dispersal capacity (Luck et al., 2012; Mammola & Cardoso, 2020; Sekercioglu, 2006). These traits encapsulate the key ecological roles of frugivorous birds in ecosystems and their responses to environmental change (Dehling et al., 2014; Luck et al., 2012; Sekercioglu, 2006). Body mass was obtained from the literature, while morphological measurements were taken from museum specimens (detailed in Dias et al., 2020). Length measurements were divided by the cubic root of body mass to obtain relative dimensions independent of absolute species size (Stiles, 1995). We prioritized continuous traits as proxies for habitat use and foraging behavior, thereby mitigating subjectivity and limitations of categorical variables (Laureto et al., 2015; Luck et al., 2012). We used the "cor" function in R's stats package (v4.4.0; R Core Team, 2024) to assess trait correlations. Wing and tarsometatarsus lengths were strongly correlated ($R = -0.75$), so we retained wing length, as it is more biologically relevant to seed dispersal (Appendix S1: Table S1.1). The remaining traits showed weak correlations (highest $R = 0.6$ between mass and wing length).

Functional diversity analysis

We began by constructing a community matrix with the number of frugivory events of each of the 16 bird species in each plant and a species-by-trait matrix using the mean trait values for each species under the assumption that interspecific variation outweighs intraspecific variation (Violle et al., 2012). The trait data were then centralized and normalized (i.e., *z*-scores). We built Gaussian kernel density *n*-dimensional hypervolumes for each plant using Euclidean distances and the three functional traits (Blonder et al., 2014, 2018; Mammola & Cardoso, 2020). This was implemented using the "kernel.build" function from the BAT package (v2.9.6; Cardoso et al., 2024) in R. We used a single bandwidth value calculated with the "estimate_bandwidth" function from the hypervolume package (v3.1.4; Ali et al., 2023; Blonder et al., 2018). Since we used abundance data (i.e., frugivory events are equivalent to abundance), the abundance-weighted argument was set to TRUE. The Gaussian method approximates trait values as stochastic point clouds based on observed species traits, with abundance data weighted by replicating each observation according to its abundance (Blonder et al., 2018; Cardoso et al., 2024). FRic, FDiv, and FReg were calculated with the "kernel.alpha," "kernel.dispersion," and "kernel.evenness" functions from the BAT package. FRic is the total volume of the *n*-dimensional hypervolume (Mammola & Cardoso, 2020). FDiv, calculated using the "kernel divergence" method, is the average distance between stochastic points and their centroid (Cardoso et al., 2024; Carmona et al., 2019). FReg measures functional evenness as the overlap between the observed and a theoretical, evenly distributed hypervolume (Cardoso et al., 2024; Carmona et al., 2016, 2019). FReg requires at least two species per sampling unit, whereas FRic and FDiv can be calculated with only one. Consequently, the number of sampling units varied across analyses ($n = 29$ for FRic, 26 for FDiv, and 22 for FReg), although species composition remained consistent. For FRic, we assumed a zero value in plants with no frugivory events.

Modeling the effect of intrinsic and extrinsic drivers on avian FDα

We aimed to assess the effect of intrinsic and extrinsic drivers on bird FDα while accounting for the effect of species richness on FRic, FDiv, and FReg (Figure 1). To do so, we used a Bayesian hierarchical approach to model the effect of predictors on species richness (S) and FDα metrics as a set of hierarchical linear equations:

$$S_i \sim \text{Student}\, t(\nu = 7, \mu_i, \sigma)$$

$$\begin{aligned}\mu_i = {} & \alpha + \tau_{\text{individual } i} + \beta_1 \text{crop size}_i + \beta_2 \text{height}_i \\ & + \beta_3 \text{fruiting duration}_i + \beta_4 \text{fruit density}_i \\ & + \beta_5 \text{tree cover}_i + \beta_6 \text{infrastructure cover}_i + \epsilon\end{aligned}$$

$$\text{FD metric}_i \sim \text{Student}\, t(\nu = 7, \mu_i, \sigma)$$

$$\begin{aligned}\mu_i = {} & \alpha + \tau_{\text{individual } i} + \beta_1 S_i + \beta_2 \text{crop size}_i + \beta_3 \text{height}_i \\ & + \beta_4 \text{fruiting duration}_i + \beta_5 \text{fruit density}_i \\ & + \beta_6 \text{tree cover}_i + \beta_7 \text{infrastructure cover}_i + \epsilon\end{aligned}$$

See the complete mathematical notation of the models in Appendix S2: Section S3. We fitted the model using *z*-scores of continuous response and predictor variables and used a Student *t* probability distribution as the likelihood function to model FDα metrics. We used Gaussian processes to conduct partial pooling across individuals, that is, τ parameter, and account for their spatial correlation. To do so, we employed a quadratic kernel to construct the covariance matrix of an *MVnormal* distribution to estimate correlated parameters (McElreath, 2020). We used as input a matrix of spatial distances among individuals calculated from their latitude and longitude coordinates (Appendix S2: Section S2). We used skeptical priors of strong effects, parameterized to encompass values within the possible range of standardized FDα metrics. To set up the Hamiltonian MCMC algorithm, we defined three chains, 4000 sampling, and 500 warming iterations, and a thinning rate of 3 (Appendix S2: Sections S4.2, S6.2, and S8.2). Finally, we conducted sampling diagnostics of the model through visual assessment of chain convergence, $Rhat < 1.05$ and $ess > 1000$ (Appendix S2: Sections S4.3, S6.3, and S8.3). We also assessed the quality of the models' fit through posterior predictive checks.

Once we verified the reliability of the models, we selected the predictors that had the highest direct or indirect effect (i.e., p [effect] ≥ 0.8) on species richness or each FDα metric. Then, we used the generative model to simulate two types of interventions: (1) total effect—effects of minimum and maximum values of the predictor *i* on species richness (S) and their joint effect on the FDα metric *j* (i.e., $X_{\text{min or max}} \rightarrow S \rightarrow FD\alpha_{\text{metric j}}$; $X_{\text{min or max}} \rightarrow FD\alpha_{\text{metric } j}$); and (2) conditional effect—effects of minimum and maximum values of predictor *i* on FDα metric *j*, while holding species richness at the minimum value (i.e., $X_{\text{min or max}} \rightarrow FD\alpha_{\text{metric } j}$). Finally, we estimated the contrast between pairs of interventions to assess the causal effect of predictor *i* on the FDα of birds. We fit the models through the Hamiltonian MCMC algorithm with Stan 2.32.2 through the *cmdstanr* 0.5.3 R package (Gabry et al., 2025); data wrangling and plotting tasks were conducted using *base* R, *dplyr* 1.1.1, *magrittr* 2.0.3, *ggplot2* 3.4.1, and *cowplot* 1.1.1 (Bache & Wickham, 2022; Wickham, 2016; Wickham et al., 2023; Wilke, 2020). See Appendix S2 for the code used in the analysis, mathematical notation, Stan code, model fitting, model diagnostics, and simulations of interventions. A protocol for reproducible functional diversity analyses (Palacio et al., 2022) is available in Appendix S3: Table S3.1.

RESULTS

A total of 13 species consumed *S. terebinthifolia* fruits. Bird species richness in plants ranged from 0 to 10 (3.2 ± 0.4 species [mean ± SE]), while abundance varied from 0 to 126 (18.7 ± 5.3). FRic had a value of 27.2 ± 2.3, FDiv 1.50 ± 0.05, and FReg 0.72 ± 0.03.

Direct and indirect effects of drivers on FRic

One intrinsic and two extrinsic drivers primarily influenced FRic (Table 1, Figure 2), with the relative importance of their direct and indirect effects varying by predictor.

Tree height increased both species richness and FRic, with comparable direct and indirect contributions. The total effect of tree height on FRic was an increase of 17.68 units (46.4%), with direct effects accounting for 11.64 units (28.7%). Infrastructure cover reduced FRic primarily by lowering species richness, with a total effect of −7.43 units (−21.4%), mostly indirect. Tree cover had a moderate direct negative effect on FRic (−6.41 units; −26.3%), with minimal effect via richness. On average, tree height was 307.03 ± 390.9% and 160.86 ± 90.29%, more important than the other drivers in explaining species richness and FRic, respectively. Model diagnostics and posterior predictive checks showed that the model was well fitted (Appendix S2: Section S4.3).

TABLE 1 Summary of direct, total, and conditional effects of drivers on three alpha functional diversity indices: Functional richness (FRic), functional divergence (FDiv), and functional regularity (FReg).

Driver	Direct—SR	Direct—FDα	Imp	Total	Conditional	Change
FRic						
Tree height	0.25 ± 0.16; 0.94	0.24 ± 0.14; 0.94	0.0	↑ 17.6 ± 8.04; ↑ 46.3 ± 17.8; 0.98	↑ 11.4 ± 6.98; ↑ 43.0 ± 28.7; 0.93	64.8; 0.93
Infrastructure	−0.19 ± 0.14; 0.89	−0.07 ± 0.13; 0.70	161.5	↓ 7.41 ± 6.5; ↓ 24.1 ± 21.4; 0.87	↓ 3.17 ± 5.80; ↓ 11.4 ± 42.5; 0.70	42.2; 0.90
Tree cover	−0.04 ± 0.15; 0.59	−0.12 ± 0.14; 0.80	229.7	↓ 6.4 ± 7.8; ↓ 19.8 ± 26.3; 0.80	↓ 5.49 ± 6.63; ↓ 27.5 ± 34.2; 0.79	0.0; 0.59
FDiv						
Tree height	0.11 ± 0.16; 0.75	0.11 ± 0.13; 0.81	0.0	↑ 0.14 ± 0.13; ↑ 8.7 ± 8.54; 0.84	↑ 0.13 ± 0.15; ↑ 8.42 ± 9.84; 0.80	0.0; 0.50
Infrastructure	−0.25 ± 0.14; 0.96	−0.21 ± 0.12; 0.96	15.3	↓ 0.27 ± 0.12; ↓ 22.8 ± 11.8; 0.98	↓ 0.22 ± 0.12; ↓ 18.8 ± 11.7; 0.95	19.4; 0.87
Crop size	0.14 ± 0.15; 0.82	0.19 ± 0.15; 0.87	32.2	↑ 0.28 ± 0.20; ↑ 15.7 ± 10.9; 0.91	↑ 0.24 ± 0.20; ↑ 13.9 ± 12.2; 0.87	13.8; 0.76
FReg						
Crop size	0.08 ± 0.16; 0.70	0.12 ± 0.15; 0.80	46.6	↑ 0.04 ± 0.10; ↑ 1.62 ± 24.1; 0.62	↑ 0.09 ± 0.1; ↑ 8.26 ± 11.3; 0.80	45; 0.68

Note: Direct—SR: Direct effect of the driver on species richness (β ± SD; p [β > 0]). Direct—FDα: Direct effect of the driver on the functional diversity index (β ± SD; p [β > 0]). Imp: Relative importance (in percentage) of the parameter explaining species richness and the functional diversity index. Total: Total effect of the driver on the functional diversity index, expressed as absolute change in index units (↑ increase/↓ decrease; mean ± SD); relative change in % (↑/↓; mean ± SD); and posterior probability (p [contrast min–max > 0]). Conditional: Effect on the functional diversity index not mediated by species richness, in the same format as Total. Change: Percent difference between total and conditional effects; p (total effect relative to conditional effect).

Direct and indirect effects of drivers on FDiv

Two intrinsic and one extrinsic driver primarily influenced FDiv (Table 1, Figure 3), with the relative importance of their direct and indirect effects varying by driver.

Tree height and crop size increased FDiv, with the latter having the strongest direct effect. Infrastructure cover reduced FDiv primarily through its effect on species richness. For all three drivers, total and conditional effects were similar in magnitude. Tree height and crop size increased FDiv by 0.14 units (8.7%) and 0.28 units (15.7%), respectively, while infrastructure cover reduced FDiv by 0.27 units (22.8%). On average, infrastructure cover was 100.2 ± 35.21% and 52 ± 53.06%, more important than the other drivers in explaining species richness and FDiv, respectively. Model diagnostics and posterior predictive checks indicated good model fit (Appendix S2: Section S6.3).

Direct and indirect effects of drivers on FReg

Crop size had a weak positive effect on species richness and a slightly stronger effect on FReg (Table 1, Figure 4). The total effect of crop size on FReg was small and variable (2.0% increase), while the conditional effect was somewhat stronger (8.3% increase). Although the increase of FReg due to the conditional effect of crop size was 45% higher compared to that of the total effect, the differences between interventions were not clear (Figure 4c–iii). Model diagnostics and posterior predictive checks indicated good model fit (Appendix S2: Section S8.3).

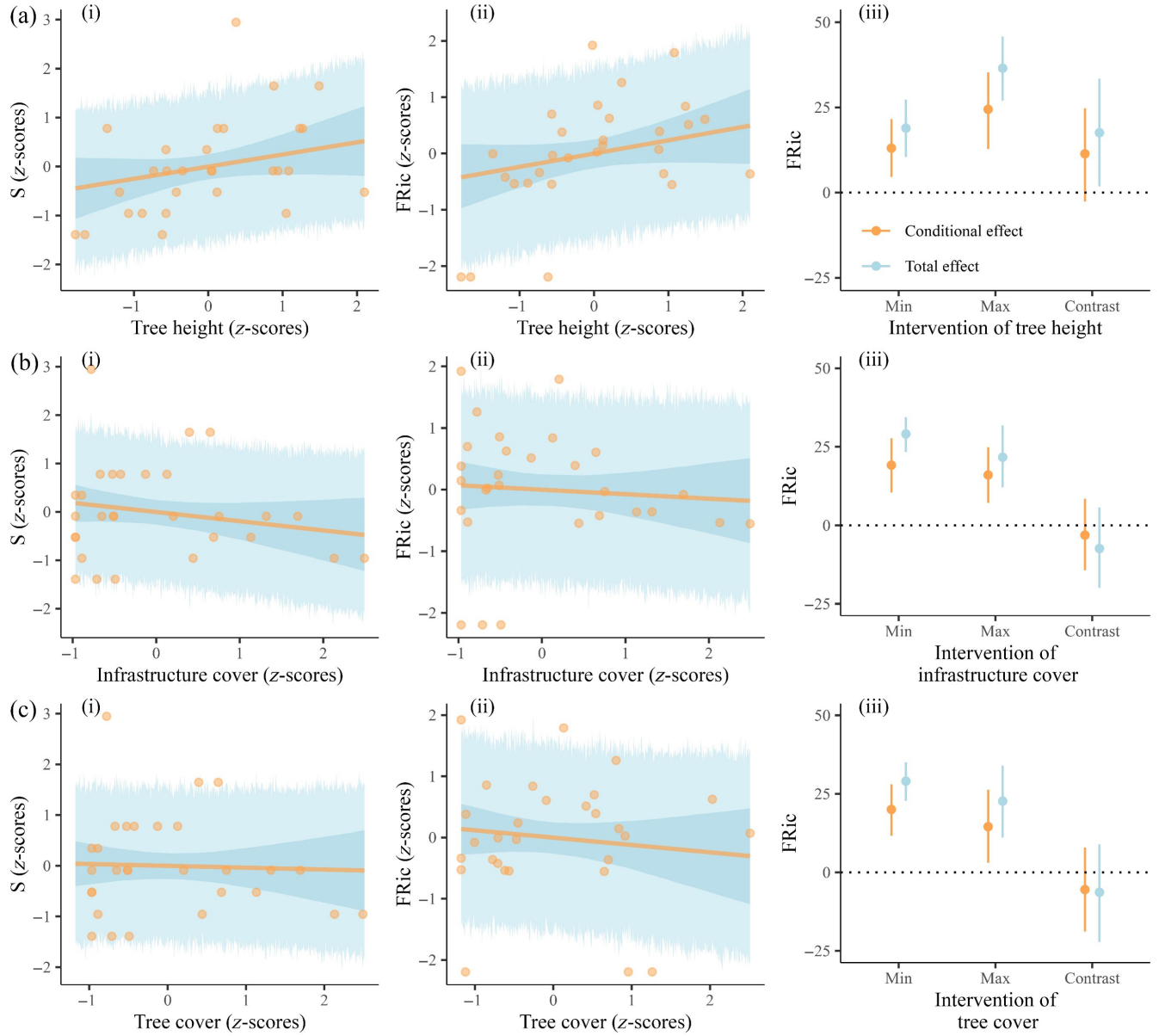


FIGURE 2 (a) Intrinsic and (b, c) extrinsic drivers influencing the functional richness (FRic) and species richness (S) of birds foraging on an *Schinus terebinthifolia* population. Effects on S (a–i to c–i–iii) imply indirect effects (i.e., X → S → FRic) on FRic, whereas effects on FRic (a–ii to c–ii) denote direct effects (a–i–ii, b–i–ii and c–i–ii). The dots indicate observed values, the solid line is the average estimation, the inner bands include 95% CI of the estimation, and the outer bands show 95% CI of the prediction. Error bars and dots in a–iii, b–iii, and c–iii show 95% credibility intervals and average values of the causal effect of intervening factors to minimum and maximum values; the contrast shows the difference between such interventions. The total effect implies both direct and indirect effects of driver *i* on FRic. In contrast, the conditional effect denotes the direct effect of driver *i* on FRic while holding S at the minimum value.

DISCUSSION

To the best of our knowledge, this is the first study to assess how the FDα of frugivorous birds responds to intraspecific characteristics of fruiting trees. Our findings show that plant phenotypic traits and local environmental settings distinctly influence multiple dimensions of avian FDα. Tree height had a strong positive effect on FRic and a moderate effect on FDiv, while human infrastructure showed strong negative effects on both indices. Crop size had a clear positive effect on FDiv and a modest positive effect on FReg, whereas tree cover had a moderate and uncertain negative effect on FRic. Most relationships, especially the strongest ones, were mediated by species richness. Previous studies examining the effect of intrinsic and extrinsic drivers of frugivory in individual plants focused primarily on taxonomic diversity (Crestani et al., 2019; Vissoto et al., 2022), while

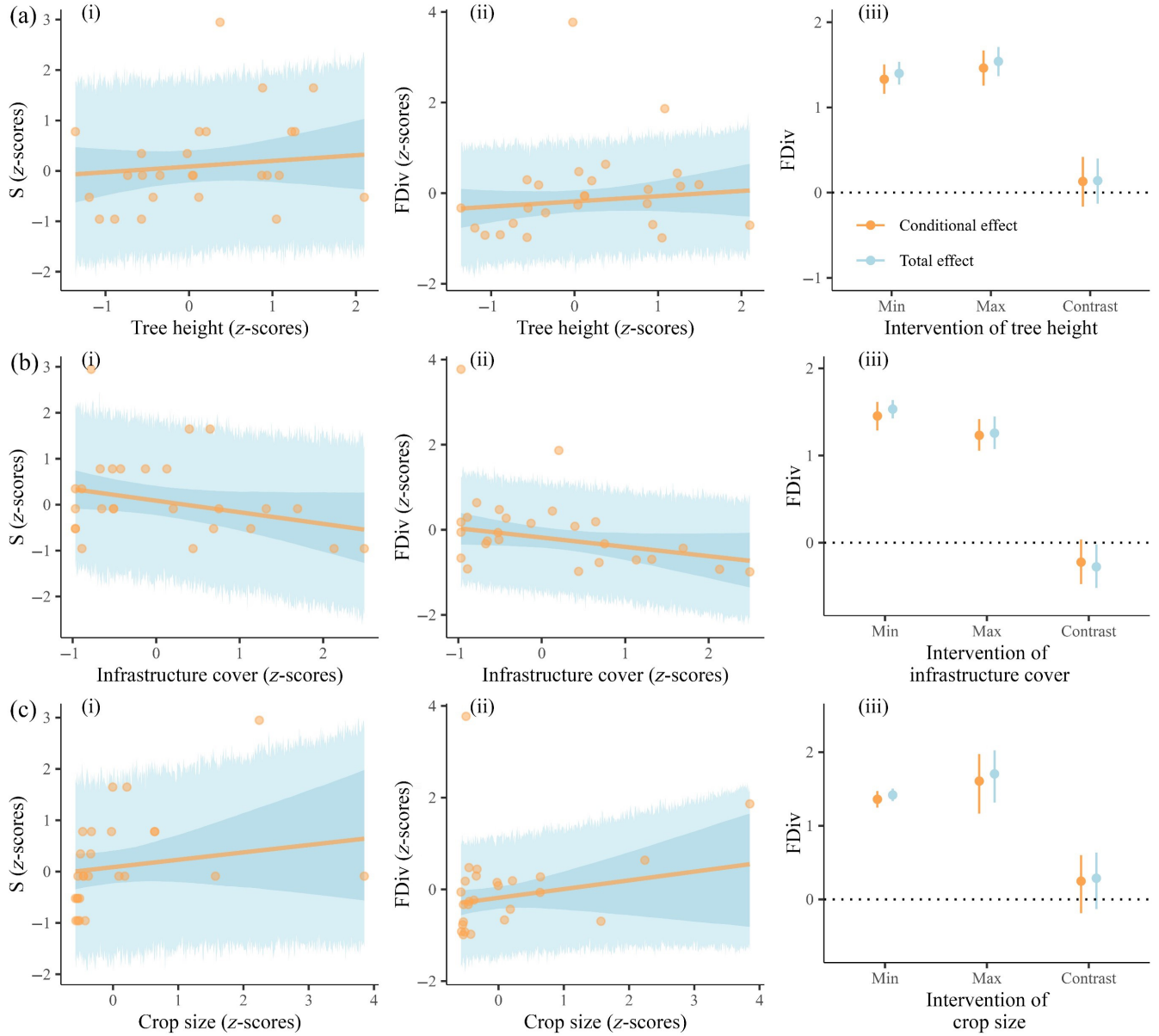


FIGURE 3 (a) Intrinsic and (b, c) extrinsic drivers influencing the functional divergence (FDiv) and species richness (S) of birds foraging on an *Schinus terebinthifolia* population. Panel structure and graphical elements follow those described in Figure 2.

functional approaches predominantly examined community-level dynamics (Bender et al., 2018; Melo et al., 2020) or, when downscaled to the population level (Blendinger, 2017; Isla et al., 2023; Lavabre et al., 2016), seldom quantified trait diversity comprehensively or explored multiple dimensions within an integrated analytical framework. By addressing these gaps, we show that intrapopulational variation in fruiting plants shapes trait-based frugivore diversity, with important implications for frugivory and seed dispersal.

As expected, plant height had a strong positive effect on FRic and a moderate effect on FDiv, primarily by increasing the number of bird species consuming *S. terebinthifolia* fruits. Taller plants may serve as visual cues and offer better foraging conditions, such as shelter and reduced disturbance, which attract a broader range of frugivores (Suhonen, 1993; Vissoto et al., 2022). Our results suggest that plant height relaxes ecological filters and promotes niche differentiation among abundant frugivores, thus increasing FRic and FDiv (Mammola et al., 2021; Mouchet et al., 2010).

Crop size had a clear and positive effect on FDiv, with a high effect size and reasonably strong posterior support. The effect was stronger than on species richness and only partly mediated by richness, indicating a trait-based mechanism. This finding was expected since plants with

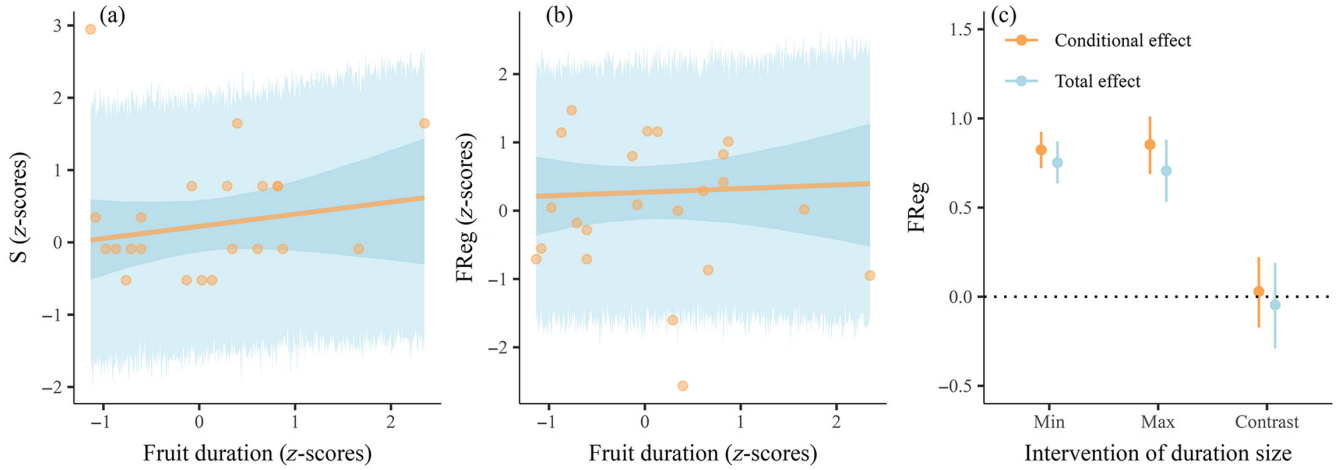


FIGURE 4 Indirect and direct effect of crop size on the functional regularity (FReg) and species richness (S) of birds foraging on an *Schinus terebinthifolia* population. Panel structure and graphical elements follow those described in Figure 2.

large crops provide abundant resources that attract frugivores with more diverse traits, fostering niche differentiation among abundant and functionally dissimilar species (Guerra et al., 2017; Mammola et al., 2021; Miguel et al., 2018). As our system is dominated by morphologically similar Passeriformes, mainly *Turdus* species plus a couple of tanagers and tyrannids (Vissoto et al., 2019, 2022), larger crops likely increase the abundance of these species or, at most, add a few functionally redundant species, shifting trait distributions and raising FDiv independently of species richness. Because these species still occupy similar regions of trait space, the overall extent of trait combinations remains unchanged, which explains the lack of effect on FRic, a metric generally more sensitive to variations in species richness (Mason et al., 2005).

Crop size also had a modest but positive effect on FReg, more evident in the direct effect than in the total effect. Taken together, our results suggest that in a functionally similar frugivore species pool, larger crops promote a more even distribution of species and abundances in trait space, which enables a more regular and effective use of resources (Mason et al., 2005; Perronne et al., 2017). Although *S. terebinthifolia* fruits are small, low-energy, and nutrient-poor (Quintero et al., 2020), they are abundant and serve as a key winter resource, amplifying the importance of crop size during periods of food scarcity (Kwit et al., 2004; Vissoto et al., 2019). This seasonal context may further enhance the influence of intrinsic drivers such as plant height and crop size, as frugivores tend to prioritize reliable resources.

Contrary to our expectations, tree cover showed a moderate negative effect on FRic that appeared largely independent of species richness, though the evidence for this relationship was limited. In our study area, few frugivores are strictly forest-dependent, and the most abundant species prefer edges and open habitats. Increased forest cover may reduce the abundance of these common frugivores and limit the occurrence of rarer, functionally distinct species more associated with open vegetation. As *S. terebinthifolia* in forested areas produces fruits only on branches facing open spaces (Vissoto et al., 2022), fruit display may be reduced, further filtering traits either by lowering frugivore abundance or excluding the few functionally distinct species, thereby shrinking the hypervolume independently of species richness.

Overall, our results indicate that intrinsic and extrinsic drivers may affect each dimension of FDα differently and that strong relationships with these indices result from the indirect effect of species richness. For example, plant height, an intrinsic driver, was the strongest predictor of FRic, while infrastructure cover, an extrinsic driver, was the strongest predictor of FDiv. In both cases, however, these relationships were mediated by species richness, which increased the range of traits in the first case but reduced trait differentiation in the latter (Mammola et al., 2021; Mouchet et al., 2010).

Our study further revealed that a more functionally diverse frugivore assemblage may also enhance the effectiveness of seed dispersal by increasing the likelihood of spatially heterogeneous seed deposition and longer distance dispersal events. This functional complementarity can benefit plant recruitment by promoting germination across a broader range of microhabitats and reducing density-dependent mortality near parent plants (Bleher & Böhning-Gaese, 2001; Isla et al., 2023). In our system, where bird species differ in body size, foraging behavior, and mobility, increased functional diversity likely translates into more diversified dispersal services at the individual plant level.

In conclusion, our findings show that phenotypic and spatial variation among fruiting trees of a single population drives the functional diversity of frugivorous birds. Drivers such as plant height, infrastructure cover, and tree cover are particularly important, as they simultaneously affect the taxonomic and functional facets of frugivore communities (Vissoto et al., 2022; this study). Our results illustrate the importance of similar studies in understanding how individual plants succeed in seed dispersal and offer practical applications in restoration ecology and invasive species management. For instance, taller individuals with larger crops can be prioritized for planting when the goal is to accelerate habitat recovery or for removal when the goal is to mitigate their spread in regions where they are invasive. Further studies should explore whether similar patterns occur in more diverse ecosystems, such as tropical forests, and assess the role of frugivore functional diversity in seed dispersal of individual plants through manipulative experiments and genetic markers. These efforts will shed light on the mechanisms linking frugivory to plant population dynamics, fitness, and evolutionary trajectories, fostering a deeper understanding of how fruiting plants and frugivores co-evolve and sustain ecosystem functions.

AUTHOR CONTRIBUTIONS

Conceptualization: Rafael A. Dias, Jeferson Vizentin-Bugoni, and Juliana H. Wolter. *Methodology*: Rafael A. Dias, Jeferson Vizentin-Bugoni, and Juliana H. Wolter. *Investigation*: Rafael A. Dias and Maiara Vissoto. *Data curation*: Rafael A. Dias, Maiara Vissoto, Juliana H. Wolter, and Andrés F. Ramírez-Mejía. *Software*: Rafael A. Dias, Andrés F. Ramírez-Mejía, and Juliana H. Wolter. *Validation*: Rafael A. Dias and Andrés F. Ramírez-Mejía. *Formal analysis*: Andrés F. Ramírez-Mejía, Juliana H. Wolter, and Rafael A. Dias. *Visualization*: Rafael A. Dias and Andrés F. Ramírez-Mejía. *Resources*: Rafael A. Dias and Jeferson Vizentin-Bugoni. *Supervision*: Rafael A. Dias and Jeferson Vizentin-Bugoni. *Project administration*: Rafael A. Dias and Jeferson Vizentin-Bugoni. *Funding acquisition*: Rafael A. Dias. *Writing—original draft*: Juliana H. Wolter and Rafael A. Dias. *Writing—review and editing*: All authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Ramírez-Mejía, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.17351425.

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REFERENCES

Ali, J. R., B. W. Blonder, A. L. Pigot, and J. A. Tobias. 2023. "Bird Extinctions Threaten to Cause Disproportionate Reductions of Functional Diversity and Uniqueness." *Functional Ecology* 37: 162–175. https://doi.org/10.1111/1365-2435.14201.

Altmann, J. 1974. "Observational Study of Behavior: Sampling Methods." *Behaviour* 49: 227–267. https://doi.org/10.1163/156853974x00534.

Bache, S., and H. Wickham. 2022. "magrittr: A Forward-Pipe Operator for R." R Package Version 2.0.3. https://CRAN.R-project.org/package=magrittr.

Bascompte, J., and P. Jordano. 2007. "Plant-Animal Mutualistic Networks: The Architecture of Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 38: 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818.

Bender, I. M. A., W. D. Kissling, P. G. Blendinger, K. Böhning-Gaese, I. Hensen, I. Kühn, M. C. Muñoz, et al. 2018. "Morphological Trait Matching Shapes Plant–Frugivore Networks across the Andes." *Ecography* 41: 1910–19. https://doi.org/10.1111/ecog.03396.

Bleher, B., and K. Böhning-Gaese. 2001. "Consequences of Frugivore Diversity for Seed Dispersal, Seedling Establishment and the Spatial Pattern of Seedlings and Trees." *Oecologia* 129: 385–394. https://doi.org/10.1007/s004420100747.

Blendinger, P. G. 2017. "Functional Equivalence in Seed Dispersal Effectiveness of *Podocarpus parlatorei* in Andean Fruit-Eating Bird Assemblages." *Frontiers in Ecology and Evolution* 5: 57. https://doi.org/10.3389/fevo.2017.00057.

Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. "The n-Dimensional Hypervolume." *Global Ecology and Biogeography* 23: 595–609. https://doi.org/10.1111/geb.12146.

Blonder, B., C. B. Morrow, B. Maitner, D. J. Harris, C. Lamanna, C. Violle, B. J. Enquist, and A. J. Kerkhoff. 2018. "New Approaches for Delineating n-Dimensional Hypervolumes." *Methods in Ecology and Evolution* 9: 305–319. https://doi.org/10.1111/2041-210X.12865.

Campagnoli, M., A. Christianini, and G. Peralta. 2024. "Plant and Frugivore Species Characteristics Drive Frugivore Contributions to Seed Dispersal Effectiveness in a Hyperdiverse Community." *Functional Ecology* 39(1): 238–253. https://doi.org/10.1111/1365-2435.14697.

Cardoso, P., S. Mammola, F. Rigal, and J. C. Carvalho. 2024. "BAT: Biodiversity Assessment Tools." R Package Version 2.9.6. https://CRAN.R-project.org/package=BAT.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. "Traits without Borders: Integrating Functional Diversity

across Scales." *Trends in Ecology & Evolution* 31: 382–394. https://doi.org/10.1016/J.TREE.2016.02.003.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2019. "Trait Probability Density (TPD): Measuring Functional Diversity across Scales Based on TPD with R." *Ecology* 100: e02876. https://doi.org/10.1002/ecy.2876.

Crestani, A. C., M. A. R. Mello, and E. Cazetta. 2019. "Interindividual Variations in Plant and Fruit Traits Affect the Structure of a Plant-Frugivore Network." *Acta Oecologica* 95: 120–27. https://doi.org/10.1016/j.actao.2018.11.003.

Cruz, J. C., J. A. Ramos, L. P. Silva, P. Q. Tenreiro, and R. H. Heleno. 2013. "Seed Dispersal Networks in an Urban Novel Ecosystem." *European Journal of Forest Research* 132: 887–897. https://doi.org/10.1007/s10342-013-0722-1.

Dehling, D. M., T. Töpfer, H. M. Schaefer, P. Jordano, K. Böhning-Gaese, and M. Schleuning. 2014. "Functional Relationships beyond Species Richness Patterns: Trait Matching in Plant-Bird Mutualisms across Scales." *Global Ecology and Biogeography* 23: 1085–93. https://doi.org/10.1111/geb.12193.

Dias, R. A., V. A. G. Bastazini, B. D. C. Knopp, F. C. Bonow, M. S. S. Gonçalves, and A. T. Gianuca. 2020. "Species Richness and Patterns of Overdispersion, Clustering and Randomness Shape Phylogenetic and Functional Diversity–Area Relationships in Habitat Islands." *Journal of Biogeography* 47: 1638–48. https://doi.org/10.1111/jbi.13849.

Díaz, S., and M. Cabido. 2001. "Vive la Différence: Plant Functional Diversity Matters to Ecosystem Processes." *Trends in Ecology & Evolution* 16: 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2.

Gabry, J., R. Češnovar, A. Johnson, and S. Bronder. 2025. "cmdstanr: R Interface to 'CmdStan'." https://mc-stan.org/cmdstanr/; https://discourse.mc-stan.org.

Gleditsch, J. M., A. M. Hruska, and J. T. Foster. 2017. "Connecting Resource Tracking by Frugivores to Temporal Variation in Seed Dispersal Networks." *Frontiers in Ecology and Evolution* 5: 98. https://doi.org/10.3389/fevo.2017.00098.

Guerra, T. J., R. L. C. Dayrell, A. J. Arruda, W. Dáttilo, A. L. Teixido, J. V. S. Messeder, and F. A. O. Silveira. 2017. "Intraspecific Variation in Fruit-Frugivore Interactions: Effects of Fruiting Neighborhood and Consequences for Seed Dispersal." *Oecologia* 185: 233–243. https://doi.org/10.1007/s00442-017-3943-z.

Herrera, C. M. 2002. "Seed Dispersal by Vertebrates." In *Plant Animal Interactions: An Evolutionary Approach*, edited by C. M. Herrera and O. Pellmyr, 185–208. Hoboken, NJ: Wiley-Blackwell.

Herrera, J. M., J. M. Morales, and D. García. 2011. "Differential Effects of Fruit Availability and Habitat Cover for Frugivore-Mediated Seed Dispersal in a Heterogeneous Landscape." *Journal of Ecology* 99: 1100–1107. https://doi.org/10.1111/j.1365-2745.2011.01861.x.

Hight, S. D., J. P. Cuda, and J. C. Medal. 2002. "Brazilian Peppertree." In *Biological Control of Invasive Plants in the Eastern United States*, edited by R. V. Driesche, B. Blossey, M. Hoddle, S. Lyon, and R. Reardon, 311–321. Morgantown: Forest Service Forest Health Technology Enterprise Team.

Hopson, R. M., R. C. Wilcox, and C. E. Tarwater. 2020. "Frugivores Vary in their Response to Neighborhood Effects in a Novel Ecosystem." *Acta Oecologica* 108: 103641. https://doi.org/10.1016/j.actao.2020.103641.

Isla, J., M. Jácome-Flores, J. M. Arroyo, and P. Jordano. 2023. "The Turnover of Plant–Frugivore Interactions along Plant Range Expansion: Consequences for Natural Colonization Processes." *Proceedings of the Royal Society B: Biological Sciences* 290: 20222547. https://doi.org/10.1098/rspb.2022.2547.

Jordano, P., P. M. Forget, J. E. Lambert, K. Böhning-Gaese, A. Traveset, and S. J. Wright. 2011. "Frugivores and Seed Dispersal: Mechanisms and Consequences for Biodiversity of a Key Ecological Interaction." *Biology Letters* 7: 321–23. https://doi.org/10.1098/rsbl.2010.0986.

Kissling, D. W., K. Böhning-Gaese, and W. Jetz. 2009. "The Global Distribution of Frugivory in Birds." *Global Ecology and Biogeography* 18: 150–162. https://doi.org/10.1111/j.1466-8238.2008.00431.x.

Kwit, C., D. J. Levey, C. H. Greenberg, S. F. Pearson, J. P. McCarty, and S. Sargent. 2004. "Cold Temperature Increases Winter Fruit Removal Rate of a Bird-Dispersed Shrub." *Oecologia* 139: 30–34. https://doi.org/10.1007/s00442-003-1470-6.

Laureto, L. M. O., M. V. Cianciaruso, and D. S. M. Samia. 2015. "Functional Diversity: An Overview of its History and Applicability." *Natureza & Conservação* 13: 112–16. https://doi.org/10.1016/j.ncon.2015.11.001.

Lavabre, J. E., L. J. Gilarranz, M. A. Fortuna, and J. Bascompte. 2016. "How Does the Functional Diversity of Frugivorous Birds Shape the Spatial Pattern of Seed Dispersal? A Case Study in a Relict Plant Species." *Philosophical Transactions of the Royal Society B* 371: 20150280. https://doi.org/10.1098/rstb.2015.0280.

Lefcheck, J. S., V. A. G. Bastazini, and J. N. Griffin. 2015. "Choosing and Using Multiple Traits in Functional Diversity Research." *Environmental Conservation* 42: 104–7. https://doi.org/10.1017/S0376892914000307.

Luck, G. W., S. Lavorel, S. McIntyre, and K. Lumb. 2012. "Improving the Application of Vertebrate Trait-Based Frameworks to the Study of Ecosystem Services." *The Journal of Animal Ecology* 81: 1065–76. https://doi.org/10.1111/j.1365-2656.2012.01974.x.

Mammola, S., and P. Cardoso. 2020. "Functional Diversity Metrics Using Kernel Density n-Dimensional Hypervolumes." *Methods in Ecology and Evolution* 11: 986–995. https://doi.org/10.1111/2041-210X.13424.

Mammola, S., C. P. Carmona, T. Guillerme, and P. Cardoso. 2021. "Concepts and Applications in Functional Diversity." *Functional Ecology* 35: 1869–85. https://doi.org/10.1111/1365-2435.13882.

Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. "Functional Richness, Functional Evenness and Functional Divergence: The Primary Components of Functional Diversity." *Oikos* 111: 112–18. https://doi.org/10.1111/j.0030-1299.2005.13886.x.

McElreath, R. 2020. *Statistical Rethinking: A Bayesian Course with Examples in R and STAN*, 2nd ed. London: CRC Press. https://doi.org/10.1201/9780429029608.

Melo, M. A., M. A. G. da Silva, and A. J. Piratelli. 2020. "Improvement of Vegetation Structure Enhances Bird Functional Traits and Habitat Resilience in an Area of Ongoing Restoration in the Atlantic Forest." *Anais da Academia Brasileira de Ciências* 92: e20191241. https://doi.org/10.1590/0001-3765202020191241.

Miguel, M. F., P. Jordano, S. Tabeni, and C. M. Campos. 2018. "Context-Dependency and Anthropogenic Effects on

Individual Plant-Frugivore Networks." *Oikos* 127: 1045–59. https://doi.org/10.1111/oik.04978.

Morales, J. M., and T. A. Carlo. 2006. "The Effects of Plant Distribution and Frugivore Density on the Scale and Shape of Dispersal Kernels." *Ecology* 87: 1489–96. https://doi.org/10.1890/0012-9658(2006)87[1489:TEOPDA]2.0.CO;2.

Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. "Functional Diversity Measures: An Overview of their Redundancy and their Ability to Discriminate Community Assembly Rules." *Functional Ecology* 24: 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Palacio, F. X., C. T. Callaghan, P. Cardoso, E. J. Hudgins, M. A. Jarzyna, G. Ottaviani, F. Riva, C. Graco-Roza, V. Shirey, and S. Mammola. 2022. "A Protocol for Reproducible Functional Diversity Analyses." *Ecography* 2022: e06287. https://doi.org/10.1111/ecog.06287.

Pavoine, S., and M. B. Bonsall. 2011. "Measuring Biodiversity to Explain Community Assembly: A Unified Approach." *Biological Reviews* 86: 792–812. https://doi.org/10.1111/j.1469-185X.2010.00171.x.

Perronne, R., F. Munoz, B. Borgy, X. Reboud, and S. Gaba. 2017. "How to Design Trait-Based Analyses of Community Assembly Mechanisms: Insights and Guidelines from a Literature Review." *Perspectives in Plant Ecology, Evolution and Systematics* 25: 29–44. https://doi.org/10.1016/j.ppees.2017.01.004.

Quintero, E., M. A. Pizo, and P. Jordano. 2020. "Fruit Resource Provisioning for Avian Frugivores: The Overlooked Side of Effectiveness in Seed Dispersal Mutualisms." *Journal of Ecology* 108: 1358–72. https://doi.org/10.1111/1365-2745.13352.

Quitián, M., V. Santillán, C. I. Espinosa, J. Homeier, K. Böhning-Gaese, M. Schleuning, and E. L. Neuschulz. 2019. "Direct and Indirect Effects of Plant and Frugivore Diversity on Structural and Functional Components of Fruit Removal by Birds." *Oecologia* 189: 435–445. https://doi.org/10.1007/s00442-018-4324-y.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramírez-Mejía, A. F. 2025. "Intrinsic and Extrinsic Drivers Shape Frugivore Functional Diversity within a Tree Population." *Ecosphere*. https://doi.org/10.5281/zenodo.17351425.

Saracco, J. F., J. A. Collazo, and M. J. Groom. 2004. "How Do Frugivores Track Resources? Insights from Spatial Analyses of Bird Foraging in a Tropical Forest." *Oecologia* 139: 235–245. https://doi.org/10.1007/s00442-004-1493-7.

Schneiberg, I., D. Boscolo, M. Devoto, V. Marcilio-Silva, C. A. Dalmaso, J. W. Ribeiro, M. C. Ribeiro, A. de Camargo Guaraldo, B. B. Niebuhr, and I. G. Varassin. 2020. "Urbanization Homogenizes the Interactions of Plant-Frugivore Bird Networks." *Urban Ecosystem* 23: 457–470. https://doi.org/10.1007/s11252-020-00927-1.

Schupp, E. W., R. Zwolak, L. R. Jones, R. S. Snell, N. G. Beckman, C. Aslan, B. R. Cavazos, et al. 2019. "Intrinsic and Extrinsic Drivers of Intraspecific Variation in Seed Dispersal Are Diverse and Pervasive." *AoB Plants* 11: plz067. https://doi.org/10.1093/aobpla/plz067.

Sekercioglu, C. H. 2006. "Increasing Awareness of Avian Ecological Function." *Trends in Ecology & Evolution* 21: 464–471. https://doi.org/10.1016/j.tree.2006.05.007.

Stiles, F. G. 1995. "Behavioral, Ecological and Morphological Correlates of Foraging for Arthropods by the Hummingbirds of a Tropical Wet Forest." *The Condor* 97: 853–878. https://doi.org/10.2307/1369527.

Suhonen, J. 1993. "Predation Risk Influences the Use of Foraging Sites by Tits." *Ecology* 74: 1197–1203. https://doi.org/10.2307/1940490.

Tonos, J., O. H. Razafindratsima, Z. S. E. Fenosoa, and A. E. Dunham. 2022. "Individual-Based Networks Reveal the Highly Skewed Interactions of a Frugivore Mutualist with Individual Plants in a Diverse Community." *Oikos* 2022. https://doi.org/10.1111/oik.08539.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. "The Return of the Variance: Intraspecific Variability in Community Ecology." *Trends in Ecology & Evolution* 27(4): 244–252. https://doi.org/10.1016/j.tree.2011.11.014.

Vissoto, M., J. Vizentin-Bugoni, O. J. F. Bonnet, G. C. Gomes, and R. A. Dias. 2019. "Avian Frugivory Rates at an Abundant Tree Species Are Constant throughout the Day and Slightly Influenced by Weather Conditions." *Journal für Ornithologie* 160: 655–663. https://doi.org/10.1007/s10336-019-01663-w.

Vissoto, M., J. Vizentin-Bugoni, S. F. Sendoya, G. C. Gomes, and R. A. Dias. 2022. "Plant Height and Spatial Context Influence Individual Connectivity and Specialization on Seed Dispersers in a Tree Population." *Oecologia* 198: 721–731. https://doi.org/10.1007/s00442-022-05142-7.

Vizentin-Bugoni, J., J. H. Sperry, J. P. Kelley, J. T. Foster, D. R. Drake, S. B. Case, J. M. Gleditsch, A. M. Hruska, R. C. Wilcox, and C. E. Tarwater. 2022. "Mechanisms Underlying Interaction Frequencies and Robustness in a Novel Seed Dispersal Network: Lessons for Restoration." *Proceedings of the Royal Society B* 289: 20221490. https://doi.org/10.1098/rspb.2022.1490.

Vizentin-Bugoni, J., J. H. Sperry, J. P. Kelley, J. M. Gleditsch, J. T. Foster, D. R. Drake, A. M. Hruska, R. C. Wilcox, S. B. Case, and C. E. Tarwater. 2021. "Ecological Correlates of Species' Roles in Highly Invaded Seed Dispersal Networks." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2009532118. https://doi.org/10.1073/pnas.2009532118.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Wickham, H., R. François, L. Henry, K. Müller, and D. Vaughan. 2023. "dplyr: A Grammar of Data Manipulation." R Package Version 1.1.1. https://CRAN.R-project.org/package=dplyr.

Wilke, C. 2020. "cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'." R Package Version 1.1.1. https://CRAN.R-project.org/package=cowplot.

SUPPORTING INFORMATION

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