Journal of Tropical Ecology

www.cambridge.org/tro

Tree density-dependence effects on seed dispersal of a large-seeded tropical tree

Fernanda Cristina Souza[1,2], Arleu Barbosa Viana-Junior[3], Pedro Uchoa Mittelman[4] and Fernando Cesar Cascelli de Azevedo[5,6]

[1]Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil; [2]Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil; [3]Programa de Pós-graduação em Biodiversidade e Evolução, Laboratório de Ecologia de Invertebrados, Coordenação de Zoologia, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; [4]Wildlife Sciences, University of Goettingen, Goettingen, Germany; [5]Departamento de Ciências Naturais, Universidade Federal de São João del Rei, São João del Rei, Brazil and [6]Instituto Pró-Carnívoros, Atibaia, São Paulo, Brazil

Research Article

Cite this article: Souza FC, Viana-Junior AB, Mittelman PU, and Azevedo FCCde (2023). Tree density-dependence effects on seed dispersal of a large-seeded tropical tree. *Journal of Tropical Ecology*. **39**(e17), 1–7. doi: https://doi.org/10.1017/S0266467423000068

Received: 8 June 2022
Revised: 27 January 2023
Accepted: 12 March 2023

Keywords:
Mutualism; predator dispersal hypothesis; seed predation; seed burial; tropical forest

Author for correspondence:
Fernando Cesar Cascelli de Azevedo,
Email: fazevedo@ufsj.edu.br

Abstract

One of the biggest issues in plant ecology is determining the interaction outcome between seeds and scatter-hoarding rodents because the latter has a dual role as dispersers and predators of seeds. Density-dependence contexts involving resource abundance largely influence the outcome of this interaction. Here, we investigated how the variation in the density of a large-seeded tropical tree (*Joannesia princeps* Vell) affects its probability of seed removal, consumption, dispersal, and burial by a neotropical rodent (*Dasyprocta azarae* Lichtenstein). We tested whether the elevated resource availability in high tree density areas would cause scatter hoarder's satiation by decreasing seed removal and consumption (predator satiation hypothesis) or increasing seed dispersal and burial (predator dispersal hypothesis). We tracked the fate of 461 seeds in 14 plots with distinct *J. princeps* abundances inside a large Atlantic Forest fragment. We used spool-and-line tracking and camera trappings to determine seed fate and identify interacting animals. Agouti was the only species removing *J. princeps* seeds. Tree density benefitted *J. princeps* by increasing seed dispersal through buried seed but not affecting seed removal and consumption. This result shows how density-dependent contexts, such as tree density, may alter seed fate in seed–rodent interactions supporting future studies aiming to reestablishing seed dispersal functions in Atlantic Forest fragments.

Introduction

One of the greatest challenges in plant ecology is determining the consequences of seed predation and dispersal for the population dynamics of plants, especially when frugivorous species have a dual functional role in the interaction networks (Xiao et al. 2013, Bogdziewicz et al. 2020). Scatter-hoarding rodents play a dual role because, in addition to preying on many species' seeds of large-seeded plants, they also disperse them (Donatti et al. 2009, Haugaasen et al. 2010). Seed predation occurs because scatter-hoarding rodents, as granivorous animals, consume mainly seeds rather than fruit pulp. However, scatter-hoarding rodents are recognised as dispersers when they remove and bury seeds for later consumption but do not recover them (Gomez et al. 2019, Smythe 1978). Many reasons prevent seeds from being retrieved, such as hoarders forgetting the cache places, hoarders dying, or seeds germinating (Lichti et al. 2017). Outcomes of seed predation and dispersal by scatter-hoarding rodents have significant consequences for the plant regenerations process, changing seed survival rates and seedlings establishment.

The balance between the costs and benefits of interactions between large-seeded plant species and scatter-hoarding rodents is highly dependent on the ecological context (Zwolak & Crone 2012). One of the main factors that can influence this interaction is the change in resource abundance. Changes in seed abundance can affect seed fates, such as predation and dispersal, due to density-dependent effects (Jones & Comita 2010, Lichti et al. 2017, Wang 2020). Seed predators might react to changes in seed abundance in two not mutually exclusive ways, which are explained by the Predator–Satiation (PS) and Predator–Dispersal (PD) hypotheses. According to the PS hypothesis, synchronised large seed production results in high seed survival because seed production exceeds the consumption capacity of granivorous animals (Silvertown 1980, Kelly & Sork 2002). Although the PS hypothesis has been widely tested in temperate and tropical forests (Visser et al. 2011, Xiao et al. 2013), it does not consider the benefits of seed dispersal and caching because the satiation of predators occurs before seed removal. Alternatively, the PD hypothesis predicts that a larger proportion of seeds should be dispersed in years of greater seed abundance (Kelly & Sork 2002, Vander Wall 2002). To the PD hypothesis, the satiation occurs after caching and not during the harvesting phase (Vander Wall 2002,

© The Author(s), 2023. Published by Cambridge University Press

Xiao et al. 2013, Zwolak et al. 2016), leading to greater survival of cached seeds and, consequently, more effective seed dispersal.

The outcome of seed–scatter-hoarding rodents' interactions in density-dependence contexts can be helpful for re-establishing ecological functions in areas undergoing natural restoration. For instance, increasing seed dispersal in high tree-density areas can improve seedling survival by reducing dispersal limitation through seed removal to safer locations (Hirsch et al. 2012). Furthermore, seeds dispersed and buried are more likely to germinate and establish because they are protected from desiccation and mortality due to natural enemies (Kuprewicz 2015). On the other hand, the decrease of seed removal or consumption in high tree-density areas can decline seedling survival due to the high mortality rate of non-dispersed seeds close to the parent tree (Comita et al. 2014). In this context, the reproductive success of plants depends on the seed fate in areas of high resource abundance with distinct consequences to seedling survival. Previous studies have addressed the effects of changes in resource abundance, focussing on the interaction between scatter-hoarding rodents and nuts (Haugaasen et al. 2010, Xiao & Huang 2020) and often estimating only seed removal rates and dispersal distance (Vieira et al. 2011, Jansen et al. 2014). However, more detailed information is needed regarding which mechanism and how resource abundance alters seed fate in seed–rodent interactions.

Due to the high nutrient content in their seeds and the high quantity of fruits produced, *Joannesia princeps* Vell (Euphorbiaceae) is a remarkable candidate for studying the relationships between large-seeded tropical trees and large rodents in density-dependence contexts (Cid et al. 2014). Furthermore, *J. princeps* is one of the few species that produce fruits in our study site from April to June. In this setting, we investigated seed removal and fate across a range of *J.princeps* tree densities in a forested fragment in the southern Atlantic Forest. We were particularly interested in understanding how the variation in the population density of *J. princeps* affects the probability of seed removal, consumption, burial, and dispersal. We hypothesised that scatter-hoarding rodents would be satiate in areas with high seed abundance. Thus, we expect (i) a lower seed removal or consumption probability if the PS hypothesis were supported or (ii) a higher seed dispersal or burial probability if the PD hypothesis is supported.

Material and methods

Study site and species

This study was conducted in the Rio Doce State Park (RDSP), located in southeastern Brazil at Minas Gerais State (19°48'S 42°38'W; Figure 1). This Park represents the larger protected fragment of Atlantic Forest in the State with approximately 36,000 hectares (ha). The vegetation consists of Semidecidual Submontane Seasonal Forest that underwent a natural regeneration process after the last fire in the 1960s. The Park presents secondary forests interspersed with stretches of primary forests (Stallings et al. 1990). Analysis of the landscape dynamics revealed that RDSP underwent minimal changes in the landscape between 1985 and 2015, and the human-altered uses are almost insignificant concerning the total area of the native forest (Oliveira et al. 2020).

Joannesia princeps is an endemic and common tree in the Brazilian Atlantic Forest, acting as a pioneer or early secondary species in secondary forests (Lopes et al. 2002). In secondary forests, the adult individuals present a height between 15 and 20 m and a diameter between 40 and 60 cm (Lorenzi 1998). Flowering occurs between June and December, and fruits mature between March and July in the Atlantic Forest of Minas Gerais State, Brazil (Carvalho 2005, Lorenzi 1998). The fleshy fruits are divided into exocarp, open in four woody valves, and indehiscent hard-husked endocarp containing two to three seeds. The endocarps present mass of 54.29 ± 11.45 g (mean ±SD, n = 439), length of 60.96 ± 6.26 mm (mean ±SD, n = 319), and diameter of 58.66 ± 5.66 mm (mean ±SD, n = 442).

Agoutis are known to be the only dispersers of *J. princeps* seeds in the Atlantic Forest (Galetti et al. 2017, Mittelman et al. 2020). The Azara's agouti (*Dasyprocta azarae* Lichtenstein) is a scatter-hoarding rodent that weighs from 1 to 4 kg and is found in forest and savannah habitats in southeast South America (Catzeflis et al. 2016). As scatter-hoarding rodents, they have the behaviour of storing seeds as a food reserve. Food reserves are formed by one or more seeds stored on the soil surface, which can be recovered for later consumption mainly during periods of scarcity (Smythe 1978). *Joannesia princeps* fruits show primary dispersal by gravity (barochory) and secondary dispersal by scatter-hoarders behaviour (synzoochory) (Carvalho 2005). After primary dispersal, only the endocarp and the seeds within it tend to remain on the forest floor to be transported by dispersers. The pulp of the *J. princeps* fruit is not widely consumed by frugivores and is quickly perishable after falling to the ground. Although agoutis interact with a wide variety of large-seeded species, only recently have the interactions between *J. princeps* seeds and agoutis received more attention. In areas undergoing natural restoration, agoutis have recovered dispersal interactions with *J. princeps* seeds and improved recruitment of their seedling (Mittelman et al. 2020).

Sample design and density of trees

To estimate the density of *J. princeps* trees, we recorded all adult individuals (DBH > 40 cm) in 15 fixed plots of 2500 m^2 that were located on a flat floor and had at least two adult *J. princeps* trees (Figure 1). Due to the absence of phytosociological studies that could inform about the variation of *J. princeps* density, we established the plots in the main trails of the RDSP where we already had previous knowledge of *J. princeps* presence. The centres of each plot were separated by at least 200 m. This distance is approximately the diameter of a circular area of three hectares which is a proxy to home ranges described for agoutis (Silvius & Fragoso 2003), making each fixed plot a spatially independent sampling unit. An adult *J. princeps* tree was chosen as the central plot tree. From this tree, a 25-m radius was established in the four cardinal directions, forming four quadrants of 25 m × 25 m each, totalling an area of 2500 m^2. This radius represents a realistic spatial scale at which agoutis can respond to food abundance (Hirsch et al. 2012).

Seed fate experiment

At the end of the fruiting period, between June and July 2016, we collected, pulped, and dried intact non-infested seeds for the seed fate experiment. We placed between 31 and 33 seeds distributed in three trees at least 5 m apart in each plot. The seeds were distributed around a young tree for plots with only two adult trees (DBH < 40 cm). The seeds distributed in each plot were selected randomly, numbered for individual recognition, and positioned at 1 m from the trunk tree (initial position). We used the spool-and-line method to track seed fate (Forget & Wenny 2005) with a line length of 50 m. To determine the seed fate, we attached spool lines to 492 experimental seeds and tracked them. Seed fates were checked 40 days after the beginning of the experiment. The time interval established was sufficient to verify the final dispersal events

https://doi.org/10.1017/S0266467423000068 Published online by Cambridge University Press

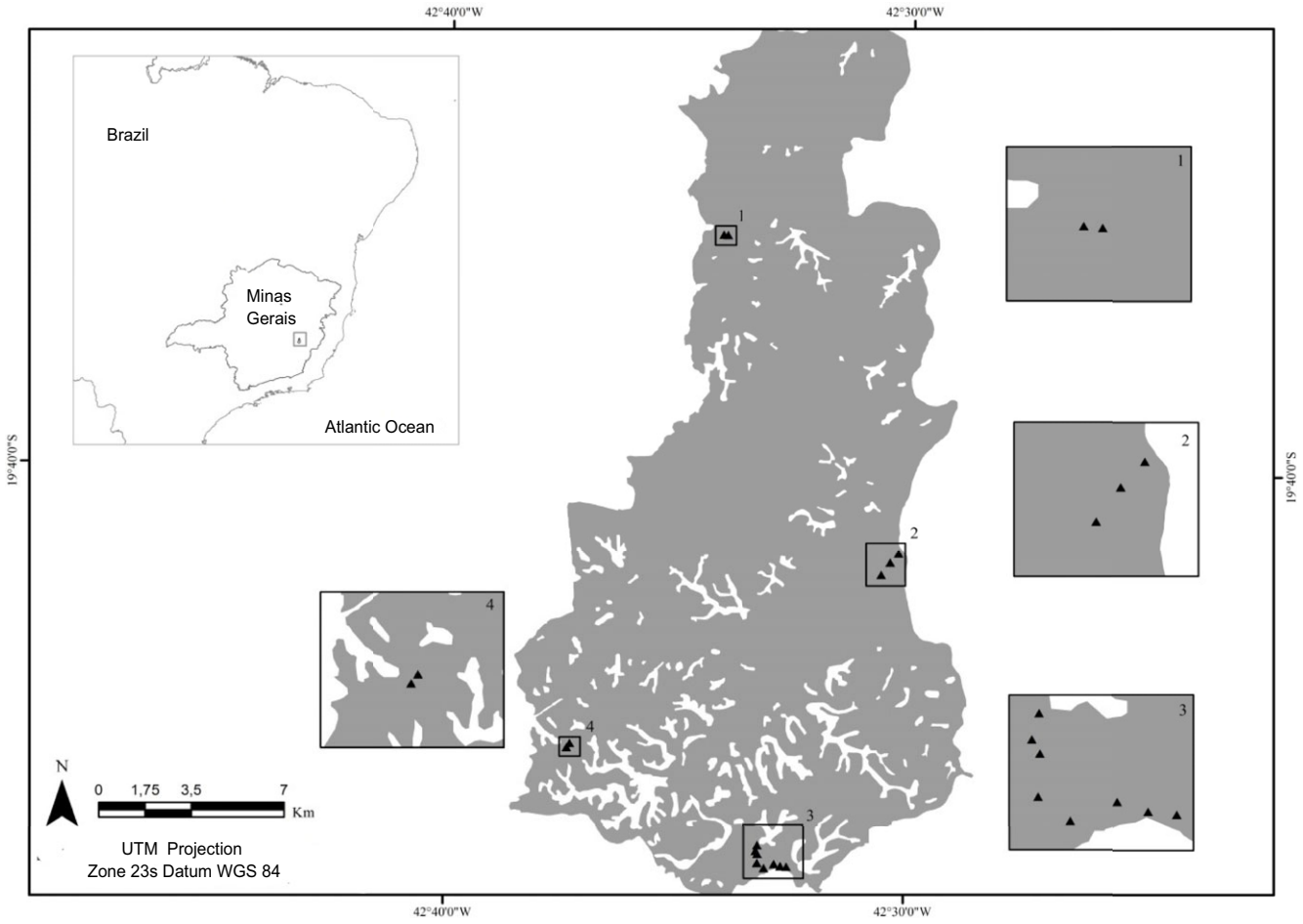


Figure 1. Locations of the 15 plots (sample units) in the trails Juquita (1), Campolina (2), Mombaça (3), and Vinhático (4). The marks indicate georeferenced points of main *Joannesia princeps* trees established between January and June 2016 at Rio Doce State Park, Minas Gerais, Brazil. Inserts in the upper left corner show the location of the state of Minas Gerais in Brazil and, within the state, the location of the Rio Doce State Park.

without underestimating them since, for this species, over 95% of cache predation events (recovery and predation of seeds after burial) occur before 40 days (Mittelman et al. 2021b).

We considered as removed seeds those found at 0.5 m or more from the initial position, with the other seeds being classified as non-removed. Removed seeds were classified as either dispersed or consumed at their final locations. Seeds were considered dispersed when found intact on the soil surface or buried. Consumed seeds were those found with the endocarp destroyed without seeds in its interior (Figure S1). The removed and lost seeds could not be classified concerning their final location. However, they were considered as removed seeds. We used the signs and marks left on seeds to identify mammal groups that potentially could remove *J. princeps* seeds.

After the seed removal and fate experiment, we collected available seeds on the surface and below the soil in 64 quadrants (1 m^2) distributed randomly and stratified inside the central area of each plot. Seed collection was used to investigate whether plots with high tree density also had high seed abundance. We found that tree density and seed abundance were positively correlated (Spearman correlation = 0.50; $P < 0.001$). Since we observed this correlation and because *J. princeps* disproportionally determines the resource abundance in the areas where it is present, we used *J. princeps* tree density as a proxy for seed abundance in the area.

Besides using signs and marks left on the seeds, we also used cameras as a complementary method to confirm which mammal species interact with *J. princeps* seeds. In September 2016, shortly after the seed fate experiment, we installed a camera trap (Bushnell® Trophy Cam Natureview-Kansas, USA) in front of the central tree of each plot (n = 15). About 20 seeds, without any tracking, were placed below each central tree. In each central tree, cameras were placed approximately 40 cm from the ground and set to record 30 s HD videos, with an interval of 60 s between videos. All cameras were set to operate 24 hr/day for 31 consecutive days.

Data analysis

We built generalised linear mixed models (GLMMs) with a binomial response to estimate the probability of seed removal, consumption, burial, and dispersal as a function of tree density (fixed effect), using the site as a random factor (n = 4; Figure 1). To test the PS hypothesis, we analysed the probability of seed removal and consumption as a function of tree density. To test the PD hypothesis, we built models testing the probability of seed dispersal and burial as a function of tree density. For the PD hypothesis, we constructed two distinct models for each seed fate (dispersal or burial) probability. The first model concerns all experimental seeds, and the second concerns only removed seeds

https://doi.org/10.1017/S0266467423000068 Published online by Cambridge University Press

(excluding the lost seeds – Table S1). Here, using removed seeds can better test the PD hypothesis because this hypothesis predicts that satiety occurs after the removal phase increasing the survival of already dispersed seeds (less buried seeds are retrieved and consumed) (Vander Wall 2002, Zwolak et al. 2016). We checked for heteroscedasticity, under/overdispersion, and residual correlation in all models. Models were built with the lme4 package in R software (Bates et al. 2015, R Core Team 2022).

Results

We tracked the fate of 461 seeds of *J.priceps* in RDSP. Unfortunately, one of our plots had the experimental seeds disrupted because of anthropic interference. From a total of 461 experimental seeds, 158 seeds were removed (34.3%). We tracked the final fate of 158 removed seeds, most of which were consumed (n = 88, 19.1%). Of those seeds dispersed (removed and intact, n = 44), 28 (6.0%) were buried, and the remaining seeds were found on the soil surface (n = 16; 3.4%). Buried seeds were intact and non-infested. A small percentage of removed seeds went missing (n = 26; 5.6%) (Figure 2).

We recorded 312 visits by frugivorous to *J. princeps* trees using camera traps (Table S2). However, only visits by agoutis resulted in interactions with the seeds of *J. princeps*. These interactions were of harvest, consumption, or removal of seeds in front of the cameras (Figure S2). Regarding the first prediction tested, we observed that the probability of seed removal and consumption was not related to tree density (Figure 3a and b – Table 1). However, testing the second prediction, we observed that the seed dispersal and burial probability increased significantly with tree density when only removed seeds were considered (Figure 3c – Table 1; GLMM fixed effect: z value = 3.043; P = 0.002; df = 1). Concerning all experimental seeds, the probability of seed dispersal and burial was not associated with tree density (Table 1).

Discussion

Our results reveal an increase in the probability of seed dispersal as a function of tree density. However, resource abundance did not affect the probability of seed removal or consumption. The direction and magnitude of interactions involving plants and scatter-hoarding rodents have recently been the subject of discussions in the literature (Zwolak & Crone 2012, Bogdziewicz et al. 2020, Moore & Dittel 2020). Nevertheless, these empirical findings have not considered the real context in which interactions occur, failing to include density-dependent effects (Moore & Dittel 2020). In the density-dependence context, our findings support the PD hypothesis (without support for the PS hypothesis). There was an increase in the probability of burial from removed seeds, but there was no increase in pre-dispersal seed survival (via decreasing seed removal or consumption). These results can have significant consequences on plant populations' dynamics and seedlings' recruitment rates (Xiao et al. 2013).

We observed positive density-dependence effects on seed fate in a high tree density context, with an increasing seed burial probability. Until recently, most studies did not approach the interaction between scatter-hoarding rodents and plants through a context-dependent point of view, failing to include density-dependence effects (Zwolak & Crone 2012, Bogdziewicz et al. 2020). Some tree species that depend on scatter-hoarding animals for seed dispersal produce massive crops at irregular intervals. Producing more fruit than predators can consume has been explained as a strategy to increase animal dispersal and reduce predation (Kelly & Sork, 2002). Although we tested hypotheses related to variations in resource production, we emphasise that resource abundance was not manipulated in this study. Instead, we used tree density as a proxy for resource abundance. Another mechanism that increases the number of dispersed seeds in high-resource areas is the diminishing of pilferage rates of seeds in the cache. In areas of high seed abundance, the intrinsic value of the seed tends to be lower, which reduces the likelihood of cache pilferage by other competitors (Moore et al. 2007). With lower cache pilferage, scatter-hoarding rodents need to harvest seeds less often. In the end, more seeds can remain stored in caches in areas with high seed abundance (Vander Wall 2002, Jansen et al. 2004).

In our study, PD hypothesis was the main mechanism to explain how resource abundance alters seed fate in seed–rodent interactions. Although PD and PS hypotheses assume that satiety occurs in high seed abundance scenarios, the main difference is in the rodent response. Seed dispersal will not always be maximised in the density-dependence context: granivorous can be satiated during seed removal phase, decreasing harvested seeds, and increasing seed survival without necessarily an increase in dispersal (PS hypothesis). Alternatively, satiation can occur after the seed is cached, increasing seed survival through dispersal or burial (PD hypothesis). In the PD hypothesis, seed survival is often attributed to a lower probability of seed consumption due to low levels of seed removal from caches (Li & Zhang 2007, Xiao et al. 2013). In areas with high tree density and resource abundance, a low proportion of the seed crop can be enough to satiate predators, and thus seeds will be spared. With predators satiated, there is an increase in the rates of dispersal and burial from removed seeds. Besides, cached seeds are more likely to remain stored in the soil if other non-harvested seeds are still available. In the end, density dependence increases effective dispersal and consequently improves the survival of cached seeds. These distinct responses are essential for plant demographics because cached seeds are dispersed and have greater chances of germination and seedlings establishment than non-dispersed seeds.

We show that consumption and dispersal of *J. princeps* seeds were performed only by agoutis. This singular interaction between agouti and agouti-tree (popularly known as "cotieira") is corroborated by Mittelman and colleagues (2020) in Atlantic Forest. The outcomes of these interactions are essential for the current context of most of the Atlantic Forest, which is present in small fragments (Ribeiro et al. 2009) and often with the absence of large frugivorous animals (Galetti et al. 2017). In these small fragmented forests, many large-seeded species can exhibit seed dispersal limitations, and scatter-hoarding rodents are often the only dispersers of these plant species (Jansen et al. 2012). Although there is no direct evidence pointing out that *J. princeps* was dispersed by megafaunal frugivore, *J. princeps*' fruit traits (colour, fruit mass, fleshy pulp, seed size, number of seeds, and thickness of endocarp) fit the description by Guimarães et al. (2008) of type 1 megafauna fruits. Furthermore, compiled evidence suggests that agoutis act as substitute dispersers of megafauna fruits as they are the only species able to disperse the largest seeds in the Neotropics (Mittelman et al. 2021a). Therefore, the singular interaction between agouti and agouti tree is an essential match for reducing dispersal limitation and improving seedling survival in Atlantic Forest fragments (Mittelman et al. 2020).

The maintenance of ecological functions performed by scatter-hoarding rodents is paramount for plant species regeneration. Since only buried *J. princeps* seeds can germinate and establish

https://doi.org/10.1017/S0266467423000068 Published online by Cambridge University Press

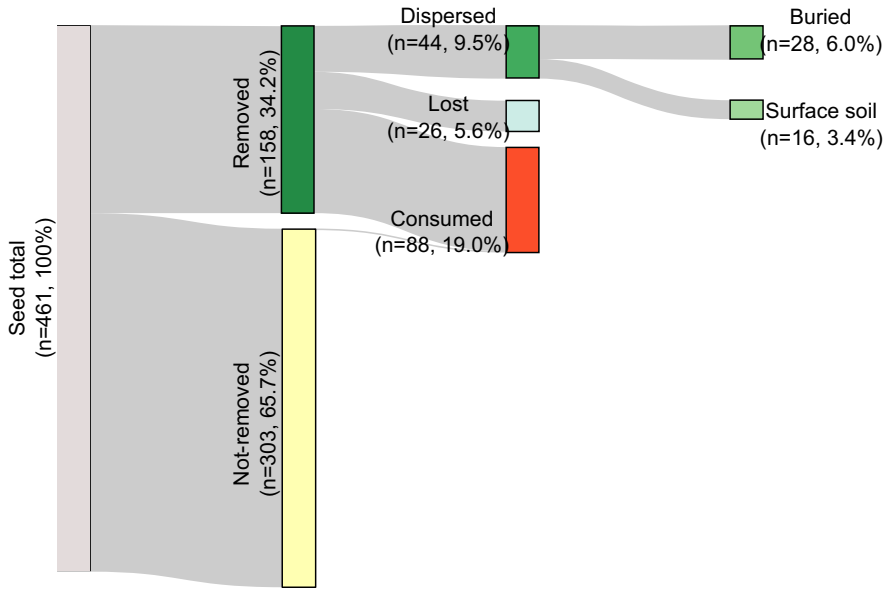


Figure 2. *Joannesia princeps* seed fate experiments. Sankey diagram shows the proportions and absolute numbers for each fate (non-removed, removed, consumed, lost, and dispersed) after 40 days of exposure at Rio Doce State Park, Minas Gerais, Brazil. The beige and dark green colours represent removed and non-removed seeds, respectively. The red colour represents removed seeds that were consumed, and the light green colours indicate removed seeds that were dispersed. The blue color represents the removed seeds that were lost. The seeds buried and seeds on the soil surface were classified as dispersed seeds.

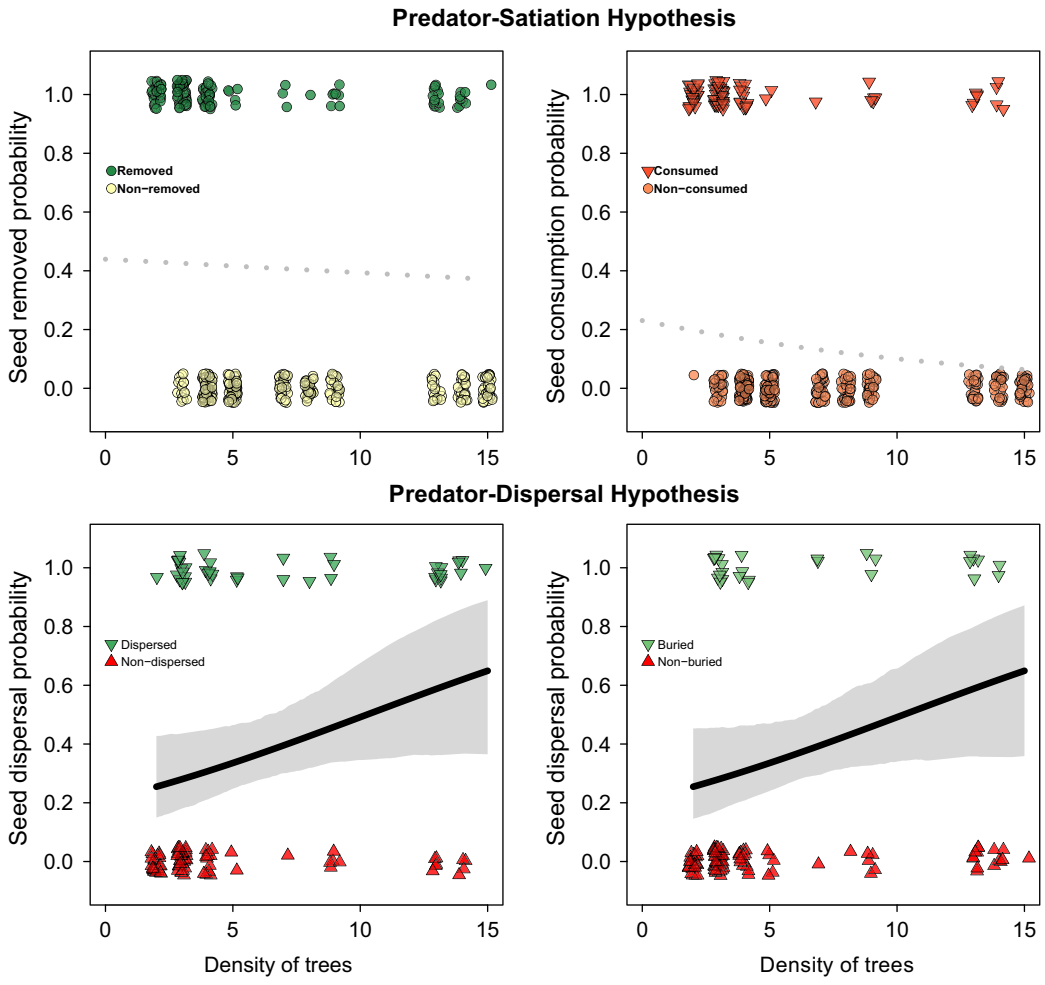


Figure 3. Removed, consumed, and dispersal probability of *Joannesia princeps* seeds by agouti as a function of the number of trees in fixed plots of 2,500m^2 at Rio Doce State Park, Minas Gerais, Brazil. A. The beige and dark green dots represent the removed and non-removed seeds, respectively. B. The orange dots represent the non-consumed and the red triangles indicate consumed seeds. C. The green and red triangles represent dispersed and non-dispersed seeds, respectively. D. The light green and red triangles represent buried and non-buried seeds, respectively. The dotted black line represents trends in GLMM global prediction for Predator–Satiation Hypothesis. The filled black line is the GLMM global prediction for the Predator–Dispersal Hypothesis with the bootstrap estimates (gray lines).

new seedlings (Mittelman et al. 2020) and agoutis seem to be the only animal able to do so, they provide a fundamental service to the plant. *J. princeps* seed dispersal decreases the risk of density-dependent mortality and increases the chances of germination and the establishment of large-seeded plants in safe locations (Haugaasen et al. 2010; Mittelman et al. 2021a). Although seed dispersal rates were greater in high tree-density areas, we did not examine seedlings' recruitment success concerning conspecific

https://doi.org/10.1017/S0266467423000068 Published online by Cambridge University Press

Table 1. Summary and analysis of deviance of mixed models to assess the effect of tree density on teed removal, consumption, dispersal, and burial at Rio Doce State Park, Minas Gerais, Southeastern Brazil

Models	Terms	df	Chisq	PseudoR^2	Estimate	SE	z-value	Pr(>|z|)	
	Intercept			R^2m = 0.0004	−0.244	1.5473	−0.157	0.875	
Removed (1)–non-removed (0)	Number of trees	1	0.2346	R^2c = 0.6891	−0.019	0.039	−0.484	0.6281	
	Residuals	459							
	Intercept			R^2m = 0.0177	−1.205	1.2171	−0.99	0.322	
Consumed (1)–non-consumed (0)	Number of trees	1	2.3935	R^2c = 0.4819	−0.099	0.0638	−1.547	0.122	
	Residuals	433							
	Intercept			R^2m = 0.0606	−1.334	0.5169	−2.58	0.0099	**
Dispersed (1)–non-dispersed (0)^R	Number of trees	1	4.5023	R^2c = 0.0951	0.1299	0.0612	2.122	0.0339	*
	Residuals	131							
	Intercept			R^2m = 0.0002	−2.22	0.4344	−5.111	0	***
Dispersed (1)–non-dispersed (0)^T	Number of trees	1		R^2c = 0.0202	0.0128	0.0439	0.292	0.77	
	Residuals	433	0.0853						
	Intercept			R^2m = 0.0268	−1.889	0.3674	−5.142	0	***
Buried (1)–non-buried (0)^R	Number of trees	1		R^2c = 0.0268	0.0994	0.0483	2.056	0.0398	*
	Residuals	131	4.2282						
	Intercept			R^2m = 0.0005	−2.885	0.7372	−3.584	0.0001	***
Buried (1)–non-buried (0)^T	Number of trees	1	0.0976	R^2c = 0.0597	0.0202	0.0646	0.312	0.755	
	Residuals	433							

The random effect for all models was (1|g1) [intercept varying among g1] when g1 = site (n = 4). df = degrees of freedom; Chisq = type II Wald chi-square tests; Pseudo R^2 = conditional (R^2c) and marginal (R^2m) coefficient of determination for generalised mixed-effect models; SE = standard error. R = Considering only removed seeds. T = Considering all experimental seeds. In all models (except the removed–non-removed model), lost seeds were excluded from the analyses.

parental trees. These results would be essential to assess the probability of seeds stored survival and emerging as seedlings (Jansen & Forget 2001). Nevertheless, agoutis usually transport seeds to areas with a lesser number of adult conspecifics (Hirsch et al. 2012). Thus, agouti dispersal is likely to help seeds in these high tree-density areas by reducing aggregation and thus minimising negative-density dependence factors causing seed and seedling mortality.

We show that density-dependent contexts, such as tree density, affected seed fate by increasing the probability of seed dispersal through buried seeds. Furthermore, agoutis were the only species that interacted with *J. princeps* seeds. Our findings support the notion that ecological interactions are vital for ecosystem functioning, exemplified by the necessity that *J. princeps* has of agoutis for its dispersal. In the long term, the presence of agoutis can be fundamental for the occurrence of *J. princeps*, minimising the probability of local extinction through the dispersal of their seeds, mainly in areas of high tree density.

Supplementary material. For supplementary material accompanying this paper visit https://doi.org/10.1017/S0266467423000068

Acknowledgments. We would like to thank National Council for Scientific and Technological Development (CNPq) for the scholarship. We thank all the members of Laboratório de Ecologia de Vertebrados LEVE-UFSJ and ECMVS-UFMG for their help with fieldwork, in particular Maria Tereza for identified cutieiras trees. We are still grateful to the members of RDSP (Vinícius, Mirlaine, Élida, Cimar, Sr. Antônio, Silas, Perpétuo, Liban, and Cláudio) for their collaboration with the infrastructure and logistics of fieldwork, mainly Lino and Neymar for having climbed cutieiras trees and collected the experimental fruits. Finally, we would like to thank Ricardo Arrais, Alexandra Cumerlato, and Álvaro Silva for their help with installing camera traps. Viana-Junior AB thanks the receiving a young researcher scholarship from the FAPESPA (Fundação de Amparo a Pesquisa do Estado do Pará) by grant #026/2021, process 2021/658276, by way of the project "Training of Human Resources for the Development of Science in the Amazon".

Author contributions. Fernanda Cristina Souza: Conceptualisation and design of the study, Data collection, Writing-Reviewing, and Editing. Arleu Barbosa Viana-Junior: Formal analysed and interpreted the data, Writing-Reviewing, and Editing. Fernando Cesar Cascelli de Azevedo: Conceptualisation, Provision of study materials, Writing-Reviewing and Editing, Supervision, Project Administration, and Funding acquisition. Pedro Mittelman: Support with data analyses, Writing-Reviewing, and Editing.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. The authors declare none.

References

Bates D, Mächler M, Bolker B and Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48.

Bogdziewicz M, Crone EE and Zwolak R (2020) Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. *Journal of Ecology* **108**, 1009–1018.

Carvalho PER (2005) *Boleira: Taxonomia e nomenclatura*. In Vencato MF (eds), *Circular Técnica*. Paraná, Brasil: Embrapa Florestas, pp. 1–9.

Catzeflis F, Patton J, Percequillo A and Weksler M (2016) *Dasyprocta azarae*. *The IUCN Red List of Threatened Species* 2016: e. T6278A22198654. https://www.iucnredlist.org/species/6278/22198654 (accessed 1 June 2022).

Cid B, Figueira L, Mello TAF, Pires AS and Fernandez FAS (2014) Short-Term success in the reintroduction of the red-humped agouti *Dasyprocta*

leporina, an important seed disperser, in a Brazilian Atlantic Forest Reserve. *Tropical Conservation Science* **7**, 796–810.

Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, Beckman N and Zhu Y (2014) Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance-and density-dependent seed and seedling survival. *Journal of Ecology* **102**, 845–856.

Donatti CI, Guimarães PR and Galetti M (2009) Seed dispersal and predation in the endemic Atlantic rainforest palm *Astrocaryum aculeatissimum* across a gradient of seed disperser abundance. *Ecological Research* **24**, 1187–1195.

Forget PM and Wenny D (2005) *How to elucidate seed fate? A review of methods used to study seed removal and secondary seed dispersal*. In Forget PM, Lambert JE, Hulme PE and Vander Wall SB (eds), *Seed Fate: Predation, Dispersal and Seedling Establishment*. Wallingford: CABI Publishing, pp. 379–393.

Galetti M, Brocardo CR, Begotti RA, Hortenci L, Rocha-Mendes F, Bernardo CSS, Bueno RS, Nobre R, Bovendorp RS, Marques RM, Meirelles F, Gobbo SK, Beca G, Schmaedecke G and Siqueira T (2017) Defaunation and Biomass collapse of mammals in the largest atlantic forest remnant. *Animal Conservation* **20**, 270–281.

Gomez JM, Schupp EW and Jordano P (2019) Synzoochory: the ecological and evolutionary relevance of a dual interaction. *Biological Reviews* **94**, 874–890

Guimarães PR, Galetti M and Jordano P (2008) Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE* **3**, 1–3.

Haugaasen JMT, Haugaasen T, Peres CA, Gribel R and Wegge P (2010) Seed dispersal of the Brazil nut tree (*Bertholletia excelsa*) by scatter-hoarding rodents in a central Amazonian forest. *Journal of Tropical Ecology* **26**, 251–262.

Hirsch BT, Kays R, Pereira VE and Jansen PA (2012) Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters* **15**, 1423–1429.

Jansen PA and Forget PM (2001) *Scatter hoarding and tree regeneration*. In Borges F, Charles-Dominique P, Forget PM and Théry M (eds), *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Dordrecht: Kluwer Academic Publishers, pp. 275–288.

Jansen PA, Bongers F and Hemerik L (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* **74**, 569–589.

Jansen PA, Hirsch BT, Emsens WJ, Zamora-Gutierrez V, Wikelski M and Kays R (2012) Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 12610–12615.

Jansen PA, Visser MD, Wright JS, Rutten G and Muller-Landau HC (2014) Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecology Letters* **17**, 1111–1120.

Jones FA and Comita LS (2010) Density-dependent pre-dispersal seed predation and fruit set in a tropical tree. *Oikos* **119**, 1841–1847.

Kelly D and Sork VL (2002) Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology and Systematics* **33**, 427–447.

Kuprewicz EK (2015) Scatter hoarding of seeds confers survival advantages and disadvantages to large-seeded tropical plants at different life stages. *PLoS One* **10**, 1–16

Li H and Zhang Z (2007) Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecology and Management* **242**, 511–517.

Lichti NI, Steele MA and Swihart RK (2017) Seed fate and decision-making processes in scatter-hoarding rodents. *Biological reviews of the Cambridge Philosophical Society* **92**, 474–504.

Lopes WP, Silva AF, Souza AL and Meira Neto JAA (2002) Estrutura fitossocióloga de um trecho de vegetação arbórea no Parque Estadual do Rio Doce - Minas Gerais, Brasil. *Acta Botanica Brasilica* **16**, 443–456.

Lorenzi H (1998) *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Brasil: Plantarum, Nova Odessa.

Mittelman P, Kreischer C, Pires AS and Fernandez FAS (2020) Agouti reintroduction recovers seed dispersal of a large-seeded tropical tree. *Biotropica* **52**, 766–774.

Mittelman P, Dracxler CM, Santos-Coutinho PRO and Pires AS (2021a) Sowing forests: a synthesis of seed dispersal and predation by agoutis and their influence on plant communities. *Biological Reviews* **96**, 2425–2445.

Mittelman P, Pires AS and Fernandez FAS (2021b) The intermediate dispersal hypothesis: seed dispersal is maximized in areas with intermediate usage by hoarders. *Plant Ecology* **222**, 221–231.

Moore CM and Dittel JW (2020) On mutualism, models, and masting: The effects of seed-dispersing animals on the plants they disperse. *Journal of Ecology* **108**, 1775–1783.

Moore JE, McEuen AB, Swihart RK, Contreras TA and Steele MA (2007) Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology* **88**, 2529–2540.

Oliveira BR, Carvalho-Ribeiro SM and Maia-Barbosa PM (2020) A multiscale analysis of land use dynamics in the buffer zone of Rio Doce State Park, Minas Gerais, Brazil. *Journal of Environmental Planning and Management* **63**, 935–957.

R Core Team (2022) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni F and Hirota M (2009) Brazilian Atlantic Forest: how much is left and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* **142**, 1141–1153.

Silvertown JW (1980) The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* **14**, 235–250.

Silvius KM and Fragoso JMV (2003) Red-rumped agouti (*Dasyprocta leporina*) home range use in an Amazonian forest: implications for the aggregated distribution of forest trees. *Biotropica* **35**, 74–83.

Smythe N (1978) The natural history of the Central American agouti (*Dasyprocta punctata*). *Smithsonian Contributions to Zoology*, **257**, 1–52

Stallings JR, Fonseca GAB, Pinto LPS, Aguiar LMS and Sábato EL (1990) Mamíferos do Parque Florestal Estadual do Rio Doce, Minas Gerais, Brasil. *Revista Brasileira de Zoologia* **7**, 663–677.

Vander Wall SB (2002) Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* **83**, 3508–3516.

Vieira EM, Ribeiro JF and Iob G (2011) Seed predation of *Araucaria angustifolia* (Araucariaceae) by small rodents in two areas with contrasting seed densities in the Brazilian Araucaria forest. *Journal of Natural History* **45**, 843–854.

Visser MD, Muller-Landau HC, Wright SJ, Rutten G and Jansen PA (2011). Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecology Letters* **14**, 1093–1100.

Wang B (2020) Seed density affects post-dispersal seed predation: evidence from a seed removal experiment of 62 species. *Integrative Zoology* **15**, 135–143.

Xiao Z and Huang X (2020) How seed defense and seed abundance predict dispersal and survival patterns in Camellia. *Integrative Zoology* **15**, 103–114.

Xiao Z, Zhang Z and Krebs CJ (2013) Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. *Journal of Ecology* **101**, 1256–1264.

Zwolak R, Bogdziewicz M, Wróbel A and Crone EE (2016) Advantages of masting in European beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia* **180**, 749–758.

Zwolak R and Crone EE (2012) Quantifying the outcome of plant-granivore interactions. *Oikos* **121**, 20–27.

https://doi.org/10.1017/S0266467423000068 Published online by Cambridge University Press