

# Endozoochory by lowland tapirs improves seed germinability and accelerates germination time of native plant species in an Amazon-Cerrado transition restoration area

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## ABSTRACT

Endozoochory by lowland tapirs (*Tapirus terrestris*) is regarded as a key seed dispersal mechanism in tropical forests and thus potentially useful for ecological restoration. Although previous studies attested the germination ability of seeds defecated by *T. terrestris*, no study has tested how tapir endozoochory affects the seed germination process in degraded lands. In an ecological restoration area in the Amazon-Cerrado transition, we ran germination trials to compare seed germination percentage and number of days until seed germination of six native plant species found in tapir feces with manually-scarified and manually-depulpd (control) seeds. For all six plant species assessed, germination percentage was statistically higher and the number of days until seed germination was statistically lower for tapir-ingested seeds and manually-scarified (compared to control seeds). Results from the germination trials showed that tapir endozoochory was associated with higher seed germinability and accelerated germination time compared to manually-depulpd seeds, likely because seed dormancy breaking is favored by the combined mechanical scarification and depulping during tapir gut passage. In summary, the seed germination advantages conferred by lowland tapir endozoochory can improve seedling recruitment and foster native vegetation restoration in South American tropical forests.

**KEYWORDS:** ecological restoration, megafrugivores, seed dispersal, seed germination, *Tapirus*

## Endozoocoria por antas brasileiras aumenta a germinabilidade e acelera o tempo de germinação de sementes de espécies de plantas nativas em uma área de restauração na transição Amazônia-Cerrado

## RESUMO

A endozoocoria por antas (*Tapirus terrestris*) é considerada um mecanismo-chave de dispersão de sementes em florestas tropicais e, logo, potencialmente útil para restauração ecológica. Embora estudos anteriores tenham atestado a capacidade de germinação de sementes defecadas por *T. terrestris*, nenhum estudo testou como a endozoocoria por antas afeta o processo de germinação de sementes em áreas degradadas. Em uma área de restauração ecológica na transição Amazônia-Cerrado, realizamos ensaios de germinação para comparar a porcentagem de germinação e o número de dias até a germinação em sementes de seis espécies de plantas nativas coletadas em fezes de anta com sementes manualmente escarificadas e manualmente despulpadas (controle). Para todas as espécies de plantas analisadas, a porcentagem de germinação foi estatisticamente maior e o número de dias até a germinação das sementes foi estatisticamente menor em sementes ingeridas por antas e manualmente escarificadas (em comparação com sementes controle). Os resultados dos ensaios de germinação mostraram que a endozoocoria por antas foi associada à maior germinabilidade e a um acelerado tempo de germinação em comparação com sementes manualmente despulpadas, provavelmente porque a quebra da dormência das sementes é favorecida pela combinação da escarificação mecânica e despulpagem durante a passagem pelo intestino da anta. Em resumo, as vantagens conferidas pela endozoocoria por antas na germinação das sementes podem favorecer o recrutamento de sementes e promover a restauração da vegetação nativa em florestas tropicais da América do Sul.

**PALAVRAS-CHAVE:** dispersão de sementes, germinação de sementes, megafrugívoros, restauração ecológica, *Tapirus*

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## INTRODUCTION

Seed dispersal is central to plant reproduction and survival (Howe and Smallwood 1982, Levey et al. 2002). Seed dispersal specifically through endozoochory (the process by which animals internally disperse viable plant seeds after consuming fruits, usually in their feces) helps plants colonize new areas, minimize competition with offspring and reduce predation near parent plants (Herrera 2002). Endozoochory is particularly relevant in tropical forests, as several tree species rely on vertebrates (especially large mammals) for effective seed dispersal (Tabarelli and Peres 2002, Fragoso et al. 2003). In this context, by helping maintain seed viability, endozoochory has far-reaching implications for forest dynamics, because it is key not only to ensure forest biodiversity, but also to the maintenance of ecosystem stability and promotion of ecosystem services (Schupp et al. 2010, Wang et al. 2013, Bello et al. 2015).

Endozoochory effects can scale up to the germination process as well. For instance, previous studies found that germination time and success of animal-ingested seeds of many species differ from those not passing through animals guts (Traveset and Verdú 2002, Fricke et al. 2019). This is because dormancy breaking of gut-passaged seeds is altered by many processes during digestion, e.g., depulping, which removes chemical inhibitors of germination, and scarification, which alters seed permeability (Samuels and Levey 2005, Robertson et al. 2006, Traveset et al. 2007). While endozoochory can enhance seed germination, frugivores vary in gut-retention time and digestion processes (Traveset et al. 2007). Together, these affect seed viability during gut passage and lead to high variation in germination patterns of ingested seeds (Fricke et al. 2019, Giombini et al. 2024). Despite continuous progress in the field of endozoochory, the germination outcomes of the frugivory by several species remain poorly understood, preventing a mechanistic understanding of the digestion effects of many animal-plant interactions (Fricke et al. 2019).

The lowland tapir (*Tapirus terrestris*, Linnaeus, 1758) is the largest terrestrial mammal in South America (up to 300 kg), occurring from northern Colombia to southern Brazil (Flesher and Medici 2022). Lowland tapirs have large home ranges (8-20 km per day) (García et al. 2012) and are generalist herbivores, consuming a wide variety of plant materials (e.g., leaves, fruits and seeds from up to 300 species) (Barcelos et al. 2013). Seeds from many fruits eaten by tapirs are excreted in their dung ('latrines'), often located far from parent plants (García et al. 2012). Multiple studies attested the viability (survival) of lowland-tapir ingested seeds (Bodmer 1991, Fragoso 1997, Fragoso and Huffman 2000, Galetti et al. 2001, Tobler et al. 2010, Barcelos et al. 2013, Paolucci et al. 2019, Giombini et al. 2024). By contributing with long-range seed dispersal of various plant

species, lowland tapirs are often regarded as the "gardeners of the forest" (Flesher and Medici 2022). Such seed-disperser ability assumedly confers lowland tapirs an important role in disturbed areas, where they could improve restoration process by dispersing native plant seeds (Paolucci et al. 2019). In Brazil, however, the lowland tapir is currently listed as a 'vulnerable' species, mostly due to gaming and habitat loss (Medici et al. 2012). Thus, the consequences of the loss of such large megafrugivore may include not only reduced plant diversity (due to its unique role as large-seed disperser), but can also scale up to significant losses in the carbon storage capacity of tropical forests (Bello et al. 2015).

While the role of lowland tapirs as seed dispersers is well-recognized, many knowledge gaps remain regarding the fate of lowland-tapir dispersed seeds, especially in the context of conservation and ecosystem dynamics (O'Farrill et al. 2013). In general, fruits ingested by lowland tapirs are de-fleshed, and the depulped seeds are slightly scarified during gut passage, which is related to enhanced germination (Fragoso et al. 2003, Giombini et al. 2024). However, increasing seed retention time in the long tapir digestive system is associated with reduced germinability (Giombini et al. 2024), and it thus remains unclear how different factors, such as scarification and depulping, influence germination rates of tapir-ingested seeds. In fact, the few available tests of the effects of lowland-tapir gut passage on seed germination yielded variable outcomes in germinability and recruitment among species (Table 1). Moreover, most studies focused on the responses of few plant species (1-2 per study) and were conducted in environmental settings different from areas under restoration (Table 1). Thus, how tapirs affect plant species recovery in degraded areas remains unexplored.

Here, we assess the effect of the endozoochory by the lowland tapir on the seed germination patterns of several native plant species in a restoration area in the Amazon-Cerrado transition, to further understand its effects on seed recruitment in degraded lands. For this purpose, we conducted germination trials to compare the germinability and mean germination time of seeds found in the lowland tapir feces with manually-depulped (control) and mechanically-scarified seeds collected from parent trees in the study area. We specifically expected that tapir-ingested seeds would have higher germinability and faster germination times compared to intact seeds (Oliveira et al. 2022, Giombini et al. 2024). Our research can make an important contribution regarding the importance of lowland tapirs in the regeneration of degraded forest areas, especially considering the current context of deforestation and degradation levels in Brazilian biomes such as Cerrado and Amazon (Projeto MapBiomass 2023), where tapir local extinction is already recorded (Flesher and Medici 2022).

**Table 1.** Summary of prior research on the effectiveness of lowland tapirs (*Tapirus terrestris*) as seed dispersers.

Search string	Source	Approach	Species	Variables	Treatments	Result	Biome
(("lowland tapir" OR "tapir" OR "Tapirus terrestris") AND "seed*" OR "dispers*" OR "tapir dispers*" OR "germin*" OR "fate"))	Giombini et al. (2024)	Laboratory experiment	<i>Syagrus romanzoffiana</i>	Germinability (G)	Tapir-ingested seeds	Tapir G < intact fruits	Atlantic Forest
			(Cham.) Glassman (Arecaceae)		Depulped seeds	Tapir G = intact seeds	(Paraguay)
					Intact fruits		
	Oliveira et al. (2022)	Laboratory experiment	<i>Dipteryx alata</i> Vog. (Fabaceae)	Germinability (G)	Tapir-ingested seeds	Tapir G = intact seeds	Cerrado (Brazil)
				Germination speed index (GSI)	Tapir-ingested fruits	Tapir GSI > intact seeds	
				Mean Germination Time (MGT)	Depulped seeds	Tapir MGT < intact seeds	
	Farias et al. (2015)	Laboratory experiment	<i>Terminalia tomentosa</i>	Germinability (G)	Tapir-ingested seeds	Tapir G > intact seeds	Cerrado (Brazil)
			Mart. Ex Eichler (Combretaceae)	Germination speed index (GSI)	Intact fruits	Tapir GSI < depulped seeds	
				Mean germination time (MGT)	Depulped seeds	Tapir MGT < intact fruits	
	Bueno et al. (2013)	Laboratory experiment	<i>Cryptocarya mandiocana</i>	Germination Time (GT)	Tapir-ingested seeds	<i>C. mandiocana</i> :	Atlantic Forest
			Meisn. (Lauraceae)		Depulped seeds	Tapir GT < depulped seeds	(Brazil)
			<i>Hyeronima alchorneoides</i>		Intact fruits	Tapir GT < intact fruits	
			Allemão (Phyllanthaceae)			<i>H. alchorneoides</i> :	
						Tapir GT = intact seeds	
	Golin et al. (2011)	Laboratory experiment	<i>Annona crassiflora</i>	Germinability (G)	Tapir-ingested seeds	Tapir G = intact seeds	Cerrado (Brazil)
			Mart. (Annonaceae)		Depulped seeds		
	Fragoso et al. (2003)	Field experiment	<i>Maximiliana maripa</i>	Survival	Tapir-ingested fruits	Tapir > intact fruits	Brazilian Amazon
			(Aubl.) Drude (Arecaceae)	(Count of viable seeds)	Intact fruits		
	Quiroga-Castro and Roldán (2001)	Field experiment	<i>Attalea phalerata</i>	Survival	Tapir latrines	Tapir = intact seeds	Bolivian Amazon
			(Mart. ex Spreng.) (Arecaceae)	(% of viable seeds)	Depulped seeds		

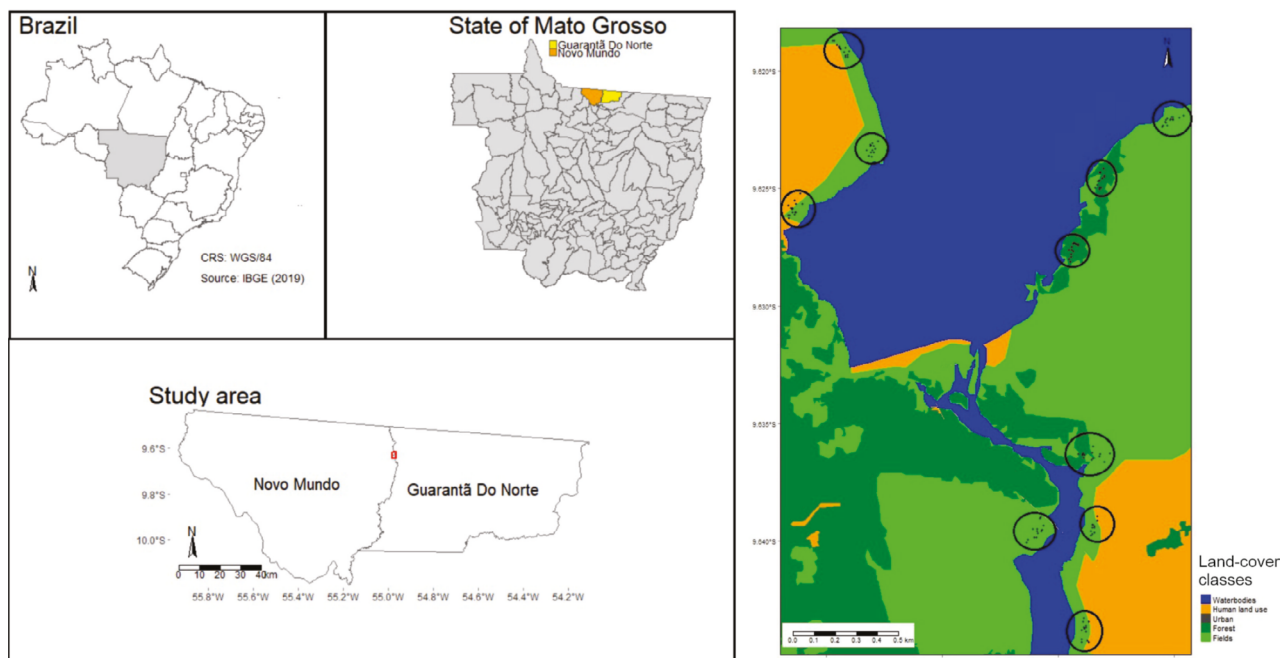
Search database: Web of Science®; Germinability = percentage of germinated seeds/total seeds

## MATERIAL AND METHODS

### Study area

The study area is located in Mato Grosso state (north Brazil) (Figure 1). The original vegetation in the area covers open ombrophilous forests, in the Amazon-Cerrado transition (Amorim and Bastos 2016). The climate in the area is tropical humid (Am), with two well-defined seasons (rainy period: October to March; dry period: April to September); the annual rainfall in the area is ~1,900 mm, and mean temperature is ~24° C (Souza et al. 2013).

Seed collection took place in a permanent protection area (APP) of a small hydroelectric plant in the watercourse of the Braço Norte River (Tapajós watershed, Amazon basin), in the border between Guarantã do Norte and Mundo Novo municipalities (northern Mato Grosso) (Figure 1; Figure S1). Since 2002, the APP is subject to an ecological restoration project consisting of the planting of seedlings from 48 native species of different succession stages (Pimentel and Rempel 2022). Until 2020, over 161,000 seedlings were planted, recovering >60 ha of native vegetation in the APP (Pinto 2024).



**Figure 1.** Location of the study area in the state of Mato Grosso and map with the spatial disposition of the fecal samples (small stars) in each latrine (large black circles).

## Field and laboratory methods

Seeds were obtained from fecal samples analyzed in a previous study assessing the diet and feeding ecology of lowland tapirs in the area (Pinto 2024), briefly summarized below. Tapir fecal samples were collected from ten previously-selected latrines located in dry soils within the APP (Figure 1). Tapir latrines were identified from previous mammal occurrence records stemming from camera-trap assessments (Figure S2) across the APP (Pinto 2019, 2024). Although lowland tapir population size in the area was not estimated to date, considering that latrines are used by at least one individual (García *et al.* 2012), the solitary habit and the tendency of lowland tapirs to use latrines as a way of marking territory boundaries (Pinho *et al.* 2014), a rough estimate of up to 10 individuals could be expected for the study area.

Distances between latrines ranged from 0.37-2.4 km. Each latrine was visited monthly over a two-year period (January 2021 to December 2022; 24 visits). In each latrine, up to 10 fecal pellets of similar sizes were collected from the top portion of dung pile with a spatula and stored in plastic bags. To avoid repeated collection of fecal material, only the freshest feces were collected (*i.e.*, not more than a few days old), determined after visual inspection of shape, color and size (Tobler *et al.* 2010). In total, we collected a sum of 140 fecal samples (Figure 1C).

Overall, 88% (N = 123) of the fecal samples contained at least one seed (Pinto 2024). In the laboratory, feces were rinsed under tap water and sieved (0.5-mm mesh size) for

seed collection. After drying in the sun for 4 h at ambient temperature, intact seeds were manually selected from the fecal material (seeds with chewing or crushing marks were discarded) for the germination experiment. The collected seeds were identified to species level through consultation to specialized literature (Lorenzi 2008) and comparison with the seed nursery.

Seeds from six native plant species that composed most part of the lowland tapir dietary content and showed the highest number of viable seeds in latrines (Pinto 2024) were selected for the experiment: *Spondias mombin* L. (Anacardiaceae, common name 'cajá-da-mata'); *Terminalia corrugata* (Ducke) Gere & Boatwr (Combretaceae, common name: 'mirindibá-do-cerrado'); *Enterolobium schomburgkii* (Benth.) Benth (Fabaceae, common name: 'angelim favela'); *Samanea tubulosa* (Benth.) Barneby & J.W. Grimes (Fabaceae, common name: 'sete-cascas'); *Psidium* sp. (Myrtaceae, common name: 'Goiabinha-domato'); and *Genipa americana* L. (Rubiaceae, common name: 'genipapo') (Figure S3). Seeds were stored in plastic bags and refrigerated at 25 °C for 30-60 days until the germination experiment.

## Germination tests

A greenhouse experiment was conducted in a nursery facility to compare the germination of seeds obtained from tapir fecal samples with seeds collected from parent trees in the study area, treated according to the following treatments: 'scarified' (seeds manually cleaned with a plier); and 'control' seeds (intact seeds obtained after

manual depulping of fruits from parent trees). For each species, a total number of 100 seeds per treatment was used in the experiment ( $N = 300$ ). In each treatment, seeds were distributed across four trays ( $N = 25$  seeds per tray). Trays were covered with a 1-cm sand layer, and seeds were distant from each other at 1.5-5 times the width of the seed to minimize competition and contamination (Brasil 2009). Seeds were watered twice a day (6:00 and 18:00) with an automatic micro-sprinkler irrigation system in the dry period; in the rainy period, irrigation was carried out according to the presence or absence of rain. The experiment was monitored daily (100 days for each species). The presence of cotyledonary leaves was used as evidence of germination.

### Data analysis

For each species, we assessed two indices related to the seed germination process: germinability and mean germination time, as seen in Rana and Santana (2006) and Lozano-Isla *et al.* (2019). To assess germinability (the proportion of germinated seeds) we counted the number of germinated seeds in each tray; for the assessment of mean germination time, we annotated the number of days until germination. We compared germinability and mean germination time among groups ('tapir faeces', 'scarified' and 'control') using a randomized-block analysis of variance (tray identity as blocking factor). Pairwise comparisons between group levels were performed with the Tukey post-hoc test. We inspected diagnostic plots to check whether model assumptions were met. All analyses were performed with R software v. 4.4.1 (R Core Team 2023). Germination indices were calculated using functions from package 'GerminAR' (Lozano-Isla *et al.* 2019).

## RESULTS

### Germination percentage

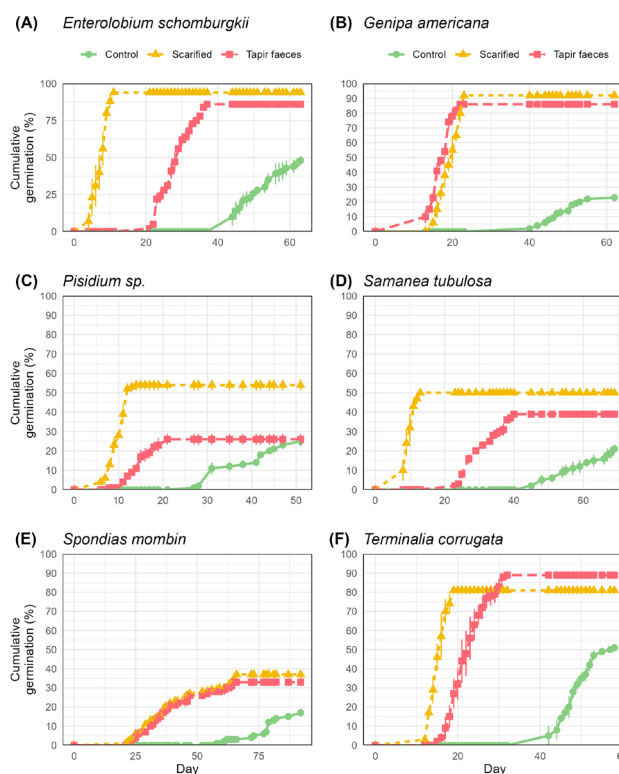
At the end of the germination trials, the total percentage of germinated seeds ranged between 17-51% for control seeds, 37-94% for scarified and 26-89% for tapir-ingested ones across plant species (Table 2). For all species, the cumulative number of germinated seeds was lower in control compared to scarified and tapir-ingested seeds (Figure 2).

Across all plant species, there were significant differences in mean germination percentage among seed treatments ( $p < 0.05$ ) (Table 3). Pairwise comparisons using Tukey post-hoc test (Table 3) revealed that seeds found in tapir faeces had higher mean germination percentage than control seeds in most species, except *Psidium* sp.; in addition, the mean germination percentage of scarified seeds was higher than control seeds across all species (Figure 3). No significant difference in germination percentage was

detected between tapir-ingested and scarified seeds for 4 species (Table 3).

### Mean germination time

Over the experiment, the number of days until seed germination ranged between 27-92 days in control seeds, 4-66 days in scarified and 8-65% in tapir-ingested ones across plant species (Table 2). In all species, control seeds required a larger number of days until germination (Figure 3). This was statistically confirmed by the randomized-block ANOVA, which detected significant differences in mean germination time among seed treatments ( $p < 0.05$ , Table 3). Tukey post-hoc analyses revealed that the number of days until seed germination was statistically higher ( $p = 0.012$ ) for control compared to both scarified seeds and seeds found in tapir faeces, across all species (Table 3). In addition, the number of days until germination in scarified seeds was significantly lower (Table 3) than in tapir-ingested seeds for 4 species (Figure 4 a,c,e,f), except *G. americana* (where tapir-ingested seeds had shorter germination times; Fig. 4b), and *S. mombim* (no difference between scarified and tapir-ingested seeds; Figure 4d) (Table 3).



**Figure 2.** Line graphs showing the cumulative germination percentage of the seeds of the native plant species assessed across treatments over the days of the experiment.

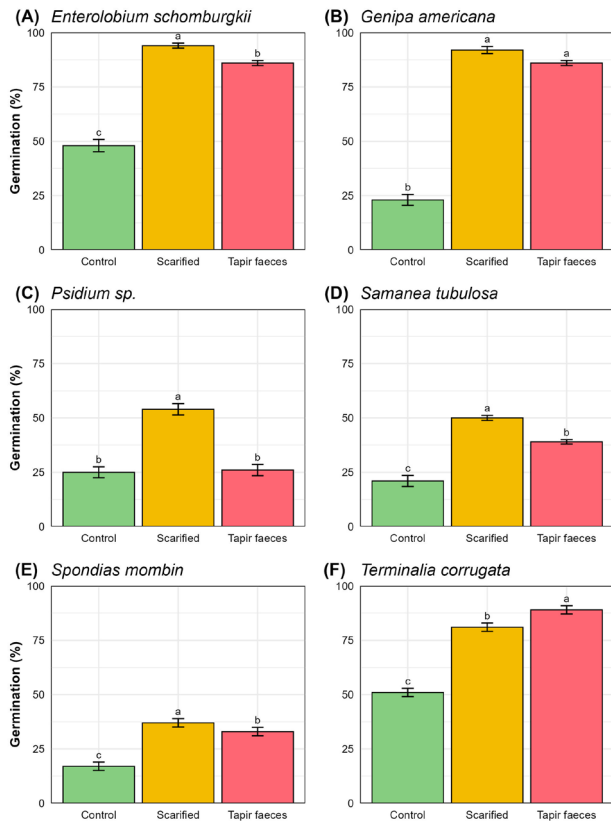
**Table 2.** Seed germination percentages and germination time (number of days until germination; range of values) of the native plant species assessed across treatments.

Family	Species	Germination percentage				Germination time		
		Status	Treatment			Treatment		
			Control	Scarified	Tapir faeces	Control	Scarified	Tapir faeces
Anacardiaceae	<i>Spondias mombin</i> L.	Germinated	17	37	33	58 - 92	22 - 66	24 - 65
		Not germinated	83	63	67			
Combretaceae	<i>Terminalia corrugata</i> (Ducke) Gere & Boatwr.	Germinated	51	81	89	42 - 58	12 - 19	15 - 32
		Not germinated	49	19	11			
Fabaceae	<i>Enterolobium schomburgkii</i> (Benth.) Benth.	Germinated	48	94	86	44 - 63	4 - 11	21 - 37
		Not germinated	52	6	14			
	<i>Samanea tubulosa</i> (Benth.) Barneby & J.W. Grimes	Germinated	21	50	39	45 - 69	8 - 13	23 - 40
		Not germinated	79	50	61			
Myrtaceae	<i>Psidium</i> sp.	Germinated	25	54	26	27 - 51	6 - 14	8 - 21
		Not germinated	75	46	74			
Rubiaceae	<i>Genipa americana</i> L.	Germinated	23	92	86	40 - 62	15 - 23	13 - 22
		Non germinated	77	8	14			

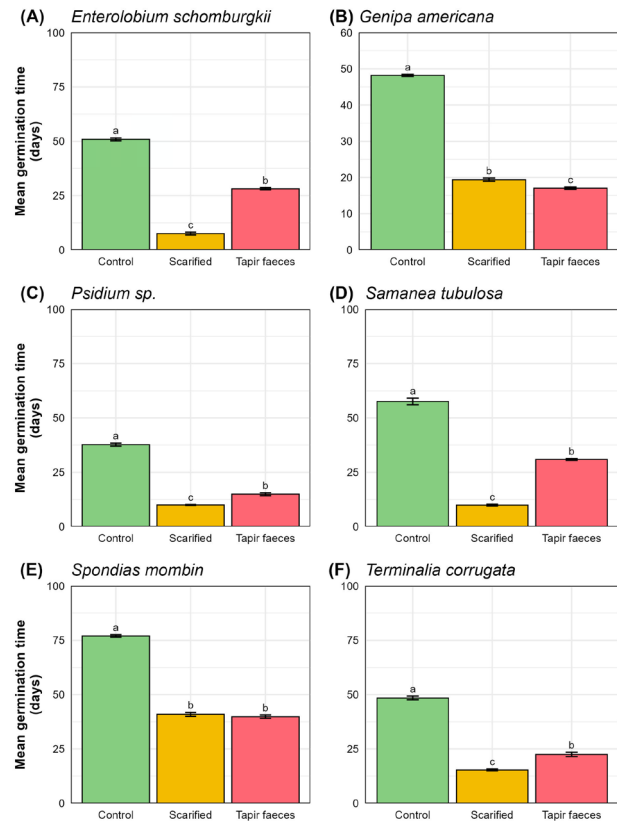
**Table 3.** Summary output of the effects of seed treatment on germination percentage and mean germination time (number of days until germination) of the native plant species assessed.

Family	Species	Germination percentage			Mean germination time	
		treatment	Average	ste	Average	ste
Anacardiaceae	<i>Spondias mombin</i> L.	Control	17 <sup>b</sup>	1.91	77 <sup>a</sup>	0.6
		Scarified	37 <sup>a</sup>	1.91	40.9 <sup>b</sup>	0.89
		Tapir faeces	33 <sup>b</sup>	1.91	39.84 <sup>b</sup>	0.77
Combretaceae	<i>Terminalia corrugata</i> (Ducke) Gere & Boatwr.	Control	51 <sup>c</sup>	1.91	48.44 <sup>a</sup>	0.87
		Scarified	81 <sup>b</sup>	1.91	15.34 <sup>c</sup>	0.45
		Tapir faeces	89 <sup>a</sup>	1.91	22.48 <sup>b</sup>	0.98
Fabaceae	<i>Enterolobium schomburgkii</i> (Benth.) Benth.	Control	48 <sup>c</sup>	2.83	50.9 <sup>a</sup>	0.66
		Scarified	94 <sup>a</sup>	1.15	7.53 <sup>c</sup>	0.67
		Tapir faeces	86 <sup>b</sup>	1.15	28.15 <sup>b</sup>	0.53
	<i>Samanea tubulosa</i> (Benth.) Barneby & J.W. Grimes	Control	21 <sup>c</sup>	2.52	57.59 <sup>a</sup>	1.49
		Scarified	50 <sup>a</sup>	1.15	9.89 <sup>c</sup>	0.39
		Tapir faeces	39 <sup>b</sup>	1	30.89 <sup>b</sup>	0.42
Myrtaceae	<i>Psidium</i> sp.	Control	25 <sup>b</sup>	2.52	37.71 <sup>a</sup>	0.71
		Scarified	54 <sup>a</sup>	2.58	9.97 <sup>c</sup>	0.18
		Tapir faeces	26 <sup>b</sup>	2.58	14.93 <sup>b</sup>	0.68
Rubiaceae	<i>Genipa americana</i> L.	Control	23 <sup>b</sup>	2.52	48.2 <sup>a</sup>	0.3
		Scarified	92 <sup>a</sup>	1.63	19.4 <sup>b</sup>	0.45
		Tapir faeces	86 <sup>a</sup>	1.15	17.05 <sup>c</sup>	0.3

Ste = standard error values; similar letters indicate significant differences ( $p < 0.05$ ) between treatments, according to the Tukey post-hoc test.



**Figure 3.** Bar plots of the seed germination percentages of the native plant species assessed across treatments.



**Figure 4.** Bar plots of the mean germination time (number of days until germination) of the native plant species assessed across treatments.

## DISCUSSION

Prior studies have shown that seeds found in lowland tapir dung remain viable in many habitats (e.g., Atlantic and Amazon forests, Cerrado and Pantanal) (Bodmer 1991, Fragoso 1997, Fragoso and Huffman 2000, Galetti *et al.* 2001, Giombini *et al.* 2009, Tobler *et al.* 2010, Barcelos *et al.* 2013). However, there is no data on the viability of the tapir-dispersed seeds in highly degraded landscapes (Paolucci *et al.* 2019), despite documented evidence that tapir move across and defecate seeds on these environments in South America (Bueno *et al.* 2013, O'Farrill *et al.* 2013, Paolucci *et al.* 2019). Here, seeds found in lowland tapir dung germinated in higher numbers than control ones in a degraded area of the Amazon-Cerrado transition. We thus provide empirical evidence for the effectiveness of lowland tapir endozoochory in increasing and speeding seed germination in degraded areas.

The importance of endozoochory by lowland tapirs for seed dispersal has been recognized (Fragoso *et al.* 2003, O'Farrill *et al.* 2013, Giombini *et al.* 2024), and the potential role of tapirs in habitat restoration has been suggested (Paolucci *et al.* 2019). However, simply evidencing the germination of seeds found in lowland tapir dung can overestimate their potential as seed dispersers, and comparison with undigested seeds is thus required to demonstrate the advantage of lowland tapir

endozoochory (Samuels and Levey 2005, Traveset *et al.* 2007, O'Farrill *et al.* 2013). However, few studies further compared the responses of seeds found in the dung of lowland tapirs with undigested seeds (Oliveira *et al.* 2022), particularly in the Amazon. The results presented here demonstrated higher germination and accelerated germination time for seeds ingested by *T. terrestris* compared to control seeds. This indicates that passage through the gut of lowland tapirs is relevant for breaking seed dormancy (Bueno *et al.* 2013, Giombini *et al.* 2024), and provide support for the role of tapir endozoochory as facilitators of seed dispersal in the study area.

The breaking of seed dormancy can be influenced by several factors acting on tapir's digestive tract (Traveset *et al.* 2007, Schupp *et al.* 2010, O'Farrill *et al.* 2013). Generally, the fruits ingested by lowland tapirs are de-pulped and, as they pass through the digestive tract, subject to both chemical transformation by microorganisms and slight scarification (Fragoso and Huffman 2000, Giombini *et al.* 2024). Scarification has been associated with shorter germination times in seeds (Campos *et al.* 2008, Farias *et al.* 2015, Giombini *et al.* 2024). Under natural conditions, seeds of *Spondias mombin* can take up to 240 days to germinate (Campos-Filho and Sartorelli 2015). Here, the results of the



germination trials showed that mechanical scarification can accelerate this process (less than 70 days).

Despite the shorter germination times of seeds passing through the lowland tapir's digestive tract (compared to intact manually-depulped ones) observed in this study, the former had longer germination time compared to mechanically-scarified seeds in all species except *G. americana* and *S. mombim*. Scarification has been related to faster seed germination in several plant species (Samuels and Levey 2005, Robertson et al. 2006, Fricke et al. 2019). This is likely because physical abrasion of the seed coat helps enable metabolism activation by improving gas and water exchange, eventually leading to an acceleration in seed dormancy breaking (Robertson et al. 2006, Traveset et al. 2007). However, despite the slight scarification to which ingested seeds are exposed in tapir gut passage, the long retention time of tapir digestion exposes them to transformation by enzymatic and microorganism activity (Traveset 1998, Traveset et al. 2007). In fact, a recent study found that increased retention time within the gut tract is associated with reduced germinability in seeds ingested by tapirs, in spite of scarification during maceration (Giombini et al. 2024). Together, the prolonged chemical exposure during tapir gut passage may counterbalance the slight positive effects of scarification and eventually delay dormancy breaking of seeds in feces, and likely explains why seeds passing through the lowland tapir's digestive tract had longer germination time compared to mechanically-scarified seeds. However, mechanical scarification may be unlikely for most examined seeds in nature, and thus the passage through tapir's gut should have a net positive effect on the acceleration of germination.

## CONCLUSIONS

Our germination trials indicate that endozoochory by the lowland tapirs can be useful to improve seed recruitment of native plant species in degraded areas. In addition, lowland tapirs can potentially foster forest restoration through increasing germination rates and long-range seed dispersal throughout their large home ranges. Conservation efforts aimed at protecting lowland tapirs are thus essential in the region not only for the species itself but also for the health and resilience of the ecosystems they support, since local extinction of the tapir could harm plant recruitment and, consequently, the capacity of natural recovery of degraded forests.

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## SUPPLEMENTARY MATERIAL

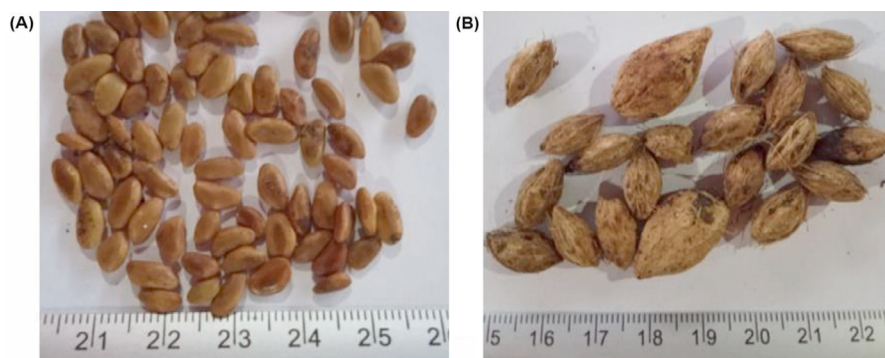
Pinto *et al.* Endozoochory by lowland tapirs improves seed germinability and accelerates germination time of native plant species in an Amazon-Cerrado transition restoration area.



**Figure S1.** Aerial photo of the study area showing a section of the permanent protection area surrounding the small hydroelectric plant in the Braço Norte River (north Mato Grosso, Brazil). Source: Guarantã Energética S.A.



**Figure S2.** Camera trap photo of a lowland tapir (*Tapirus terrestris*) individual in the study area.



**Figure S3.** Seeds of *Enterolobium schomburgkii* (Benth.) Benth. (A) and *Terminalia corrugata* (Ducke) Gere (B) found in fecal samples of *Tapirus terrestris* in the study area.