

Lowland tapirs facilitate seed dispersal in degraded Amazonian forests

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Abstract

The forests of southeastern Amazonia are highly threatened by disturbances such as fragmentation, understory fires, and extreme climatic events. Large-bodied frugivores such as the lowland tapir (*Tapirus terrestris*) have the potential to offset this process, supporting natural forest regeneration by dispersing a variety of seeds over long distances to disturbed forests. However, we know little about their effectiveness as seed dispersers in degraded forest landscapes. Here, we investigate the seed dispersal function of lowland tapirs in Amazonian forests subject to a range of human (fire and fragmentation) and natural (extreme droughts and windstorms) disturbances, using a combination of field observations, camera traps, and light detection and ranging (LiDAR) data. Tapirs travel and defecate more often in degraded forests, dispersing much more seeds in these areas [9,822 seeds per ha/year (CI_{95%} = 9,106; 11,838)] than in undisturbed forests [2,950 seeds per ha/year (CI_{95%} = 2,961; 3,771)]. By effectively dispersing seeds across disturbed forests, tapirs may contribute to natural forest regeneration—the cheapest and usually the most feasible way to achieve large-scale restoration of tropical forests. Through the dispersal of large-seeded species that eventually become large trees, such frugivores also contribute indirectly to maintaining forest carbon stocks. These functions may be critical in helping tropical countries to achieve their goals to maintain and restore biodiversity and its ecosystem services. Ultimately, preserving these animals along with their habitats may help in the process of natural recovery of degraded forests throughout the tropics.

Abstract in Portuguese is available with online material.

KEYWORDS

Brazil, forest restoration, frugivory, natural regeneration, seed dispersal, *Tapirus terrestris*, understory fires

1 | INTRODUCTION

Tropical rain forests have experienced widespread deforestation and degradation over the past decades, resulting in severe losses in biodiversity, carbon storage, and climate regulation capacity (Lewis, Edwards, & Galbraith, 2015). For instance, the southeast Amazon

region is the largest agricultural frontier in Brazil and among the largest in the world. Human activities have degraded forests in the region via two main mechanisms. First, widespread deforestation has created a fragmented landscape in the Upper Xingu basin, where ~8% of the forests are located at <100 m from a cleared area (Brando et al., 2014). Second, the fires typically used to clear

land and manage pastures often escape into forest edges, burning up to 10–12 percent of the region's forests during drought years (Brando et al., 2014). Between 1999 and 2010, fires burned more than 85,000 km² of forests in the southern portion of the Amazon (Morton, Le Page, DeFries, Collatz, & Hurtt, 2013). Additionally, windstorms can interact with forest fragmentation and fires by increasing the mortality of large trees, particularly at forest edges (Silvério et al., 2018), thus increasing fuel loads and consequently forest flammability (Schwartz et al., 2017).

As climate and land use change, forest fires, forest edges, and windstorms will likely become more common (Davidson et al., 2012), with compounding negative effects on the structure and diversity of Amazon forests in the future. These disturbances not only degrade forests but also have cascading ecological effects, including species losses and directional shifts in the composition of faunal communities (Andrade, Balch, Carreira, Brando, & Freitas, 2017; Paolucci, Schoederer, Brando, & Andersen, 2017). Recovering large tracts of these degraded and deforested areas would provide benefits such as biodiversity conservation, ecosystem service provisioning, and carbon sequestration (Barlow et al., 2007; Chazdon et al., 2016). This scenario would ensure not only a healthier ecosystem but also the opportunity for tropical nations to achieve national targets to reduce net carbon emissions (Maser, Ordóñez, & Dirzo, 1997). On average, secondary tropical forests can accumulate 122 Mg/ha of carbon for the first 20 years of regrowth, 11 times higher than the uptake rate of old growth forests (Poorter et al., 2016). Despite these benefits, the high cost of active restoration represents a barrier to large-scale restoration of degraded forests (Chazdon & Guariguata, 2016). For instance, two major Brazilian Amazon states (Mato Grosso and Pará) need to restore 841,564 and 3,951,664 ha, respectively, to comply with the Brazilian Forest Code. Doing so would cost an estimated US \$0.5–1.1 billion in Mato Grosso and US \$2.1–5.2 billion in Pará (Azevedo et al., 2017).

Natural regeneration is among the most cost-effective techniques to restore degraded forests, but it depends on the availability of resources for plant growth and a supply of propagules such as seeds and sprouts (Chazdon & Guariguata, 2016). Several animals play a key role as seed dispersers, contributing to the recovery of disturbed forests by facilitating the establishment of woody plants and increasing the diversity of seed rain in tropical rain forests (Carlo & Morales, 2016; Herrera, Jordano, Lopez-Soria, & Amat, 1994; Rey & Alcántara, 2000). Vertebrates are particularly important for the dispersal of many tropical forest tree and shrub species (Howe & Smallwood, 1982; Wandrag, Dunham, Duncan, & Rogers, 2017), including many large-seeded late-successional species (Tabarelli & Peres, 2002). However, the large frugivores that disperse large seeds are threatened by habitat loss and hunting, which could result in losses of animal-dispersed species, and eventually shift tree community composition and forest dynamics (Harrison et al., 2013).

Lowland tapirs (*Tapirus terrestris*) are large, voracious herbivores that play a key role in dispersing seeds, especially large ones, although they might predate seeds during digestion (reviewed by O'Farrill, Galetti, & Campos-Arceiz, 2013). Lowland tapirs consume

the fruits of approximately 300 plant species, distributed in 66 families (Barcelos, Bobrowiec, Sanaiotti, & Gribel, 2013). Their home range is large, varying from 220 to 470 ha (Tobler, 2008), and they are capable of straight-line movements of over 20 km, thus potentially dispersing seeds over large distances (Fragoso, Silvius, & Correa, 2003). Usually, tapirs defecate in latrines, which consist of deposits of dung clumps from several individuals. These latrines, which are spaced up to 2 km apart, may serve as regeneration hotspots (Fragoso, 1997).

Lowland tapirs are known to be seed dispersers throughout undisturbed forests (e.g., Fragoso, 1997; Fragoso & Huffman 2000; Galetti, Keuroghlian, & Morato, 2001; Bueno et al., 2013), but they frequently use degraded forests and traverse open areas (Bueno et al., 2013), as do Baird's tapirs (*Tapirus bairdii*; Foerster & Vaughan, 2002). Nevertheless, their role in seed dispersal and their contribution to natural regeneration of disturbed areas remain understudied. This study took advantage of long-term experimental burns in southeastern Amazonia to investigate whether lowland tapirs use forests that have been degraded by recurrent experimental fires, windstorms, and fragmentation, and to evaluate their role in dispersing seeds across these habitats. To accomplish this, we combined data from aerial light detection and ranging (LiDAR) surveys, camera traps, and field surveys to map and quantify forest degradation, habitat use, and seed dispersal by tapirs in burned and unburned forests.

2 | METHODS

2.1 | Study site

This study was conducted in southeastern Amazonia (Mato Grosso, Brazil, 13°04'S, 52°23'W; Figure 1). The local vegetation is tropical evergreen forest, and soils are oxisols with a water table at 12–15 m depth (Balch et al., 2008). Annual air temperature averages 23.5°C and annual rainfall varies from 1,800 to 2,000 mm, with marked rainy (October–April) and dry (May–September) seasons (Rocha et al., 2014).

2.2 | Experimental burns

Experimental burns began in 2004, aiming to investigate forest resilience and drivers of forest degradation in the Amazonian agricultural frontier. A full description of the experiment and main results can be found in Balch et al. (2008, 2015) and Brando et al. (2014). Briefly, the fire experiment took place in an undisturbed forest bordering a soybean field. Three adjacent plots of 1000 × 500 m each were subjected to one of three treatments: burned every year (B1yr) from 2004 to 2010 (except for 2008); burned triennially in 2004, 2007, and 2010 (B3yr); or unburned, which served as the control (Figure 1). The study area is crossed by north–south and east–west trails, each 2 m wide and crossing every 50 m, forming 50 × 50 m quadrants throughout the study area. The plots were not replicated due to logistical, legal, and financial limitations, but the large plot size allows fire behavior to mimic that of actual fires in Amazon forests (Balch

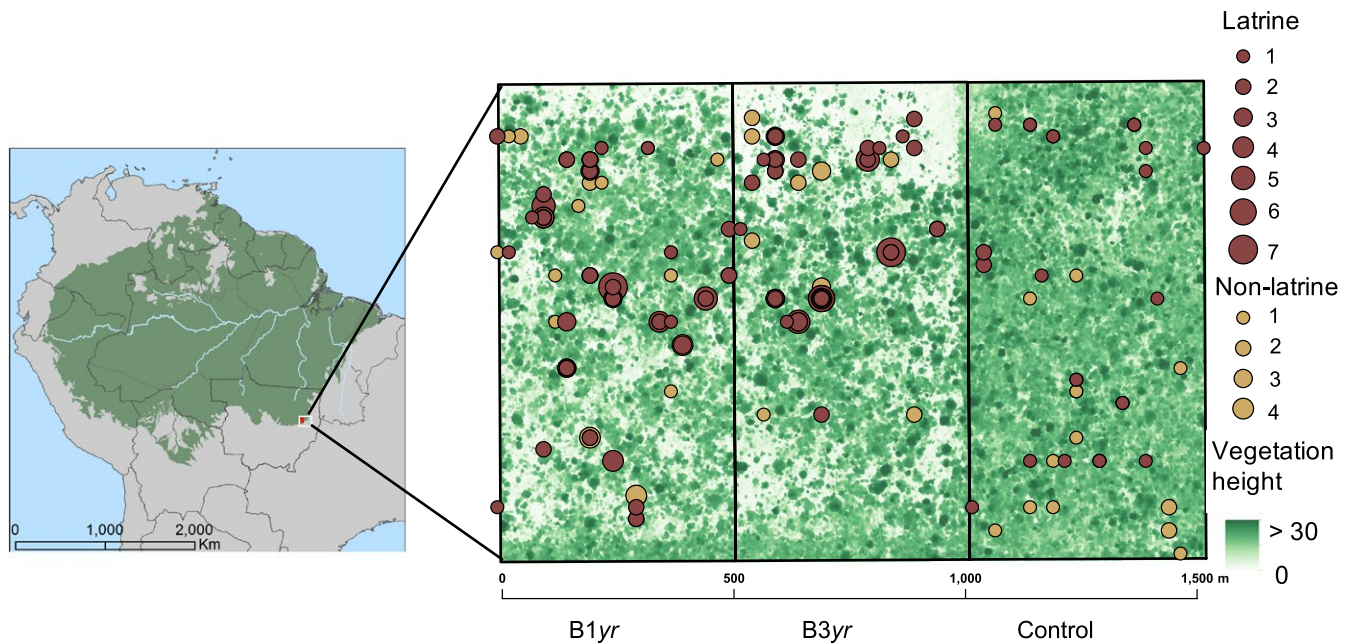


FIGURE 1 Map showing the location of the Tanguro experimental burn plots in southeastern Amazonia. Inset: vegetation height of the experimental forest in 2014 (from airborne LiDAR), with the location of dung clumps sampled during the study. Darker greens represent taller canopies, which correlated positively with leaf area density. Brown and beige dots represent the number of dung clumps found at a given location. Treatments included an annually burned (from 2004 to 2010, except 2008; B1yr), triennially burned (2004, 2007, 2010; B3yr), and unburned Control plot

et al., 2015). Importantly, the large size also allows for movement of large vertebrates across these plots. Pre-fire sampling showed no differences among the plots with respect to several vegetation and microclimatic variables (Balch et al., 2008), suggesting that any observed differences in vegetation structure could be attributed to the fire treatments rather than to local effects.

The experimental fires were generally low-intensity, understory fires. Fire intensity and burned area were larger in B3yr than in B1yr due to higher fuel accumulation during non-burning years (Balch et al., 2015). Fires resulted in the massive mortality of large trees, especially during the drought years of 2007 and 2010 (Brando et al., 2014) and after a major windstorm event in 2012 (Silvério et al., 2018). These disturbances caused a marked reduction in canopy cover (B1yr: 23% and B3yr: 31%) and aboveground biomass (B1yr: 12% and B3yr: 30%; Figure 1; Brando et al., 2014). Recurrent experimental fires, coupled with extreme climate events, thus triggered forest conversion to derived savannas—defined as forests degraded by human activities that lack continuous canopy cover and have an established grassy layer with low plant diversity (Veldman, 2016).

2.3 | Data sampling

We sampled tapir dung in all treatment plots during four different sampling events (lasting 3–5 days each) in January, April, June, and September 2016. Fruit productivity (abundance and weight) in our study area peaked in April and September, so we did not miss any important fruiting events during the months between sampling (Supporting Information Figure S1). During the first three sampling

events, we walked along 31 north–south trails and nine east–west trails (at 100-m intervals between 100 and 900 m from the forest edge). We searched for dung clumps deposited on trails and up to 2 m on either side. The total area sampled was thus 17.8 ha per sampling event. To estimate the error associated with searching only on established trails, we did a complete survey of the entire study area (150 ha) during the last sampling event in September 2016, when we also looked for dung located in the area off of the main trails. For that, four people walked side-by-side searching for dung in each 50 × 50 m quadrant of the entire study area.

When encountering a dung clump during a sampling event, we georeferenced it, noted whether it was located in a latrine (i.e., when a large amount of dung of different ages was visibly clumped within a radius of 5 m), and arbitrarily sampled 10 pellets from the clump (defined as a sample). We washed samples in sieves of 0.25 mm thread and 6 × 6 mm mesh, and manually separated seeds from fibers. We counted all seeds from each sample, except when seeds were very small (<3 mm), in which case we counted them in 0.5-g samples and extrapolated based on the total weight of the sample. Whenever possible, we identified seeds to species based on the Angiosperm Phylogeny Group III system (Bremer et al., 2009) and specialists' expertise. We confirmed species names according to the Species List of the Brazilian Flora data base (Flora do Brasil 2020). We checked all seeds for physical damage and considered them as predated if broken or chewed. We then classified seeds by successional stage (climax or pioneer), life-form (liana, palm, shrub, or tree), and size (small: <0.5 cm; medium: 0.5–1.5 cm; or large: >1.5 cm).

2.4 | Camera trapping

As a complementary sampling method to evaluate tapir habitat use, we placed three camera traps (Bushnell Trophy Cam HD Essential E2 119836C) in each treatment plot. Cameras were placed at 30–40 cm height, facing the trail near latrines, and were kept in the field for 9 months (March–November 2016) for a total sampling effort of 2,196 days per camera. We considered records registered 30 min apart as independent events. However, given tapirs' mobility, events do not represent the relative number of tapirs in each area. Rather, they represent independent opportunities for defecation and seed dispersal.

2.5 | LiDAR survey

Forest degradation increases canopy opening, which in turn increases mortality rates and may delay or impair the recovery of carbon stocks (Longo et al., 2016). To characterize forest degradation, we used an airborne LiDAR to calculate leaf area density (LAD) and quantify openness along the forest profile. LiDAR data were collected in October 2014 by GEOID Ltd. (Belo Horizonte, MG) at 1-m resolution, as part of a joint project (Sustainable Landscapes Brazil) of the Brazilian Corporation of Agricultural Research (EMBRAPA) and the United States Forest Service (USFS). For each dung sample, we drew a 5-m radius and extracted the associated information from the altitude normalized LiDAR at 10-m resolution. We then computed LAD using standard methods, as described in Bouvier, Durrieu, Fournier, and Renaud (2015). We set the bottom limit of the vegetation profile to 1 m due to data reliability above this height. We used the resulting digital elevation model to correct the tree heights for biases associated with the terrain elevation.

2.6 | Statistical analyses

To test whether tapirs defecate more frequently in degraded forests, we built generalized linear models (GLMs) with a Poisson distribution, using LAD as an explanatory variable and the number of dung clumps deposited by tapirs as the response variable. For that, we counted the number of dung clumps deposited in each LAD class, classified in 0.5-m intervals varying from 0.5 to 9 m²/m².

We estimated the number of seeds dispersed by tapirs per ha/year for our study area as follows. First, we obtained the average number of seeds dispersed per day in the interval between each sampling event. For that, we divided the number of seeds found in a sampling event by the number of days elapsed since the previous sampling event. We then averaged the number of seeds dispersed per day between each sampling event, multiplied it by 365 to obtain the average number of seeds dispersed each year, and divided this number by 150 (the total area of our study site in hectares) to obtain the number of seeds dispersed per ha/year. Finally, we adjusted our estimate to account for the fact that we sampled just 10 pellets per dung clump (see SI for further details on this correction; the R script and associated dataset used for this analysis are available on the Dryad Digital Repository; Paolucci et al., 2019).

We used two-way ANOVAs to analyze whether the number of seeds dispersed by tapirs varied as a function of groups (i.e., successional stage, life-form, and seed size) across treatment plots. For that, we built a generalized linear mixed model (GLMM) with a Poisson error distribution, using the treatment plot and seed groups as explanatory variables; number of seed as a response variable; and sampling event and dung clump identity as random factors. Finally, we compared the number of seed species dispersed across treatment plots from a rarefied $n = 43$ dung clumps and extrapolated values of $n = 72$ (the minimum and maximum number of dung clumps found, in the unburned and B1yr treatment plots, respectively). We then extrapolated using presence/absence data (Hill numbers of order 0).

We conducted all analyses using the software R (R Core Team, 2018) and analyzed the residuals to check for distribution suitability and model fit in all models. We asserted a “quasi” correction for Poisson models with overdispersion. We used the *lme4* v1.1-18-1 package for GLMM models; *multcomp* v.1.4 (function *glht*) for post hoc comparisons, *rgdal* v1.3-2 and *rasterVis* v0.45 for LiDAR analyses; *iNEXT* v 2.0.12 for sample-based extrapolation curves; *lidR* v1.6.1 for leaf area density calculation; and *ggplot2* v3.0 for plotting.

3 | RESULTS

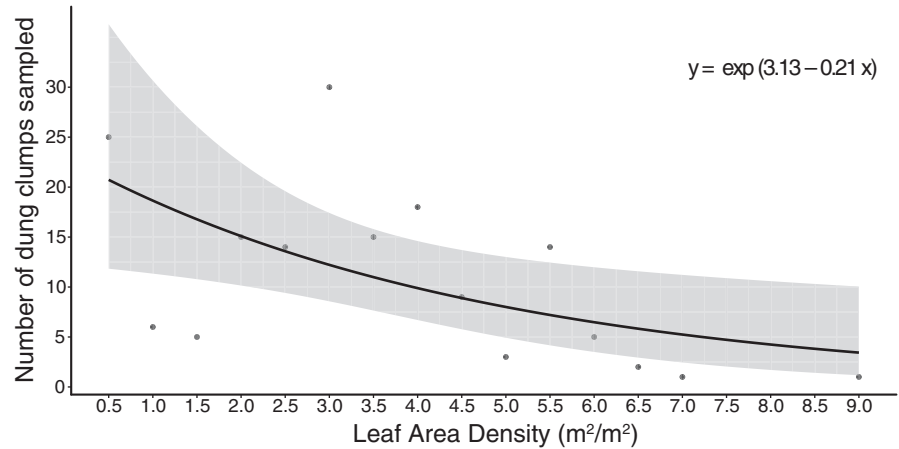
We found a total of 163 dung clumps, 43 in the unburned plot, 48 in the B3yr, and 72 in the B1yr treatment plots (Table 1; Figure 1). Of these dung clumps, 74% were deposited in latrines. They contained a total of 129,204 seeds from 24 species, six of which (25%) were not previously documented in our study area (Supporting Information Table S1). Less than one percent of all seeds were damaged. We obtained a total of 306 independent camera records of lowland tapirs in our study area, each representing a potential defecation event. The records in burned plots were twofold higher (B3yr = 125 records; 41% and B1yr = 120; 39%) than in the unburned plot (61; 20% of all records).

We found more tapir dung clumps under open canopy forests ($F_{1,13} = 6.5$, $p = 0.024$; Figure 2) than under closed canopy forests. By open canopy, we mean a lower leaf area density along the entire forest profile within a 5 m radius from each sample, which occurred more often in burned plots (Supporting Information Figure S2). Tapirs dispersed an estimated total of 7,531 seeds ($CI_{95\%} = 6,844; 8,945$).

TABLE 1 Number and proportion of tapir dung clumps and seeds, and the ratio seeds/dung found in each treatment plot in southeastern Amazonia, Brazil. These numbers represent the sum of occurrence across different four sampling events (each lasting 3–5 days) in January, April, June, and September 2016

	Unburned	B3yr	B1yr
Number of dung clumps	43 (26%)	48 (30%)	72 (44%)
Number of seeds	18,468 (14%)	48,406 (38%)	62,330 (48%)
Ratio seeds/dung	429	1008	866

FIGURE 2 Negative relationship between leaf area density and the number of tapir dung clumps sampled in an unburned and in an experimentally burned forest in southeastern Amazonia. Leaf area density was measured with airborne LiDAR in a 5 m radius around each dung clump, which values were classified into 0.5-m intervals. The experimental forest was subjected to either annual or triennial experimental fires over 6 years; an adjacent plot was studied as an unburned Control



per ha/year across our entire study area. Considering each treatment plot separately, we estimate that tapirs disperse 2,950 ($CI_{95\%} = 2,961; 3,771$) seeds per ha/year in the unburned plot, 8,587 ($CI_{95\%} = 7,999; 10,395$) seeds per ha/year in the B3yr plot, and 11,057 ($CI_{95\%} = 10,214; 13,281$) seeds per ha/year in the B1yr plot (9,822 seeds per ha/year on average across both burned plots). Our complete survey of the 150 ha study area (during the fourth sampling event) showed that 39% of dung clumps were deposited far from established trails. Assuming this distribution was consistent with that of the first three sampling events, we may be underestimating the number of seeds dispersed per hectare by as much as 40 percent.

Lowland tapirs dispersed many (~120 times) more climax than pioneer seed species ($\chi^2 = 242.7, df = 1, p < 0.001$; Figure 3A), which did not vary across treatment plots ($\chi^2 = 0.16, df = 2, p = 0.92$). They dispersed 60 times more seeds from tree species than from lianas and shrubs ($\chi^2 = 239.6, df = 2, p < 0.001$; Figure 3B), which was also consistent across treatments ($\chi^2 = 0.51, df = 2, p = 0.77$). Finally, tapirs dispersed 25 times more small than medium and large seeds ($\chi^2 = 120.1, df = 2, p < 0.001$; Figure 3C), which also did not differ across treatment plots ($\chi^2 = 0.02, df = 2, p = 0.98$). These results were highly influenced by the massive dispersal of *Bellucia grossularioides* (Melastomataceae), a small-seeded climax tree species that represented 83% of all seeds found in dung. Seed species richness found in dung clumps did not vary across treatments (unburned: observed richness = 21 ± 3.61 spp., extrapolated to 72 samples = 24.52 ± 3.61 spp.; B3yr: observed richness = 21 ± 1.39 spp., extrapolated to 72 samples = 21.61 ± 1.8 spp; and B1yr: observed richness = 23 ± 2.9 spp; Supporting Information Figure S3).

4 | DISCUSSION

Our results indicate that lowland tapirs play an important role as seed dispersers in disturbed tropical forests. Camera records suggest that tapirs used burned forests twice as often as undisturbed, closed canopy forests. We speculate that this preference for degraded forests is related to the fact that open areas are hotter, allow greater light penetration, and tend to have a higher proportion of palatable plants from early-successional stages. These results are

broadly consistent with previous work showing that Baird's tapirs utilized secondary forests much more than primary forests in Costa Rica, because those secondary forests housed more palatable plants and higher densities of understory vegetation (Foerster & Vaughan, 2002). It is possible that the tapirs in our study preferred degraded forests for the same reasons, although the burned forests had lower leaf area density than unburned forests (Supporting Information Figure S2). Regardless of the explanation, higher usage of open areas by tapirs resulted in a greater density of tapir dung in those areas, and hence, more seeds dispersed across burned forests. The majority of dispersed seeds belonged to small-seeded climax tree species (Figure 3), and very few seeds were predated.

Several factors have been found to limit the capacity of animal dispersal in promoting natural recovery of disturbed forests, including: (a) few forest seeds reaching degraded areas; (b) dispersed seeds concentrated below trees rather than in more open areas; and (c) predominance of early-successional species in the pool of dispersed seeds (Duncan & Chapman, 2002). Our results suggest that lowland tapirs may help overcome these limitations to dispersal via several mechanisms. Tapirs not only disperse more seeds across burned than unburned forests (Table 1), but also deposit more dung clumps under open canopies (Figure 2). Moreover, half of the dispersed seed species were arboreal and nearly 40% of them were late-successional species (Supporting Information Table S1). Finally, tapirs dispersed four native species (*Byrsonima crispera*, *Emmotum nitens*, *Senna* sp., and *Solanum* sp.) that were not previously documented in our study area, suggesting their potential to increase seed diversity in degraded forests. Although there are other important barriers to seedling establishment such as competition, predation, and soil condition, seed arrival is a critical one. Tapirs may thus make a crucial contribution to the natural recovery of disturbed forests.

Some traits associated with tapir seed dispersal could jeopardize the efficacy of natural recovery, but our findings suggest that the positive effects offset the negative. For example, most of the dung samples (>70%) from our study site were found in latrines. This implies that most tapir-dispersed seeds are aggregated in the landscape, which could facilitate attacks by natural enemies (Terborgh, 2012). On the other hand, seeds located in tapir latrines have been shown to suffer 100-fold less mortality by bruchid beetles than those near parent

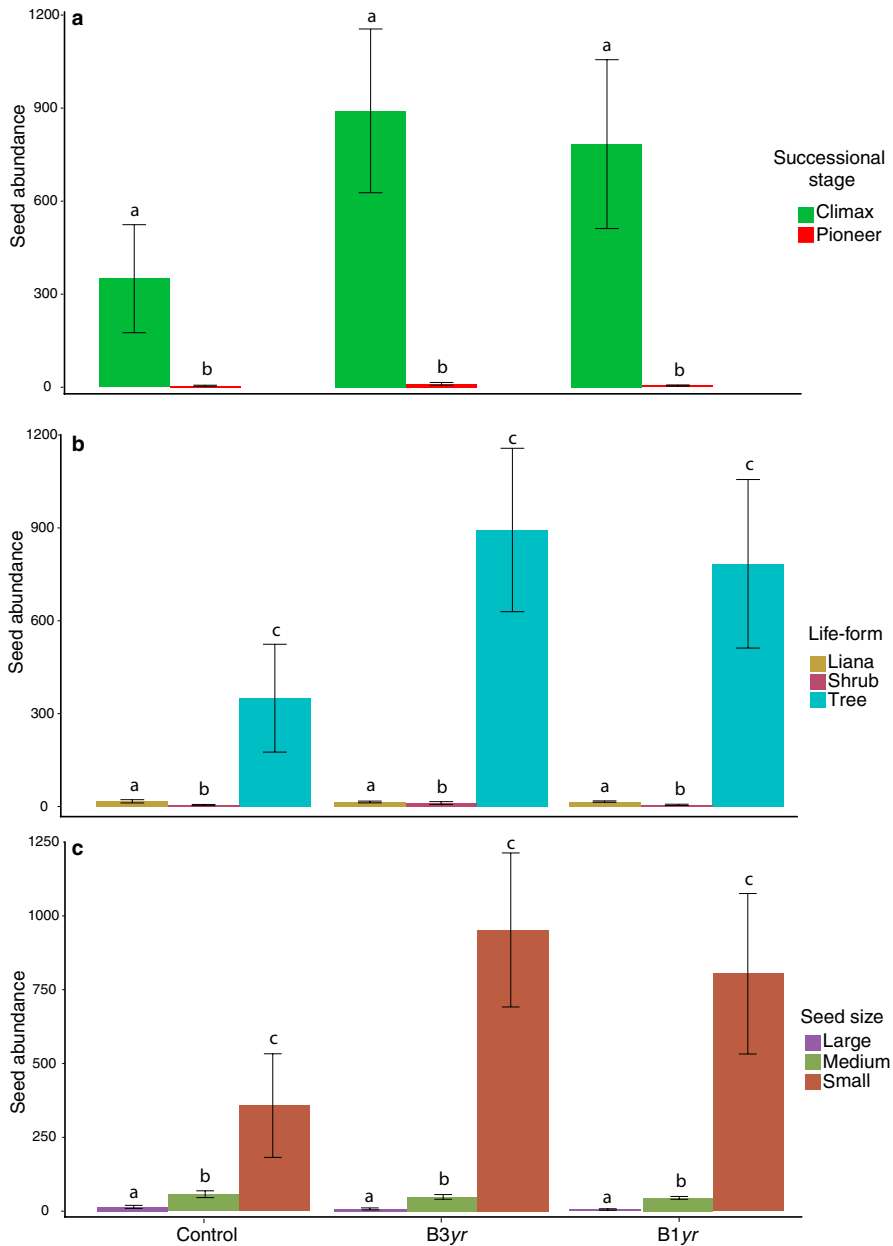


FIGURE 3 Average seed abundance found per dung clump across treatment plots (unburned Control: $N = 42$; B3yr: $N = 48$; and B1yr: $N = 73$) in southeastern Amazonia. Seeds are classified in different types according to (A) successional stage, (B) life-form, and (C) size (small: <0.5 cm; medium: 0.5 – 1.5 cm; and large: >1.5 cm). According to two-way ANOVA, variation in seed type abundance was not different across treatment plots; different letters indicate significant differences among seed type abundance within each treatment plot. Bars represent SEs

trees in an undisturbed Amazonian forest (Fragoso, 1997), which has been attributed to seed protection by the dung (Rios & Pacheco, 2006). Tapir dung may also act as a fertilizer for seedling development (O'Farrill et al., 2013). Previous studies have argued that tapirs are poor seed dispersers due to seed predation during digestion (Campos-Arceiz, Traeholt, Jaffar, Santamaria, & Corlett, 2012; Janzen, 1981) and due to a preference for defecating in water or seasonally flooded areas (e.g., Janzen, 1981; Salas & Fuller, 1996). In contrast, our findings show a low level of seed predation and high incidence of tapir dung clumps in disturbed upland forests, comparable to levels reported in undisturbed upland rain forests (Bueno et al., 2013).

Although we did not check for seed viability, previous studies have found high rates of seed survivorship (Bodmer, 1990, 1991; Fragoso, 1997; Fragoso & Huffman, 2000; Rodrigues, Olmos, & Galetti, 1993) and shortened germination times (Bueno et al., 2013) following lowland tapir ingestion. While some of these seeds may not establish

(e.g., soybeans), many others have the potential to do so, including pioneer shrub species and climax tree species. Lowland tapirs thus play a noteworthy role among vertebrates by effectively dispersing seeds into disturbed forests. They are large-bodied animals with long gut retention times and large home ranges, providing longer-distance movement of seeds from a wider range of sizes than other vertebrates (O'Farrill et al., 2013). Tapirs also complement seed dispersal by other large vertebrates such as the miqui monkey (*Brachyteles arachnoides*), dispersing larger seeds to distinct habitats (Bueno et al., 2013). Taken together, these factors suggest that tapirs play a net positive role in seed dispersal and seedling recruitment.

By helping to maintain the distribution and abundance of plant species (O'Farrill et al., 2013), tapirs can ultimately contribute to natural regeneration. This ecosystem function may be particularly critical in severely disturbed forests like our study area, where tree survivorship remained low and grass invasion high even after 7 years of

natural recovery. For context, the number of seeds dispersed per ha/year by tapirs in burned forests (9,822 seeds ha/year from 24 spp.) was equivalent to 3.5% of the minimum density and 96% of the minimum richness of seeds typically used in a large reforestation program in the southeast Amazon's Xingu Basin (*muvuca* method, led by Instituto Socioambiental–ISA; <http://sementesdoxingu.org.br/>). This further supports the idea that tapirs can provide an important complement to restoration programs and ultimately reduce the level of effort required.

Extirpation or population decline of large seed dispersers such as tapirs could be even more detrimental than previously recognized. It would not only impair the recruitment of plants and vegetation dynamics in undisturbed forests, but also the natural recovery of degraded forests by disrupting long-distance dispersal of large-seeded species into isolated remnants. Given that many large tropical trees rely on them for seed dispersal and regeneration, large-bodied vertebrate seed dispersers support critical ecosystem functions such as maintaining forest carbon stocks (Bello et al., 2015). Our results show that tapirs are important seed dispersers that can help some species escape dispersal limitation, ultimately favoring a more efficient natural recovery of tropical forests.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q8d17km> (Paolucci et al., 2019).

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SUPPORTING INFORMATION

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