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REVIEW

Frugivory and seed dispersal by tapirs: an insight on their ecological role

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Abstract

Tapirs are one of the last extant megafauna species that survived the Pleistocene extinctions. Given their size and digestive system characteristics, tapirs might be the last potential seed disperser of plant species that were previously dispersed by other large mammal species that are now extinct. We compiled evidence from 39 published scientific studies showing that tapirs have a key role as seed dispersers and seed predators. Tapirs play an important role either through seed predation or by facilitating the recruitment of seeds over long distances, therefore influencing the diversity of plant species in the ecosystem. Neotropical tapirs might have a unique role as long-distance seed dispersers of large seeds (<20 mm) because they are capable of depositing viable large seeds in favorable places for germination that even large-bodied primates cannot disperse. Given the high diversity of seed species found in tapir diet, more information is needed on the identification of seed traits that allow the survival of seeds in the tapir's gut. Moreover, further studies are necessary on the role of tapirs as seed dispersers and predators; in particular considering spatial patterns of dispersed seeds, seed viability, effect of dung, and seed density in tapir latrines, and the effect of deposition sites on germination and seedling survival. Because all tapir species are highly threatened, it is paramount to identify gaps in our knowledge on the ecological role of tapirs and, in particular, on critical and endangered plant–tapir interactions to avoid possible trophic cascading effects on ecosystem function.

Key words: defaunation, ecological function, long-distance dispersal, megafaunal dispersal syndrome, trophic cascades

INTRODUCTION

Seed dispersal is a key stage in the life cycle of plants with profound implications for the succession, regener-

ation and conservation of ecosystems (Wang & Smith 2002). Large-bodied frugivores play an important role shaping the structure of plant communities at different scales and maintaining plant diversity, because they are able to ingest more fruits, eat larger seeds and disperse them to larger distances than small bodied frugivores (Jordano *et al.* 2007; Guimãraes *et al.* 2008). One of these megafrugivores is the tapir (*Tapirus* spp., Perissodactyla).

Tapirs are one of the few species that survived the vast megafaunal extinctions of the Late Pleistocene, be-

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tween 50 000 and 10 000 years ago (Koch & Barnosky 2006). Tapirs (Tapiridae) are among the most primitive extant large mammals (Feldhamer *et al.* 2007). At least 22 species of tapirs were known between the Oligocene and the Pleistocene and were distributed worldwide (Janis 1984). Today, there are only 4 extant tapir species, all of them included in the genus *Tapirus*. Of these, 3 species are distributed in the American continent, Baird's tapir [*Tapirus bairdii* (Gill, 1865)], the lowland tapir [*Tapirus terrestris* (Linnaeus, 1758)] and the mountain tapir [*Tapirus pinchaque* (Roulin, 1829)], and 1 in Asia, the Malayan tapir (*Tapirus indicus* Desmarest, 1819). All tapir species are considered threatened by poaching, fragmentation and habitat loss (see www.redlist.org), so it is paramount to understand their role in forest succession and regeneration.

In the present study, we review the role of tapirs in the seed dispersal process. In particular, we look for broad scale patterns and particularities that could explain their frugivorous habits in different environments, the effects of tapir gut passage on seed viability and the spatial seed deposition patterns provided by tapirs. Ultimately, we show that the fruit diet of tapirs varies among ecosystems and populations with no clear pattern. We identify gaps in our knowledge that are key for the understanding of the importance of the ecological role of tapirs and the potential consequences of their extinction.

FRUGIVORY

The relative occurrence of fruits *versus* plant vegetative parts in tapir diet varies among habitats, biomes and populations; however, all tapir species eat fruits,

and, therefore, are potential seed dispersers and predators (Bodmer 1990; Rodrigues *et al.* 1993; Fragoso & Huffman 2000; Tobler *et al.* 2010). The relative occurrence of fruits in the tapir's diet ranges from 3% in Guatemala for the Baird's tapir (García-Vetorazzi 2006) to 33% in the Amazonian Peru for the lowland tapir (Bodmer 1991; Fig. 1). The low relative occurrence of fruits in the tapir diet might be associated with the availability of fallen fruits, season, productivity, competition with other ungulates (e.g. peccaries) and fruit selection; however, further studies are necessary to identify the factors that influence the degree of frugivory of tapirs along their distribution range.

PLANT DIVERSITY

The diversity of plant species dispersed is an important component of the community-level effectiveness of a seed disperser (Bascompte *et al.* 2003; Dennis & Westcott 2006). Tapirs consume a wide variety of plant species (Schupp *et al.* 2010), which might be determining their variable role as seed dispersers and predators among habitats and populations (Table 1). For instance, lowland tapirs have been reported to eat more than 460 plant species in the Neotropical region, with fruits from 194 plant species (Hibert *et al.* 2011), many of which are not dispersed by Ateline primates. For Baird's tapir, seeds of as many as 81 species (33 families) have been reported in tapir dung, with 67 species reported with viable or intact seeds (Table S1). In French Guiana, Hibert *et al.* (2011) found 42 identified and 16 unidentified fruit species as part of the lowland tapir; however, the fate of the seeds in the dung is not reported. In the most comprehensive study to date, Downer (2001) stud-

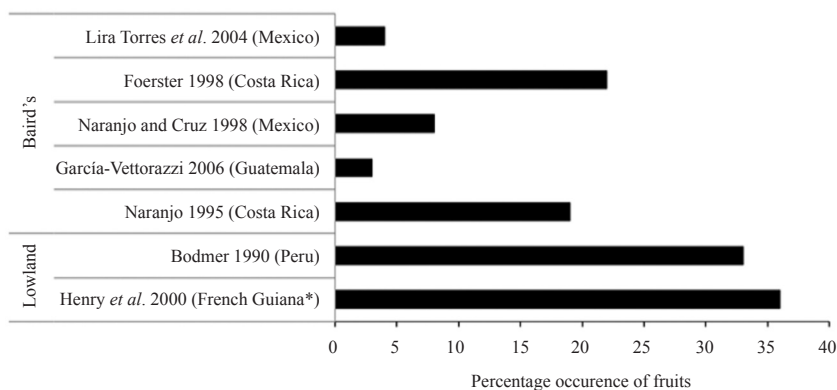


Figure 1 Percentage occurrence of fruits in lowland and Baird's tapir diets. *Percentage occurrence in stomachs.

Table 1 Fruit species richness in the diet of the lowland tapir (*Tapir terrestris*) in South America

Site	Habitat	Sample size	Fruit species richness	Reference
RE Ilha de Maracá, RR, Brazil	Amazon forest	356	25	Fragoso and Huffman (2000)
Rio Tahuayo and Quebrada Blanco, Peru	Amazon forest	44 (25 scats)	at least 16	Bodmer (1991)
Tabaro Valley, Venezuela	Amazon forest	206	33	Salas and Fuller (1996)
French Guiana	Amazon forest	27 stomachs	42	Henry <i>et al.</i> (2000)
Bacia Solimões, AM, Brazil	Amazon forest	113	48	Morais (2006)
Madre de Deus, Peru	Amazon forest	135	122	Tobler (2008)
Virúá National Park, AM, Brazil	Amazon forest	111	75	Barcelos <i>et al.</i> (2013)
PE Carlos Botelho, SP, Brazil	Atlantic forest	49	6	Bueno <i>et al.</i> (unpubl. data)
PE Serra do Mar, SP, Brazil	Atlantic forest	38	7	Oliveira (2011)
Usina Serra Grande, Alagoas, Brazil	Atlantic forest	10	19	Bachand <i>et al.</i> (2009)
PE Serra do Tabuleiro, SC, Brazil*	Atlantic forest (restinga)	81 observations	33	Santos <i>et al.</i> (2005)
Faz. Barra do Moeda, MS, Brazil	Cerrado	39	53	Prado (2012)
PE Serra Azul, MT, Brazil	Cerrado	105	13	Fraias <i>et al.</i> (2011)
Serra do Caraça, MG, Brazil	Cerrado/Atlantic forest	147	9 (families)	Talamoni and Assis (2009)
Faz. Rio Negro, MS, Brazil	Pantanal	285	11	Donatti <i>et al.</i> (2007)
Nhecolândia, MS, Brazil	Pantanal	263	54	Zorzi (2009)
EE Caetetus, SP, Brazil	Semideciduous forest	46	9	Galetti <i>et al.</i> (2001)
PE Morro do Diabo, SP, Brazil	Semideciduous forest	172	58	Tófoli (2006)
Sierra de San Javier, Argentina*	Yungas	not mentioned	12	Richard and Juliá (2000)
El Rey National Park, Argentina	Yungas	88	57	Chalukian <i>et al.</i> (2012)

*semi-captive animals

ied mountain tapirs in Sanguay National Park, Ecuador and found that they consumed as many as 205 plant species and seeds from 86 species (or 32.6% of the vascular plants recorded in the study area) germinated from tapirs' dung (Table 2).

The high variation in fruit consumption by tapirs might be explained by forest productivity. Nevertheless, Oliveira (2011) did not find any relation between number of species eaten by lowland tapirs and forest productivity, or any abiotic variable (rainfall and temperature; Table 1). However, further studies are necessary with other tapir species. In particular, studies on the relationship between species diversity in the field and diversity of seeds dispersed by tapirs are necessary to identify possible patterns of fruit choice and preference.

Despite the high diversity of seeds reported in tapirs' dung or as dispersed by tapirs, only a few studies evaluate the germination probabilities of the seeds found in the dung (i.e. Janzen 1982a; O'Farrill *et al.* 2012). We

focus the present study on all the reports on tapir diet and assume that tapirs potentially disperse the seeds found in tapir dung (meaning seeds can germinate in their deposition sites). However, further conclusions on the seed dispersal role of tapirs should consider the fate of the seeds dispersed.

Future studies should focus on the distribution of the most commonly represented families of the seeds found in tapir dung to evaluate whether the variability of seeds in dung represents the variability of family species along the distribution range of tapirs. We established that the species found in dung and reported as dispersed in the literature corresponded to 46 families for the lowland tapir, 34 families for the Baird's tapir and 14 families for the mountain tapir (Fig. S1). The family Rubiaceae was the most common family represented in the species reported as dispersed by the Baird's tapir (10 species). This family also represented one of the most common families in the lowland tapir dispersed species (29 spe-

Table 2 Number of plant species reported to be found in tapir dung and from stomach analyses and likely to be dispersed by tapirs

<i>Tapirus</i> spp.	Country	<i>N</i> spp	Habitat	Reference
<i>T. terrestris</i>	Peru	122	Old growth lowland	Tobler <i>et al.</i> (2010)
	Peru	15 [†]	Amazonian moist forest	Bodmer (1991)
	Brazil	58	Atlantic forest	Tófoli <i>et al.</i> (2007)
	Brazil	9	Semi-deciduous tropical forest	Galetti <i>et al.</i> (2001)
	French Guiana	34	Evergreen primary forest	Hibert <i>et al.</i> (2011)
	French Guiana	42 [†]	Tropical rain forest	Henry <i>et al.</i> (2000)
	Brazil	39	Old growth tropical evergreen lowland rain forest	Fragoso and Huffman (2000)
	Venezuela	33	Seasonal swamp forest in upland valleys	Salas and Fuller (1996)
<i>T. pinchaque</i>	Ecuador	86 [‡]	Cloud forest and wet paramo	Downer (2001)
<i>T. bairdii</i>	Costa Rica	14	Deciduous tropical forest	Janzen (1982a)
	Costa Rica	10	Montane cloud forest	Tobler (2002)
	Costa Rica	23	Tropical forest	Naranjo (1995)
	Guatemala	5	Tropical forest	García-Vettorazi (2006)
	Mexico	21 (genera)	Tropical forest	Naranjo and Cruz (1998); Cruz (2001); Lira Torres <i>et al.</i> (2004)
<i>T. indicus</i>	Malaysia	>6	Tropical rain forest	William and Petrides (1980)

[†]Plants found during stomach analyses, included because stomach contents is potentially found in dung as well. [‡]Plants found to germinate in tapir feces, showing that tapirs are effective seed dispersers.

cies). Moraceae was the most common family represented in the species dispersed by the lowland tapir (36 species). For the mountain tapir, the Asteraceae family was the most represented (4 species), followed by Poaceae (3 species).

Even though tapirs have been documented to have mutualistic interactions with the large-seeded plant species they disperse, further study is required on plant species with potential tapir syndromes (e.g. with large seeds, falling to the ground at maturity and using smell to attract dispersers) to evaluate their dependency on tapirs for recruitment (Janzen & Martin 1982; Guimarães *et al.* 2008; Donatti *et al.* 2011).

SEED SIZE CONSUMPTION

Tapirs can ingest small seeds (e.g. those of *Ficus* spp. approximately 1 mm) and large seeds, varying in size from 20–30 mm (*Spondias mombim* and *Manilkara zapota*) up to mango seeds (*Mangifera* spp. >50 mm; Fragoso & Huffman 2000). Tapirs can ingest and defecate a large number of even large seeds (Janzen 1982b; Williams 1984). For example, in Brazil, Galetti *et al.*

(2001) found up to 2103 seeds (>3 mm) in a single tapir dung in a semi deciduous forest. In the Yucatan Peninsula in Mexico, a single dung pile of a Baird's tapir contained up to forty 20 mm long *M. zapota* seeds (O'Farrill *et al.* 2012), while in Brazil, Rodrigues *et al.* (1993) found 300 seeds of *Euterpe edulis*, each measuring 8–14 mm. In a study in Taman Negara National Park, Malaysia, fruit parts and seeds were present in all but one of the Malayan tapir dung piles inspected (the number of piles is unknown). These included many species, with a fruit diameter ranging from 10 to 60 mm (Williams & Petrides 1980). Unfortunately, most of these species remained unidentified.

We compiled the information available on the seed sizes of species found in tapir dung (*N* = 156). In most studies, seeds found in tapir dung are reported as dispersed despite that no germination or viability tests confirmed the status of the seeds. In addition, only the species names are reported and no data is presented on the number of seeds per plant species in most studies. We found that most of the seeds that had been reported as dispersed by tapirs are small: 66% of the species corresponded to seeds ≤10 mm, 21% to seeds between 10 and

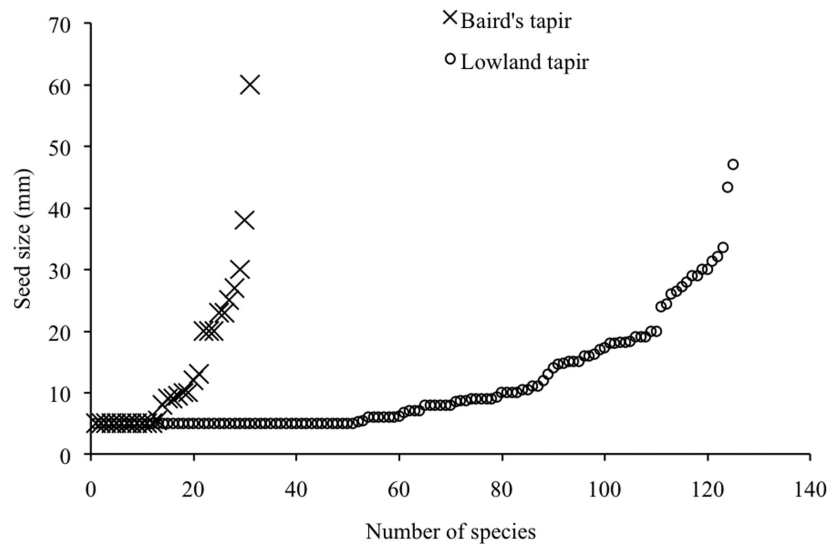


Figure 2 Distribution of seed sizes of seeds reported as 'dispersed' by tapirs, for Baird's and lowland tapirs. Seed sizes (length) ≤ 5 mm where recorded as 5 mm for graphical purposes. Seeds were found in dung and in stomachs; however, in most cases no germination or viability analyses were carried out to verify the status of the seed.

20 mm, 9% to seeds from 20 to 30 mm and only 4% to seeds larger than 30 mm (Fig. 2). This high percentage of small seeds remains when observing seed sizes by tapir species: 61% of the seeds were ≤ 10 mm for Baird's tapir and 66% for the lowland tapir. In French Guiana, Henry *et al.* (2000) found a similar pattern for the lowland tapir, where 67% of 40 seed species were < 10 mm in diameter. Even though tapirs might not be dispersing a high diversity of large-seeded plant species, their unique role as dispersers of large seeds should not be underestimated, especially in those habitats where there are no redundant species.

SEED PREDATORS *VERSUS* SEED DISPERSERS

Tapirs can spit or accidentally drop many seeds from the fruits they eat (Janzen 1982b; Bodmer 1991; Campos-Arceiz *et al.* 2012); however, the fate of those seeds is commonly ignored. Of those seeds that are actually swallowed, many do not survive the passage through the guts; some are crushed during mastication or destroyed by gastric acids and excessive hydration in tapirs' guts (Janzen 1981; Campos-Arceiz *et al.* 2012).

There is controversy regarding the role of tapirs as either disperser or predator for certain plant species. For example, in a feeding trial with a captive Baird's tapir, Janzen (1981) found that the tapir's digestive process killed 78 and 100% of guanacaste (*Enterolobium cyclo-*

carpum) and carao (*Cassia grandis*) seeds, respectively. In contrast, Williams (1984) found live carao seeds in tapir dung in Santa Rosa National Park in Costa Rica. Also in Costa Rica, Baird's tapir predated *M. zapota* seeds (Janzen 1982a; Williams 1984), while in Mexico viable *M. zapota* seeds were observed in several Baird's tapir dung piles (O'Farrill *et al.* 2012). Campos-Arceiz *et al.* (2012) found that seeds ingested by captive Malayan tapirs showed survival rates ranging from 0 to 50% for different species. Although tapirs can act both as seed predators or seed dispersers, even within plant species, further study is necessary to understand what seed traits determine the survival of seeds in the tapir gut.

TAPIR EFFECTIVENESS IN THE DISPERSAL OF LARGE SEEDS

Effective seed dispersal includes the movement of viable seeds to favorable places for germination and the successful survival of the seeds and establishment of adult individuals (Harper 1977). Tapirs have been reported as effective seed dispersers of large seeds: for example, *Mauritia flexuosa* and *Maximiliana maripa* palms in Costa Rica (Bodmer 1991; Fragoso & Huffman 2000), *M. zapota* in Mexico (O'Farrill *et al.* 2012) and *Syagrus romanzoffiana* in Argentina (Giombini *et al.* 2009; Table 3). However, the role of tapirs as seed dispersers needs to be compared with their role as seed

predators for a particular plant species and the effects of the location where seeds are deposited should be considered. For example, in the Calakmul region in Mexico, only 53% of 345 dung piles collected between 2005 and 2008 contained intact *M. zapota* seeds (large seeds length >20 mm) or seedlings (G. O’Farrill, unpubl. data). In addition, the same authors found that in 164 dung piles analyzed, 54% of the seeds were intact while 46% were predated (O’Farrill *et al.* 2006), suggesting that tapirs play a significant role both in the seed dispersal and seed predation of *M. zapota* seeds. However, O’Farrill *et al.* (2012) found that of 512 *M. zapota* seeds collected from tapir dung, only 30% germinated, suggesting that reports on seed dispersal by tapirs based only on

seed presence in tapir dung might overestimate the seed dispersal role of these species. In Kerinci Seblat, Sumatra, Malayan tapirs consumed large fruits, such as jackfruits (*Artocarpus* sp.) and durians (*Durio* sp.), and durian seedlings were often found sprouting from tapir dung (Holden *et al.* 2003). In contrast, a study with captive tapirs showed that although Malayan tapirs readily consume large fruits, such as *Artocarpus integer*, very few large seeds survive to passage through their guts (Campos-Arceiz *et al.* 2012). Even though tapirs might predate a vast amount of large seeds, the dispersal of just a few large seeds to favorable places for germination and survival might enhance the recruitment of large-seeded plant species not dispersed by other animal species.

Table 3 Species with large seeds >20 mm reported as potentially dispersed by tapirs

Species	Seed size (mm)	Tapir species	Reference
<i>Manilkara</i> sp.	20	B	Naranjo and Cruz (1998)
<i>Pouteria</i> sp.	20	B	Brooks <i>et al.</i> (1997)
<i>Virola</i> sp.	20	B	Williams (1984)
<i>Enterolobium cyclocarpum</i>	23	B	Janzen (1981); Williams (1984)
<i>Manilkara zapota</i>	23	B	O’Farrill <i>et al.</i> (2006)
<i>Hymenaea courbaril</i>	25	B	Janzen (1982a)
<i>Brosimum alicastrum</i>	27	B	Janzen (1982a); Olmos (1997)
<i>Astrocaryum standleyanum</i>	30	B	Brooks <i>et al.</i> (1997)
<i>Spondias mombim</i>	38	B	Williams (1984); Naranjo (1995); Cruz (2001)
<i>Bactris gasipaes</i>	60	B	Naranjo (1995)
<i>Calatola</i> sp.	20	L	Tobler <i>et al.</i> (2010)
<i>Mimosa</i> sp. 1	20	L	Tobler <i>et al.</i> (2010)
<i>Sarcaulus</i> sp. 2	24.3	L	Tobler <i>et al.</i> (2010)
<i>Oenocarpus batua</i>	26	L	Tobler <i>et al.</i> (2010)
<i>Mauritia flexuosa</i>	26.5	L	Tobler <i>et al.</i> (2010)
<i>Sarcaulus</i> sp. 1	27.2	L	Tobler <i>et al.</i> (2010)
<i>Oenocarpus mapora</i>	28	L	Tobler <i>et al.</i> (2010)
<i>Fussaea longifolia</i> cf.	29	L	Tobler <i>et al.</i> (2010)
<i>Mutisia cordata</i>	29	L	Tobler <i>et al.</i> (2010)
<i>Spondias mombin</i>	30	L	Tobler <i>et al.</i> (2010)
<i>Syagrus romanzoffiana</i>	30	L	Giombini <i>et al.</i> (2009)
<i>Anomospermum</i> cf. <i>reticulatum</i>	31.4	L	Tobler <i>et al.</i> (2010)
<i>Hymenaea oblongifolia</i>	32	L	Tobler <i>et al.</i> (2010)
<i>Pouteria putamen-ovii</i>	33.5	L	Tobler <i>et al.</i> (2010)
<i>Astrocaryum murumuru</i>	43.3	L	Tobler <i>et al.</i> (2010)
<i>Elephantomene eburnea</i>	47	L	Henry <i>et al.</i> (2000)

The species are reported as dispersed by the references (found intact in tapir dung); however, in most cases, no germination probabilities were reported. B = Baird’s tapir; L = lowland tapir.

TAPIR EFFECTS ON SEED RECRUITMENT

Tapirs defecate seeds in a large amount of dung that can act as fertilizer in the early stages of seedling development. In Mexico, germination of *M. zapota* seeds collected from tapir dung was significantly higher when planted in tapir dung than when planted in soil near water ponds commonly frequented by tapirs, suggesting a positive effect of tapir dung on germination (O'Farrill *et al.* 2012).

Dung can also act as a physical protection against predation by bruchid beetles, as reported by Fragoso *et al.* (2003), and can attract other seed predators, such as hyacinth macaws in Pantanal (M. Galetti, unpubl. data). In addition, secondary seed dispersal from tapir dung can influence the fate of the dispersed seeds. In Bolivia, predation of *Attalea phalerata* seeds by bruchid beetles was significantly lower when seeds were planted in tapir dung than when seeds were left exposed or partially covered (Rios & Pacheco 2006).

In addition, tapirs have been described to defecate repeatedly in latrines (Acosta *et al.* 1996; Fragoso & Huffman 2000; Holden *et al.* 2003), but this behavior does not seem to be universal. Based on molecular analysis, researchers have found that several individuals can use the same latrine (A. Sanches, unpubl. data). Therefore, defecation in latrines can increase the concentration of seeds and result in higher density-dependent mortality. In the Pantanal, tapirs are known to defecate in salt-water lakes (salinas), where seeds are unable to recruit. However, many seeds are also dispersed in latrines in the forests and cerrado vegetation (M. Galetti, unpubl. data). In conclusion, the advantages and disadvantages of the creation of latrines by tapirs and their seed dispersal role remain unclear.

It has been documented that tapirs have a tendency to defecate in water, a hostile environment for the survival and establishment of most seeds. However, it is unclear how widespread this behavior is. For example, in Costa Rica, Janzen (1981) concluded that Baird's tapirs defecated exclusively in water or in dry areas that flood seasonally, while in Mexico, dung piles of this same species were found both in inundated areas and in sites never reached by water (G. O'Farrill, pers. observ.). In Venezuela, lowland tapirs were observed to defecate exclusively in flooded or seasonally flooded areas (Salas & Fuller 1996). In contrast, Fragoso (1997) found lowland tapir latrines at upland forest sites in Brazil. Also in Brazil, Talamoni and Assis (2009) found tapir dung in

water, suggesting the deposition of seeds in hostile environments.

TAPIRS' EFFECTS AT A LANDSCAPE LEVEL

The spatial distribution of dispersed seeds by tapirs is determined by the time the seeds are retained in the animal guts (i.e. time from consumption to defecation) and by the animal's movement in that time (Jordano *et al.* 2007; Morales & Carlo 2006). Janzen (1981) found that bigger seeds are retained longer than small seeds in tapir guts, with retention times varying from 48 to 52 h. A recent study with captive lowland and Malayan tapirs showed mean fluid and particle retention times ranging from 25 to 81 h (Clauss *et al.* 2010). Feeding trials with Malayan tapirs using seeds of 9 different plant species showed mean retention times of up to 13 days for some large seeds (Campos-Arceiz *et al.* 2012). This shows that tapirs have relatively long retention times for their body size. For instance, the seeds of *Tamarindus indica* eaten by Malayan tapirs are retained 4 times longer than by Asian elephants (*Elephas maximus* Linnaeus, 1758) (Campos-Arceiz *et al.* 2008).

Having long gut retention times can have a positive and negative effect on seed survival. This can cause more seeds to be predated by the gut fluids but can favor the dispersal of seeds farther away from parent trees, therefore reducing density-dependent mortality and promoting large-scale processes such as fragment connectivity, re-colonization of disturbed patches and plant migration (e.g. as a result to climate change).

In addition to long gut retention times, tapir movement patterns determine the spatial pattern of seed dispersal. Tapirs have large home ranges, although smaller than expected by their body size. For example, in Peru, Tobler *et al.* (2009) reported lowland tapir individuals moving up to 13 km in 24 h periods, with a mean daily movement of 5.2 km (range 3.6–6.7 km). These movements over long distances or through large home ranges allow tapirs to move seeds over many kilometers, spacing the seeds in the tapir's dung (Janzen 1981), and, therefore maximizing seed dispersal effectiveness and increasing the probability of the deposition of seeds in favorable places for germination (far from parent trees where density-dependent competition occurs). Hence, tapirs can facilitate the regeneration of several plant species and the maintenance of their populations on a large scale, as reported by Fragoso (1997) in Brazil, where the large-scale aggregation of *Ma. maripa* palms might

result from the defecation characteristics of tapirs. Talamoni and Assis (2009) found several dense clumps of *Psidium myrtoides* (a tapir-dispersed seed) located next to rivers, which suggests that tapirs, among other dispersers, might be influencing the distribution of this particular plant species. Bueno (2010) showed that low-land tapirs move across open or highly degraded areas not suitable for primates or other arboreal frugivores, therefore ensuring the dispersal of seeds across the landscape.

UNIQUENESS OF TAPIRS

All species of tapirs are locally threatened, due to overexploitation, habitat loss and road kill (Castellanos *et al.* 2008; Diaz *et al.* 2008; Lynam *et al.* 2008; Naveda *et al.* 2008). Today, tapirs represent the largest mammal of a once highly diverse megafauna in the Neotropical region. Although some regions still support large abundances of tapirs, most of their populations are declining.

Tapirs are seed dispersers and seed predators of a wide variety of plant species, therefore influencing the dynamics of plant populations. Given their frugivorous habits, tapirs consume small and large seeds, which are moved over long distances. However, given their size, long gut retention times, large home ranges and defecation patterns, tapirs might be the only species capable of dispersing large-seeded plants over long distances and to favorable places for germination. Therefore, tapirs might have a unique role as long-distance seed dispersers of large-seeded plants. The deposition of seeds in favorable places helps to maintain plant populations in both the short term and on a large scale. For example, Giombini *et al.* (2009) found that *S. romanzoffiana* seeds were present in 98% of dung piles observed in Argentina, and that dung piles showed a clumped deposition pattern, reflecting the use of latrines and influencing the distribution of seedlings. Fragoso *et al.* (2003) found that the aggregated pattern of *Ma. maripa* palms in Brazil was associated with tapir latrine sites, suggesting that tapirs might be shaping the distribution patterns of the species they disperse.

Even though most of the large-seeded plant species reported as dispersed by tapirs are consumed by other frugivore species (e.g. peccaries, spider and howler monkeys; Donatti *et al.* 2011; Table 4); it remains unclear whether other potential dispersers are capable of transporting viable seeds over long distances, as most studies do not test for viability or germination probabilities. For example, *M. zapota* seeds are reported as

uniquely dispersed by tapirs in the Yucatan Peninsula in Mexico (O'Farrill *et al.* 2012). Other potential dispersers in the area are howler monkeys (*Alouatta pigra* Lawrence, 1933), but this species has been observed to spit out *M. zapota* seeds (S. Calmé, pers. comm.). In a study in French Guiana, Ratiarison and Forget (2011) report that even though *Alouatta seniculus* (Linnaeus, 1766) and *Ateles paniscus* (Linnaeus, 1758) swallowed *M. huberi* seeds, their sedentary behavior causes the dispersal of seeds only over short distances. *Cebus apella* Linnaeus, 1758 and *Saguinus midas* Linnaeus, 1758 were often observed in *Man. bidentata* crowns; however, these species spit out the seeds. This suggests that for *Manilkara* spp. seeds, tapirs might act as the sole long-distance seed dispersers. Further comparative studies are necessary to evaluate the role of tapirs as long-distance seed dispersers of other large-seeded species in comparison with other potential seed dispersers in the Neotropics. In Asia, tapirs might not play a unique role as long-distance seed dispersers as other larger mammals disperse large-seeded plants. For example, Campos-Arceiz *et al.* (2012) found that Malayan tapirs effectively dispersed small-seeded plants but acted as seed predators for large-seeded plants (e.g. *Artocarpus integer*, seed length >20 mm).

Perhaps the main difference between the role of Asian tapirs and their North, Central and South American counterparts in seed dispersal effectiveness is a matter of context (Hansen & Galetti 2009). In Southeast Asia, Malayan tapirs are one order of magnitude smaller than the largest seed dispersers (i.e. Asian elephants). In the Neotropics, in contrast, tapirs are the largest living seed dispersers. This confers American tapirs a more unique role in the dispersal of large-seeded plants and long-distance dispersal events. In Southeast Asia, however, if the loss of very large mammals continues unabated, Malayan tapirs are expected to acquire in the future a relatively more important role as seed dispersers.

CASCADING EFFECTS IN TAPIR DEFAUNATED SITES

Through their seed dispersal role, tapir might promote gene flow via seeds of the plant species they disperse. The extinction of tapirs, due to overexploitation or habitat loss, would have demographic and genetic consequences for some plants they disperse, particularly as some large-seeded plant species have not been reported as dispersed over long distances by any other species other than tapirs. Tapirs consume high quantities

Table 4 Potential dispersers of large seeds[†]

	<i>Manilkara</i> sp.	<i>Pouteria</i> sp.	<i>Hymenaea</i> sp.	<i>Brosimum</i> sp.	<i>Astrocaryum</i> sp.	<i>Bactris</i> sp.	
<i>Agouti paca</i>		X					Gutierrez-Granados (2011)
<i>Alouatta palliata</i>	X						Anzures-Dadda <i>et al.</i> (2011)
<i>Alouatta seniculus</i>	X				X		Wright <i>et al.</i> (2000)
		X					Ratiarison and Forget (2011)
<i>Ateles chamek</i>		X					Julliot (1997)
<i>Ateles geoffroyi</i>					X		Felton <i>et al.</i> (2010)
<i>Ateles paniscus</i>	X						Wright <i>et al.</i> (2000)
				X			Ratiarison and Forget (2011)
<i>Bassaricyon gabbii</i>					X		Andresen (1999)
<i>Cebus apella</i>	X						Wright <i>et al.</i> (2000)
<i>Cebus capucinus</i>					X		Ratiarison and Forget (2011)
<i>Cebus olivaceus</i>	X						Wright <i>et al.</i> (2000)
<i>Dasyprocta leporina</i>		X	X	X	X		Ratiarison and Forget (2011)
<i>Dasyprocta punctata</i>		X					Silvius and Fragoso (2003)
					X		Gutierrez-Granados (2011)
<i>Dasyprocta</i> spp.			X			X	Silva and Tabarelli (2001)
					X		Donatti <i>et al.</i> (2009)
<i>Eira barbara</i>					X		Galetti <i>et al.</i> (2006)
<i>Nasua narica</i>					X		Wright <i>et al.</i> (2000)
<i>Pecari tajacu</i>					X		Wright <i>et al.</i> (2000)
<i>Pteropus tonganus</i>		X					Wright <i>et al.</i> (2000)
<i>Potos flavus</i>					X		McConkey and Drake (2006)
<i>Sanguinus midas</i>	X						Wright <i>et al.</i> (2000)
							Ratiarison and Forget (2011)
	<i>Virola</i> sp.	<i>Spondias</i> sp.	<i>Calatola</i> sp.	<i>Enterolobium</i> sp.	<i>Syagrus</i> sp.	<i>Oenocarpus</i> sp.	
<i>Agouti paca</i>					X		Keuroghlian and Eaton (2009)
					X		Silva and Tabarelli (2001)
<i>Alouatta palliata</i>						X	Beckmand and Muller-Landau (2007)
<i>Alouatta seniculus</i>	X						Julliot (1997)
<i>Ateles geoffroyi</i>						X	Beckman and Muller-Landau (2007)
<i>Ateles paniscus</i>	X						Russo (2003)
<i>Cebus capucinus</i>						X	Beckman and Muller-Landau (2007)
<i>Cerdocyon thous</i>					X		Silva and Tabarelli (2001)
<i>Dasyprocta azarae</i>					X		Silva and Tabarelli (2001)
<i>Elephas maximus</i>		X					Kitamura <i>et al.</i> (2007)
<i>Nasua narica</i>						X	Beckman and Muller-Landau (2007)
					X		Silva and Tabarelli (2001)
<i>Odocoileus virginianus</i>		X					Mandujano <i>et al.</i> (1994)
<i>Pecari tajacu</i>					X		Keuroghlian and Eaton (2009)
<i>Potos flavus</i>						X	Beckman and Muller-Landau (2007)
<i>Sanguinus geoffroyi</i>						X	Beckman and Muller-Landau (2007)
<i>Tayassu pecari</i>					X		Keuroghlian and Eaton (2009)

[†]Animal species are reported as dispersers despite the lack of germination and viability analysis in most of the studies.

of seeds, many of which are predated, causing the depletion of seedling abundance or promoting seed dispersal of those seeds that survive the digestive system (Gill 2006); hence, their loss can cause a cascade of ecological effects on other species interacting with the plant species tapirs consume (Giombini *et al.* 2009). In the Sangay National Park in Ecuador, Downer (2001) found a positive correlation between tapirs' feeding preferences for plant species and their germination frequency in dung, suggesting that mountain tapirs might be exerting a positive influence in their habitat by helping to regenerate their preferred food items. In the Brazilian Pantanal, a long-term community study found that plants dispersed by large mammals (particularly tapirs) form a distinct subset in the community, suggesting the irreplaceable role of these mammals on seed dispersal processes (Donatti *et al.* 2011). Therefore, the extinction of tapirs or changes in their movement patterns due to human-driven changes would result in a reduction of the quality and quantity of dispersal for many plants. For example, according to Galetti *et al.* (2001), the removal of lowland tapir from its habitat would have deleterious consequences for 50 out of 1380 Atlantic forest plant species, especially those with large seeds. Further studies on the potential consequences of tapir-defaunated or low tapir population sites are necessary to prevent a cascade of ecological effects. The decline of animal-mediated seed dispersal results in an increased dominance of wind-dispersed species (Muller-Landau & Hardesty 2005). Therefore, it is of great relevance to understand the ecological role of tapirs and to guarantee their conservation as functional elements of the very ecosystems they inhabit. In addition, future decisions on the conservation of tapir populations and their habitat areas require actions based on the information gathered in field studies.

Tapirs are important given their unique evolution and their role in promoting the coexistence of species by controlling recruitment (eating seedlings or seeds) and by promoting the seed dispersal of many species. Despite their endangered status all along their distribution range, the information available on their ecology, populations and the interactions with other species is limited. Further studies on tapirs are necessary, especially those focused on the ecological cascade effects on tapir defaunated sites and on the ecological consequences of the disruption of their movement patterns.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1 List of fruit species reported in tapir dung of Baird's tapir.

Figure S1 Families and number of species per family represented in the species potentially dispersed by lowland, Baird's and mountain tapirs.

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