BIOTROPICA
THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 0(0): 1–9 2017 10.1111/btp.12507

White-tailed deer as the last megafauna dispersing seeds in Neotropical dry forests: the role of fruit and seed traits

Andrea Jara-Guerrero[1], **Gema Escribano-Avila**[1,2,4], **Carlos Iván Espinosa**[1], **Marcelino De la Cruz**[3], and **Marcos Méndez**[3]

[1] Departamento de Ciencias Biológicas, Universidad Técnica Particular de Loja, CP.: 11-01-608 Loja, Ecuador

[2] IMEDEA- Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Esporles, Illes Balears, Spain

[3] Departamento de Biología y Geología, Física y Química Inorgánica, Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, E-28933 Madrid, Spain

ABSTRACT

Endozoochory is a prominent form of seed dispersal in tropical dry forests. Most extant megafauna that perform such seed dispersal are ungulates, which can also be seed predators. White-tailed deer (*Odocoileus virginianus*) is one of the last extant megafauna of Neotropical dry forests, but whether it serves as a legitimate seed disperser is poorly understood. We studied seed dispersal patterns and germination after white-tailed deer gut passage in a tropical dry forest in southwest Ecuador. Over 23 mo, we recorded *ca* 2000 seeds of 11 species in 385 fecal samples. Most seeds belonged to four species of Fabaceae: *Chloroleucon mangense*, *Senna mollissima*, *Piptadenia flava*, and *Caesalpinia glabrata*. Seeds from eight of the 11 species dispersed by white-tailed deer germinated under controlled conditions. Ingestion did not affect germination of *C. mangense* and *S. mollissima*, whereas *C. glabrata* showed reduced germination. Nevertheless, the removal of fruit pulp resulting from ingestion by white-tailed deer could have a deinhibition effect on germination due to seed release. Thus, white-tailed deer play an important role as legitimate seed dispersers of woody species formerly considered autochorous. Our results suggest that more research is needed to fully understand the ecological and evolutionary effects of the remaining extant megafauna on plant regeneration dynamics in the dry Neotropics.

Abstract in Spanish is available with online material.

Key words: anachronistic traits; deinhibition; dry fibrous pulp; germination; gut passage; herbivore; legume; megafauna fruits.

Seed dispersal is a key process in the life of a plant because it promotes genetic connectivity and diversity of plant communities (Nathan & Muller-Landau 2000, Jordano *et al.* 2007), as well as for the colonization of vacant habitats (Escribano-Avila *et al.* 2014). Zoochory (seed dispersal by animals) is a major dispersal syndrome in tropical forests (Howe & Smallwood 1982, Jordano 2000), including dry tropical ecosystems, where fruit availability is seasonally limited (Bullock 1995, Jordano 2000, Jara-Guerrero *et al.* 2011). Not all dispersers are equally effective in tropical systems (Brodie *et al.* 2009, McConkey & Brockelmanm 2011). Large-sized dispersers, like mammals, have no limitations of gape width and present higher movement capacity and gut retention time, thus generating more diverse, long-distance dispersal patterns than smaller dispersers (Jordano *et al.* 2007, Nathan *et al.* 2008, O′Farrill *et al.* 2013). Therefore, large-sized mammals (>35 kg) are especially important endozoochorous species, because they are long-distance dispersers of many seeds of various sizes (Escribano-Ávila *et al.* 2015).

The extinct Neotropical megafauna consisted mostly of wide trophic-range herbivores (Corlett 2013). The role of herbivorous megafauna as effective seed dispersers has been challenged due to the low probability of seeds surviving passage through the gut (Janzen 1981, Bodmer 1991, Picard *et al.* 2015). For instance, tapirs (*Tapirus terrestris*), the largest members of the extant Neotropical megafauna, have been identified as seed predators, (Janzen 1981) or effective seed dispersers (O′Farrill *et al.* 2013), depending on the plant species. One of the few tropical studies comparing seed dispersal by different species of deer, peccaries, and tapirs, showed that 0.4–1 cm seeds had better survival probabilities than larger ones (Bodmer 1991). While deer and peccaries acted mainly as seed predators, almost half of the seeds dispersed by tapirs were still viable (Bodmer 1991). These findings highlight the species-specific seed-dispersal effects of large herbivores, the effectiveness if which depends on not only their own characteristics, but also seed traits (*e.g.*, size and shape) (Janzen 1982, O′Farrill *et al.* 2013, Albert *et al.* 2015). For example, small round seeds seem more resistant to gut passage and suffer less damage from chewing (Mouissie *et al.* 2005).

White-tailed deer are among the last extant and common megafauna inhabiting Neotropical dry forests (NTDFs) (Ficcarelli *et al.* 2003), probably the most endangered tropical biome due to deforestation and climate change (Janzen 1988, Miles *et al.* 2006). Given their body size and broad diet, white-tailed deer are likely to disperse a wide spectrum of plant species (Myers *et al.* 2004, Williams *et al.* 2008), which may include the so-called 'anachronistic fruits' (*i.e.*, fruits dispersed by Pleistocene megafauna; Janzen & Martin 1982, Guimarães *et al.* 2008). In addition, white-tailed

Received 27 February 2017; revision accepted 10 August 2017.
[4]Corresponding author; e-mail: gema.escribano.avila@gmail.com

deer are long-distance dispersers (Myers *et al.* 2004, Williams *et al.* 2008). Therefore, dispersal by white-tailed deer may promote functional connectivity between fragmented patches (*sensu* Auffret *et al.* 2017), as well as aid NTDF species to track new available habitats resulting from climate change (Cain *et al.* 2000). Hence, similar to their extinct counterparts or to tapirs in rainforests, white-tailed deer may play a relevant ecosystem function. Unfortunately, most studies about seed dispersal by white-tailed deer have been conducted in temperate areas of North America and mainly focused on invasive herbaceous species (Williams *et al.* 2008, Habeck & Schultz 2015). The scarce literature about dispersal of NTDF species by white-tailed deer reports anecdotic dispersal events of a handful of species (*Spondias mombin*: Janzen 1985, *Opuntia* sp.: González-Espinosa & Quintana-Ascencio 1986, *Maximiliana maripa*: Fragoso 1997, *Spondias purpurea, Brosimum alicastrum, Jacquinia pungens*: Arceo *et al.* 2005) and fails to provide crucial data on the capacity of seed germination of NTDF woody species after white-tailed deer gut passage. Accordingly, we do not know whether white-tailed deer are legitimate seed dispersers or seed predators of NTDF species (Bodmer 1991). Ungulate species differ greatly in diet, suggesting that fruit consumption is not random and therefore acts as an ecological filter for species with particular traits (Albert *et al.* 2015). Thus, we expect that traits of fruits and seeds will determine the role of white-tailed deer as seed dispersers or seed predators.

In this study, we address the role of white-tailed deer as legitimate seed dispersers in a well-preserved NTDF in Ecuador. We asked several specific questions: (1) Which plant species are more frequently dispersed by white-tailed deer? (2) Are white-tailed deer consuming fruits and seeds with a particular subset of traits? and (3) Do seeds of those species differentially survive and germinate after white-tailed deer gut passage?

METHODS

Study area.—We conducted this study at the Arenillas Ecological Reserve (REA), located in El Oro province, Southwest Ecuador (03°34′15.44″ S; 80°08′46.15″ E, 30 m asl), (Figure S1). The REA has been protected for approximately 60 yr, formally included in the National System of Protected Areas of Ecuador since 2001 (BirdLife International 2014). Annual mean precipitation is 667 mm, mainly concentrated between January and May, with a strong dry season from June to December. Mean maximum daily temperature is 25.2°C, with a variation of 3.4°C between the coldest and warmest month (Espinosa *et al.* 2015).

The REA covers 13,170 ha of one of the last remnants of NTDFs on the Ecuadorian Pacific Coast (Espinosa *et al.* 2015). The most conspicuous tree species in the area are *Tabebuia chrysantha* and *T. billbergii* (Bignoniaceae), along with *Cynophalla mollis* (Capparaceae), *Erythroxylum glaucum* (Erythroxylaceae), *Eriotheca ruizii* (Malvaceae), *Leucaena trichodes, Chloroleucon mangense* (Fabaceae), and *Cochlospermum vitifolium* (Bixaceae). In the central REA, one of the best- preserved areas, we established a 9-ha permanent plot consisting of transitional vegetation between tropical dry forest and lowland dry scrubland (Figure S1). Since 2009, all individual trees with a diameter at breast height ≥5 cm have been inventoried within the plot (Jara-Guerrero *et al.* 2015), and we inventoried shrubs and subshrubs in the central hectare of the plot. A total of 49 woody species have been recorded. Fabaceae is the predominant family, with 10 species (or 20 percent) of the recorded individuals.

Natural history of white-tailed deer.—*Odocoileus virginianus*, white-tailed deer, is the only deer species reported for the REA. Although distribution of *Mazama americana* includes areas of NTDF of southwestern Ecuador, there are no records for the REA. Recently, camera trap sampling in the area did not detect *M. americana* but pointed to *O. virginianus* as the mammal species with the greatest number of records (0.13 individuals/day/trap; Espinosa *et al.* 2016). This species is a large cervid (50–120 kg), usually solitary, but also forming small groups. Because of its robust body and branched horns, it is more common in open areas. Like other deer, it is a herbivorous ruminant (Eisenberg & Redford 1999); as a browser, it feeds mainly on leaves, twigs, and young shoots of trees and shrubs (Hoffman 1989), but also consumes fruits during the dry season (Tirira 2007).

Quantitative dispersal pattern: seed diversity and abundance in feces.—We established a 3.4 km transect in the central portion (4.8 ha) of our 9-ha permanent plot, and surveyed this transect monthly for 23 mo, between October 2011 and September 2013. Each month, we collected all white-tailed deer feces detected in a 2-m-wide band along the transect. We considered each group of spatially aggregated pellets as an individual sample. Each fecal sample was placed in a plastic bag and labeled, and air-dried in the lab. In addition, we collected mature fruits from plants within the study area to build a reference seed collection for identification of the dispersed seeds.

All seeds present in the feces were extracted by sample disaggregation. We identified each seed with the aid of the reference seed collection and scored the number of seeds per plant species for each fecal sample. We visually inspected seeds to assess viability, *i.e.* identify possible damage during the ingestion, physical damage signals or putrefaction.

For the most frequently dispersed seeds, we evaluated the overlap between the period of fallen fruits and that of white-tailed deer dispersal. The fall of fruits upon ripening (or even before) has been considered a part of the megafauna dispersal syndrome (Janzen & Martin 1982). A parallel study of seed rain for trees and shrubs (Jara-Guerrero 2015) provided data used to compare the phenology of seed-fruit fall with the presence of the most frequently encountered seeds in our samples: *Chloroleucon mangense, Caesalpinia glabrata, Leucaena trichodes, and Senna mollissima*. The species *Piptadenia flava* was excluded as no seeds were detected in the seed traps. Additionally, we explored the match between seed abundance in the seed rain and presence in white-tailed deer feces, by comparing the percentage of seeds in our samples with the total availability of seeds in the seed rain, as an indirect measure of availability.

FRUIT AND SEED TRAITS.—To analyze if white-tailed deer were consuming fruits and seeds with a particular subset of traits, we compiled information for six traits in the 49 species present in the plot (Table S1). We classified fruit type in seven categories following Jara-Guerrero *et al.* (2011), and measured fruit length and width to the nearest mm in samples collected in the study site. Number of seeds per fruit, seed mass, and volume were measured in the same samples or taken from the literature (Romero-Saritama & Pérez-Ruíz 2016). We used only the seed volume to represent the seed size. Dispersal syndromes – zoochory, anemochory, or autochory – were scored following Jara-Guerrero *et al.* (2011).

GERMINATION PATTERNS.—Seeds dispersed by white-tailed deer were sown in plastic trays filled with moist peat and kept under greenhouse conditions. To record the presence of unobserved seeds, we sowed the remaining fecal material with the seeds. We monitored germination for 90 d to determine the germination percentage. We considered a seed germinated when the radicle emerged from the seed coat. Seeds that failed to germinate were visually inspected for possible damage after sowing.

To assess the effect of gut passage on seed germination, we compared the germination capacity of white-tailed deer-dispersed vs. control seeds. Control seeds were collected in June and July 2013 from at least five trees per species. We randomly selected 100 control seeds and separated them into four trays of 25 seeds, sown under the same conditions as dispersed seeds. We used three species that were abundant enough in white-tailed deer feces ($N \geq 70$, Table 1): *Chloroleucon mangense*, *Caesalpinia glabrata,* and *Senna mollissima*. Our experiment assessed the scarification effect resulting from white-tailed deer gut passage, given that pulp from control seeds was removed by hand, but not the deinhibition effect resulting from pulp removal, as no intact fruits were sown (Samuels & Levey 2005, Robertson *et al.* 2006).

TABLE 1. *Seed frequency and abundance in white-tailed deer feces and germination.*

Family	Species	*F*	*G/N*
Fabaceae	*Chloroleucon mangense*	206	136/1183
	Caesalpinia glabrata	32	6/75
	Leucaena trichodes	10	0/12
	Piptadenia flava	26	11/104
	Senna mollissima	96	13/544
	Vigna sp.	11	3/16
Cactaceae	Unidentified	1	1/1
Convolvulaceae	Unidentified	6	0/10
Primulaceae	*Bonellia sprucei*	1	1/1
Rubiaceae	*Randia aurantiaca*	2	0/7
Unidentified		7	1/8

Seeds of plant species present in 385 white-tailed deer feces collected during 23 mo. *F*: Frequency, number of fecal samples containing at least one seed of a given species. *G/N*: Number of germinated seeds (*G*) and total abundance of dispersed seeds (*N*). Seeds coded as *Unidentified* showed similar characteristics and were assumed to belong to the same species.

DATA ANALYSIS.—To assess if white-tailed deer were dispersing fruits and seeds with a particular subset of traits, we performed two kinds of tests. We used a Mann–Whitney test for each quantitative variable to test whether the distributions of fruit and seed traits differ between dispersed and not dispersed. We used a Fisher exact test to explore whether fruit type was associated with dispersal or non-dispersal by white-tailed deer. We used the functions wilcox.test and fisher.test implemented in R. These tests were performed only including the species for which trait values were available (Table S1): fruit length, 40 species; fruit width, 43; seed volume, 39; number of seeds per fruit, 35; and fruit type, 50. The percentage of species used in the analyses, with respect to those present, varied between 78–100 percent.

To evaluate the effect of scarification after gut passage on seed germination, we fitted Generalized Linear Models (GLM) with germination occurrence as the response variable and origin (white-tailed deer dispersal or control) as the independent variable. We considered a binomial distribution of errors and a logit link function. All data analyses were performed in the R environment (R Core Team 2016).

RESULTS

QUANTITATIVE DISPERSAL PATTERN: SEED DIVERSITY AND ABUNDANCE IN FECES.—A total of 385 white-tailed deer fecal samples were recorded, mainly detected between the end of the rainy season (May) and the end of the dry season (January), with an abundance ranging between 0 and 86 feces per month (mean $\pm$ SE = 19 $\pm$ 4). 65.3 percent of fecal samples contained seeds. The number of seeds ranged from one to 54 (mean $\pm$ SE = 7.8 $\pm$ 0.59 seeds per fecal sample, Table S2), giving a total of 1961 seeds belonging to 11 species from at least five families (Table 1). We found up to five species in a fecal sample, although 57 percent contained seeds of a single species. All recorded seeds were intact with no apparent damage to the seed coat. The most frequent and abundant species dispersed by white-tailed deer was *Chloroleucon mangense*, followed by *Senna mollissima*, *Caesalpinia glabrata*, and *Piptadenia flava* (Table 1). Although the period of seed rain and white-tailed deer dispersal sampling did not completely coincide, there was a trend that showed white-tailed deer dispersal of these species several months after peak fruit fall (Figure S2). Among the species dispersed by white-tailed deer, the match between seed abundance in feces and seed rain was variable (Fig. 1). From the ten species present in the seed rain, *C. mangense* was abundant both in the seed rain and in feces (Fig. 1), while *C. glabrata* showed a low abundance in both. Conversely, *R. aurantiaca, S. mollissima, L. trichodes,* and *Vigna* sp. were abundant in the seed rain but very scarce in our samples (Fig. 1). Among the other four species recorded in the white-tailed deer feces that were absent in the seed rain sampling, *P. flava* was most abundant.

CHARACTERISTICS OF THE FRUITS DISPERSED.—The most frequent fruits dispersed by white-tailed deer were dehiscent legumes, 61–250 mm in length and 13–20 mm in width with 8–15 seeds, and

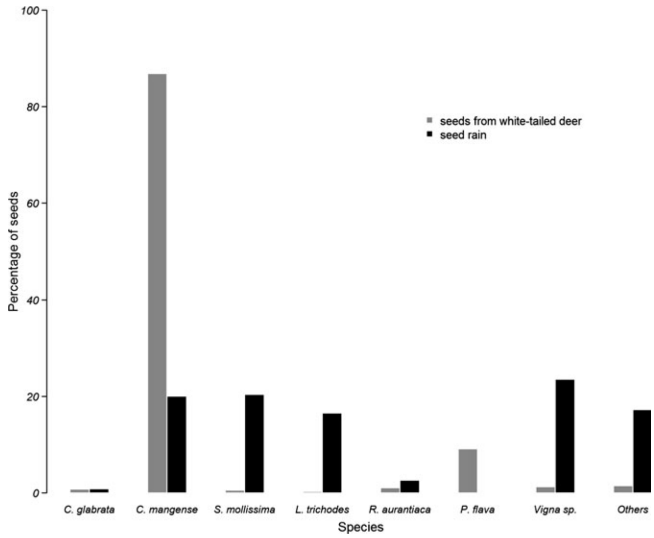

FIGURE 1. Percentage of seeds per species in white-tailed deer feces and in the seed traps, with respect to the total number of seeds in white-tailed deer feces (N = 824) and in seed traps (N = 287) from October 2011 to July 2012.

varying in seed volume from 12 to 323 mm^3, and in seed mass from 0.016 to 0.176 g. Large-sized berries (length: 30–55 mm; diameter: 17–40 mm) and dehiscent capsules were the other fruit types dispersed by white-tailed deer, though in much lower amounts than dry pods (Table S1). This pattern was confirmed by the Fisher test, which indicated significant association between fruit type and dispersal by white-tailed deer (Fig. 2). Mann–Whitney tests showed significant differences between species dispersed and not dispersed by white-tailed deer in relation to fruit length, fruit width, and number of seeds, but not seed volume (Fig. 2).

Compared to the average available fruit, white-tailed deer consumed fruits that were longer, wider, and had more seeds. The fruit types dispersed by white-tailed deer were primarily legumes, although berries were found in a low frequency; drupes and achenes were never recorded in our samples.

Germination after white-tailed deer gut passage.—Eight out of the eleven plant species dispersed by white-tailed deer germinated (Table 1). From the four most frequent and abundant species, three (*C. mangense*, *P. flava*, and *C. glabrata*) presented a germination percentage around 10 percent, while only 2 percent of *S. mollissima* seeds germinated. A very small sample size was available for the remaining species (Table 1). From *B. sprucei* and the Cactaceae species, only one seed each was present in the feces and both species germinated, while seeds of *Randia aurantiaca, Leucaena trichodes*, and the unidentified Convolvulaceae species did not germinate. We did not find any external damage on seeds that failed to germinate.

No significant differences in germination percentage were found for *C. mangense* and *S. mollissima* seeds after white-tailed deer gut passage, compared to controls (Fig. 3 and Table 2). However, we found a significant reduction in germination capacity (10% vs. 90%) for *C. glabrata* gut-passed seeds compared to control seeds (Fig. 3; Table 2).

DISCUSSION

White-tailed deer dispersal patterns in Neotropical Dry Forest.—White-tailed deer was a frequent seed disperser in the NTDF of southwestern Ecuador. First, white-tailed deer consumed, and therefore potentially dispersed by via endozoochory, 20 percent (10 out of 49) of all woody species in the study area, and 35 percent (10 out of 28 species) of those species that can be dispersed by animals (Table S1). In addition, one climber species, not sampled in the seed rain experiment, was found in the fecal samples. Although only a few species were dispersed in large numbers, these are among the most frequent and abundant species in the study area (Fabaceae species). Second, 65 percent of white-tailed deer feces contained seeds, indicating that dry fruits are a regular component of its diet. Thus, white-tailed deer moved seeds of 11 species belonging to five families. Third, plant species dispersed by deer shared particular fruit traits, such as large size and many seeds. The most frequently dispersed fruits were dry pods from legumes, which had fibrous pulp but no apparent adaptations for assisted dispersal and were previously considered autochorous (Jara-Guerrero *et al.* 2011, López-Martínez *et al.* 2013). Arceo *et al.* (2005) showed that species commonly dispersed by white-tailed deer fructified during the dry months, which was also the case in this study. During the dry months, the proportion of feces with seeds was higher than in the rainy season. However, this pattern must be taken with caution due to the low quantity of feces recorded during the rainy months, which could be related to a lower detectability rate (Wiles 1980, Aulak & Babińska-Werka 1990). Fourth, contrary to our expectations, white-tailed deer dispersal did not adversely affect seed survival or germination of the three species evaluated; the majority were able to germinate to some extent. Together, these findings point to white-tailed deer a pivotal seed-dispersal species, maintaining regeneration dynamics and colonization capacity.

Anemochory and zoochory are considered the most relevant dispersal modes in NTDFs (Jara-Guerrero *et al.* 2011, López-Martínez *et al.* 2013, Hilje *et al.* 2015). Among zoochorous species, birds and bats seem the most relevant dispersers (Nassar *et al.* 2013), with a minor role recognized for reptiles and terrestrial mammals (but see Benítez-Malvido *et al.* 2003 and Hilje *et al.* 2015). Specialist frugivorous bats (Phyllostomidae) are rather common in NTDF assemblages (4–10 species: Ríos-Blanco & Pérez-Torres 2015) in contrast to specialist frugivorous birds (1–3 plant species: Ramos-Robles *et al.* 2016), which are usually absent (Nassar *et al.* 2013). According to our study, white-tailed deer disperse a similar number of species as other NTDF specialized frugivores, although this comparison is made from different study areas and therefore should be taken with caution. However, it seems clear that the species and fruit type dispersed by white-tailed deer (mainly dry legumes) are distinctive and complementary to those dispersed by other frugivores (fleshy drupes, berries,

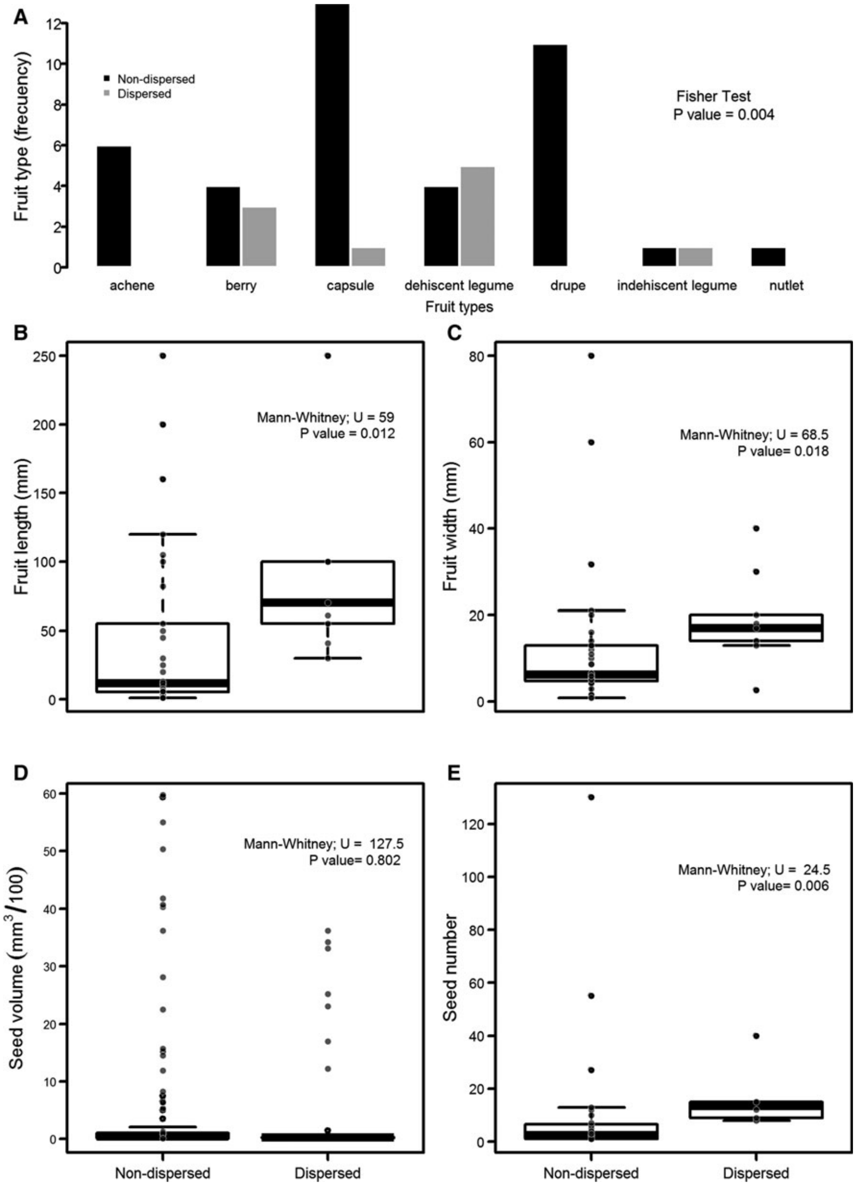

FIGURE 2. (A) Frequency of fruit types dispersed (black bars) and not dispersed (gray bars) by white-tailed deer. Box plots for (B) fruit length, (C) fruit width (D), seed volume, and (E) seed number of fruits dispersed and not dispersed by white-tailed deer. Segments in box plots indicate minimum and maximum values, the box denotes first and third quartile. Bolded line denotes the median value.

and syconia, Ramos-Robles *et al.* 2016, Ríos-Blanco & Pérez-Torres 2015). In addition, the longer seed dispersal distances (up to 3–5 km) performed by white-tailed deer (Myers *et al.* 2004, Williams *et al.* 2008), compared to smaller-bodied frugivores, such as birds and bats (up to 1 km, Carlo *et al.* 2013, Abedi-Lartey *et al.* 2016, González-Varo *et al.* 2017, Jordano 2017), probably make this species a relevant and complementary disperser of NTDF plants.

Interaction between white-tailed deer and fruit-seed traits: the importance of the deinhibition effect for indehiscent species.—Seed survival after ingestion by ungulates depends mainly seed treatment, such as chewing, swallowing, or spiting (Gardener *et al.* 1993, Myers *et al.* 2004, Mouissie *et al.* 2005). According to our results, white-tailed deer defecated undamaged seeds. Thus, the negative effects found on germination for *C. glabrata* seem to be due to excessive scarification, likely related to seed size, and not to chewing. Herbivore body size and feeding type (*i.e.*, grazer or browser) greatly influence seed retention time, which in some cases has been negatively related to seed survival probability (Janzen 1982, Bodmer 1991, Picard *et al.* 2015). White-tailed deer, as browsers, consume plant materials that require a rumination process. This may lead to a strong scarification of seeds that, together with high acid secretion in white-

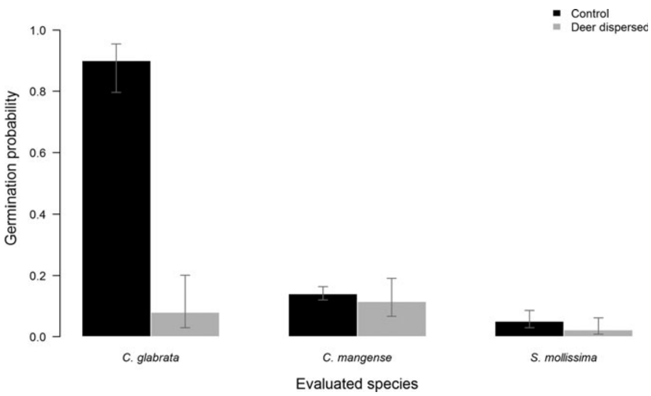

FIGURE 3. Germination probability (mean ± SD) resulting from seeds dispersed and not dispersed by white-tailed deer.

tailed deer gut (Clauss *et al.* 2008), may produce internal damage to seed embryos. *Caesalpinia glabrata* seeds are twice the size of all other studied species that were not negatively affected by gut passage. A larger seed size implies greater surface contact and exposure to digestive effects, which may explain the costs of herbivore gut passage on seed germination, as previously seen in other large-seeded species (Pakeman *et al.* 2002, Mouissie *et al.* 2005).

A seldom recognized advantage of endozoochory is the release of seeds from the pulp (Miller 1995, Samuels & Levey 2005). This depulping can entail a positive effect on seed germination (*i.e.*, deinhibition effect), by removing inhibitory substances present in the pulp, (Traveset *et al.* 2007) and removing pathogens and attractants to seed predators (Fricke *et al.* 2013). For the dehiscent species studied, whose seeds are spontaneously released, the deinhibition effect may be irrelevant, but it may be important for the fleshy or indehiscent legumes species dispersed by white-tailed deer, such as *C. glabrata*. Legumes are known to suffer high rates of pre-dispersal loss owing to bruchiids and other beetles. In addition, ongoing research (GEA, unpubl. data) suggests that several species dispersed by white-tailed deer show very low rates of germination when kept in the fruits. Notably, <1 percent of *C. glabrata* seeds inside pods germinated, while released seeds germinated up to 80 percent (GEA, unpubl. results). For *C. glabrata*, the beneficial deinhibiton effect resulting from seed release of the dry, thick, fibrous pulp may offset the excessive scarification, yielding an overall positive effect of white-tailed deer dispersal.

The few experiments on gut passage that have utilized intact fruits as controls, found that deinhibition had either a species-specific response, or a greater effect than scarification, on germination success (Robertson *et al.* 2006, Traveset *et al.* 2007). Therefore, the release of seeds from indehiscent pods may be an underestimated service performed by white-tailed deer with a net effect on plant regeneration. The dependence of plant regeneration on the release of seeds from inhibition is poorly understood and deserves further attention, especially in highly defaunated ecosystems in which plants may be deprived of their dispersers.

An ungulate dispersal syndrome previously overlooked in dry ecosystems.—Several studies report that woody species with thick pods, dry fibrous pulp, and no apparent adaptations for animal dispersal, are frequently consumed by large herbivores (Gardener *et al.* 1993, Granados *et al.* 2014). Similar results were found in this study, suggesting a *herbivore dispersal syndrome*. Contrary to Janzen (1984), this may not be related to the foliage but to diaspore characteristics (*i.e.*, pods), mainly of Fabaceae species. Apart from African savannas, where the relationship between *Acacia* species and large African herbivores has been documented (Tybirk 1997), a *herbivore dispersal syndrome* has rarely been considered for seed dispersal in NTDFs or other dry ecosystems. Yet, in a recent review of seed dispersal and frugivory by large herbivores in Asia, pods were a common fruit type among those consumed by several herbivore families, especially elephants, bovids, and large cervids (Sridhara *et al.* 2016). Thus, the *herbivore dispersal*

TABLE 2. *Effect of white-tailed deer dispersal on germination.*

Deviance table				Parameters estimates				
Model	Residual df	Deviance	Pr(>X^2)	Fixed Factor	Estimate	SE	z-Value	*P*(>|z|)
Caesalpinia glabrata								
NULL	174			Intercept	**2.197**	**0.333**	**6.592**	**<0.001**
Treatment	**173**	**134.12**	**<0.001**	Dispersed	**−4.64**	**0.54**	**−8.58**	**<0.001**
Chloroleucon mangense								
NULL	1282			Intercept	**−1.82**	**0.29**	**−6.30**	**<0.001**
Treatment	1281	0.53	0.47	Dispersed	−0.23	0.30	−0.75	0.46
Senna mollissima								
NULL	643			Intercept	**−2.94**	**0.46**	**−6.42**	**<0.001**
Treatment	642	2.15	0.14	Dispersed	−0.85	0.54	−1.56	0.12

Deviance table (left) of the GLMs performed. Treatment is a factor with two levels: Dispersed, seeds recovered from deer feces; and Control, seeds collected from the trees. Note that degrees of freedom (df) differ among species according to the number of seeds used for testing the effects of deer dispersal. Parameter estimates, standard errors (SE), and *P*-values are shown (right). Significant effects are shown in bold.

syndrome warrants further research; it may provide new insights about why species previously considered as autochorous have been surprisingly successful colonizers (Pakeman 2001, Jara-Guerrero *et al.* 2015). Therefore, in our study area, white-tailed deer dispersal might explain the random spatial distribution of *Senna mollissima* (Jara-Guerrero *et al.* 2015), instead of the aggregated distribution pattern expected for autochorous species. On the contrary, the other species dispersed by white-tailed deer, previously classified as autochorous, show the expected spatial pattern (Jara-Guerrero *et al.* 2015). Furthermore, white-tailed deer could move seeds and facilitate gene flow, but without modifying the aggregate distribution pattern. Other factors, such as differences in seed germination and survival, might be related to these differences in the white-tailed deer dispersal effects among species.

Megafauna dispersing megafauna fruits.—Previous evidence showed that white-tailed deer may disperse seeds matching the description of *megafauna fruits,* those with traits that extinct megafauna species would have consumed (Janzen & Martin 1982, Guimarães *et al.* 2008). This is also supported by our results, since species regularly dispersed by white-tailed deer were large, brownish fruits, with dry fibrous pulp, usually indehiscent and contained in thick pods (Janzen 1984, Janzen & Martin 1982, Gautier-Hion *et al.* 1985). The large, fleshy-fruited species occasionally dispersed by white-tailed deer in this and previous studies also match the megafauna fruits (Janzen 1985, González-Espinosa & Quintana-Ascencio 1986, Fragoso 1997, Arceo *et al.* 2005). Another trait related to the megafauna dispersal syndrome is high availability of fruits on the forest floor (Janzen & Martin 1982). In this study, white-tailed deer dispersed seeds after peak fruit fall, indicating those fruits were available on the ground. White-tailed deer, together with tapirs, peccaries, and a handful of other cervids, are the only extant Pleistocene megafauna in the NTDF that may function as seed dispersers. These species present unique evolutionary and morphological characteristics that make them relevant and likely non-replaceable, from an ecological functioning perspective (Malhi *et al.* 2016). Our findings provide further support to such a relevant and unique ecological role: plants with larger diaspores are not adapted to other ways of dispersal, making white-tailed deer a conservation priority (Pires *et al.* 2014). It has recently been suggested that medium to large cervids may replace the ecological functions played by larger megaherbivores, such as tapirs and elephants, at higher risk of extinction and already gone in many ecosystems. This highlights the conservation value of common and extant megafauna, such as medium to large deer (Sridhara *et al.* 2016).

Limitations and further research priorities.—Despite the robustness of our data and the clear importance of white-tailed deer as seed dispersers, we acknowledge that this study included only one forest community. Accordingly, further research along the Neotropics should be performed to establish the generality of white-tailed deer as an important seed disperser. This can also be extended to other ecosystems in which megaherbivores are still present, as there is a serious empirical gap in this respect. Clearly, further efforts should try to unveil the dispersal networks established between megaherbivores and fruiting plants, their functional traits, and the ecological and evolutionary consequences of such interaction.

CONCLUSIONS

White-tailed deer effectively dispersed at least 11 native woody species typical of NTDFs, about half of them were considered autochorous. Species dispersed by white-tailed deer had fruit traits matching the megafauna fruits, with large size and numerous seeds; most of these were dry pods with fibrous pulp, which stay on the floor for many months. This dispersal service is especially relevant considering these fruits could not be dispersed by other means in the study area. Even the plant species that suffered a decrease in germination due to white-tailed deer gut passage seems to benefit from other dispersal services such as pod-release. Therefore, white-tailed deer played a relevant ecological role in NTDFs by dispersing viable seeds of a wide array of species, contributing to local recruitment and long-distance dispersal. This is particularly important in NTDFs, given their high levels of fragmentation and the possibility of recovery in newly available niches resulting from climate change (Cain *et al.* 2000, Miles *et al.* 2006). White-tailed deer are among the few extant megafauna functioning as seed dispersers in the NTDF. Consequently, white-tailed deer dispersal services and associated ecological functions are likely unique.

ACKNOWLEDGMENTS

This work was partially supported by project PROY_CCNN_1054 financed by Universidad Técnica Particular de Loja. The authors thank Ministerio del Ambiente del Ecuador for facilities and operational support during field work. GEA is grateful to the Prometeo Program of the Ecuadorian National Secretariat for Education, Science and Technology for the funding provided for her post-doctoral stay in Loja, Ecuador and further support during the period of manuscript writing was provided by Spanish ministry for Science (Juan de la Cierva-Formación program). We are grateful to two anonymous reviewers and the subject matter editor T. Carlo for their valuable suggestions and comments.

DATA AVAILABILITY

Data available from the Dryad Repository: https://doi.org/10.5061/dryad.43d3g (Jara-Guerrero *et al.* 2017), and *ámbar*: http://ambar.utpl.edu.ec/dataset/deer-seed-dispersal.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Map and location of the study area.

FIGURE S2. Monthly proportion of seed density in seed rain and white-tailed deer feces for the four most abundant species in white-tailed deer feces.

TABLE S1. *Fruit and seed traits of woody species in the 9 ha plot of Arenillas Ecological Reserve.*

TABLE S2. *Number of feces collected each month and number of feces with seeds.*

LITERATURE CITED

Abedi-Lartey, M., D. K. Dechmann, M. Wikelski, A. K. Scharf, and J. Fahr. 2016. Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. Glob. Ecol. Conserv. 7: 12–24.

Albert, A., A. G. Auffret, E. Cosyns, S. A. O. Cousins, B. D'Hondt, C. Eichberg, A. E. Eycott, T. Heinken, M. Hoffmann, B. Jaroszewicz, J. E. Malo, A. Mårell, M. Mouissie, R. J. Pakeman, M. Picard, J. Plue, P. Poschlod, S. Provoost, K. A. Schulze, and C. Baltzinger. 2015. Seed dispersal by ungulates as an ecological filter: A trait-based meta-analysis. Oikos 124: 1109–1120.

Arceo, G., S. Mandujano, S. Gallina, and L. Perez-Jimenez. 2005. Diet diversity of white tailed white-tailed deer (*Odocoileus virginianus*) in a tropical dry forest in Mexico. Mammalia 6: 159–168.

Auffret, A. G., Y. Rico, J. M. Bullock, D. A. Hooftman, R. J. Pakeman, M. B. Soons, A. Suarez-Esteban, A. Traveset, H. H. Wagner, and S. A. Cousins. 2017. Plant functional connectivity–integrating landscape structure and effective dispersal. J. Ecol. https://doi.org/10.1111/1365-2745.12742.

Aulak, W., and J. Babińska-Werka. 1990. Estimation of roe deer density based on the abundance and rate of disappearance of their faeces from the forest. Acta Theriol. 35: 111–120.

Benítez-Malvido, J., E. Tapia, I. Suazo, E. Villaseñor, and J. Alvarado. 2003. Germination and seed damage in tropical dry forest plants ingested by iguanas. J. Herpetol. 37: 301–308.

BirdLife International. 2014. Important bird areas factsheet: Reserva Ecológica Arenillas. Downloaded from http://www.birdlife.org on 07/10/2014

Bodmer, R. 1991. Strategies of seed dispersal and seed predation in amazonian ungulates. Biotropica 23: 255–261.

Brodie, J., O. E. Helmy, W. Y. Brockelman, and J. L. Maron. 2009. Functional differences within a guild of tropical mammalian frugivores. Ecology 90: 688–698.

Bullock, S. H. 1995. Plant reproduction in neotropical dry forests. *In* S. Bullock, H. Mooney, and E. Medina (Eds.). Seasonally dry tropical forests, pp. 277–297. Cambridge University Press, Cambridge, UK.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. Am. J. Bot. 87: 1217–1227.

Carlo, T. A., D. García, D. Martínez, J. M. Gleditsch, and J. M. Morales. 2013. Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. Ecology 94: 301–307.

Clauss, M., T. Kaiser, and J. Hummel. 2008. The morphophysiological adaptations of browsing and grazing mammals. *In* I. J. Gordon, H. H. T. Prins (Eds.). The ecology of browsing and grazing, pp. 47–88. Springer, Berlin, Heidelberg.

Corlett, R. 2013. The shifted baseline: Prehistoric defaunation in the tropics and its consequences for biodiversity conservation. Biol. Conserv. 163: 13–21.

Eisenberg, J. F., and K. H. Redford 1999. Mammals of the neotropics. 3. The central neotropics: Ecuador, Perú, Bolivia, Brasil. The University of Chicago Press, Chicago, IL.

Escribano-Avila, G., M. Calvino-Cancela, B. Pías, E. Virgós, F. Valladares, and A. Escudero. 2014. Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. J. Appl. Ecol. 51: 1701–1711.

Escribano-Ávila, G., B. Pías, A. Escudero, and E. Virgós. 2015. Importancia ecológica de los mamíferos frugívoros en la dinámica de regeneración de tierras abandonadas en ambientes mediterráneos. Ecosistemas 24: 35–42.

Espinosa, C. I., M. de la Cruz, A. Jara-Guerrero, E. Gusmán, and A. Escudero. 2015. The effects of individual tree species on species diversity in a tropical dry forest change throughout ontogeny. Ecography 39: 329–337.

Espinosa, C. I., A. Jara-Guerrero, R. Cisneros, J. D. Sotomayor, and G. Escribano-Ávila. 2016. Reserva Ecológica Arenillas ¿un refugio de diversidad biológica o una isla en extinción? Ecosistemas 25: 5–12.

Ficcarelli, G., M. Coltorti, M. Moreno-Espinosa, P. L. Pieruccini, L. Rook, and D. Torre. 2003. A model for the Holocene extinction of the mammal megafauna in Ecuador. J. S. Am. Earth Sci. 15: 835–845.

Fragoso, J. M. 1997. Tapir-generated seed shadows: Scale-dependent patchiness in the Amazon rain forest. J. Ecol. 85: 519–529.

Fricke, E. C., M. J. Simon, K. M. Reagan, D. C. Haak, D. J. Levey, J. A. Riffell, T. A. Carlo, and J. J. Tewksbury. 2013. When condition trumps location: Seed consumption by fruit-eating birds removes pathogens and attractants to seed predators. Ecol. Lett. 16: 1031–1036.

Gardener, D. J., G. McIvor, and A. Jansen. 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. J. Appl. Ecol. 30: 63–74.

Gautier-Hion, A., J. M. Duplaintier, R. Ouris, F. Feer, C. Sourd, J. P. DeCoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Moungazi, C. Roussilhon, and J. M. Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324–337.

González-Espinosa, M., and P. F. Quintana-Ascencio. 1986. Seed predation and dispersal in a dominant desert plant: Opuntia, ants, birds, and mammals. *In* A. Estrada and T. H. Fleming (Eds.). Frugivores and seed dispersal, pp. 273–284. Springer, Netherlands.

González-Varo, J. P., C. S. Carvalho, J. M. Arroyo, and P. Jordano. 2017. Unravelling seed dispersal through fragmented landscapes: Frugivore species operate unevenly as mobile links. Mol. Ecol. https://doi.org/10.1111/mec.14181

Granados, D., L. Tarango, G. Olmos, J. Palacio, F. Clemente, and G. Mendoza. 2014. Dieta y disponibilidad de forraje del venado cola blanca *Odocoileus virginianus thomasi* (Artiodactyla: Cervidae) en un campo experimental de Campeche, México. Rev. Biol. Trop. 62: 699–710.

Guimarães, Jr, P. R., M. Galetti, and P. Jordano. 2008. Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. PLoS One 3: e1745.

Habeck, C. W., and A. K. Schultz. 2015. Community-level impacts of white-tailed white-tailed deer on understory plants in North American forests: A meta-analysis. AoB Plants 7: plv119.

Hilje, B., J. Calvo-Alvarado, C. Jiménez-Rodríguez, and A. Sánchez-Azofeifa. 2015. Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica. Trop. Conserv. Sci. 8: 76–94.

Hoffman, R. R.. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. Oecología 78: 443–457.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13: 201–228.

Janzen, D. H. 1981. Digestive seed predation by a Costa Rican Baird's tapir. Biotropica 59: 59–63.

Janzen, D. H. 1982. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. Oikos 38: 150–156.

Janzen, D. H. 1984. Dispersal of small seeds by big herbivores: Foliage is the fruit. Am. Nat. 123: 338–353.

Janzen, D. H. 1985. *Spondias mombin* is culturally deprived in megafauna free forest. J. Trop. Ecol. 1: 131–155.

Janzen, D. H. 1988. Management of habitat fragments in a tropical dry forest: Growth. Ann. Mo. Bot. Gard. 75: 105–116.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: The fruits the gomphotheres ate. Science 215: 19–27.

Jara-Guerrero, A. 2015. Ecología de la dispersión de plantas en los bosques secos del suroccidente Ecuatoriano. PhD Dissertation. Universidad Politécnica de Madrid, España.

Jara-Guerrero, A., M. De La Cruz, C. Espinosa, M. Méndez, and A. Escudero. 2015. Does spatial heterogeneity blur the signature of dispersal syndromes on spatial patterns of woody species? A test in a tropical dry forest. Oikos 124: 1360–1366.

Jara-Guerrero, A., G. Escribano-Avila, G. Iván Espinosa, M. De la Cruz, and M. Méndez. 2017. Data from: White-tailed deer as the last megafauna dispersing seeds in Neotropical dry forests: The role of fruit and seed traits. Dryad Digital Repository. https://doi.org/10.5061/dryad.43d3g

Jara-Guerrero, A., M. Méndez, and M. De La Cruz. 2011. Seed dispersal spectrum of woody species in South Ecuadorian dry forests: Environmental correlates and the effect of considering species abundance. Biotropica 43: 722–730.

Jordano, P. 2000. Fruits and frugivory. *In* M. Fenner (Ed.). Seeds: The ecology of regeneration in plant communities (2nd Edition), pp. 125–165. CABI Publishing, Wallingford, UK.

Jordano, P. 2017. What is long-distance dispersal? And a taxonomy of dispersal events. J. Ecol. 105: 75–84.

Jordano, P., C. García, J. A. Godoy, and L. García-Castaño. 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proc. Natl Acad. Sci. USA 104: 3278–3282.

López-Martínez, J. O., L. Sanaphre-Villanueva, J. M. Dupuy, J. L. Hernández-Stefanoni, J. A. Meave, and J. A. Gallardo-Cruz. 2013. β-diversity of functional groups of woody plants in a tropical dry forest in Yucatan. PLoS One 8: e73660. https://doi.org/10.1371/journal.pone.0073660.

Malhi, Y., C. E. Doughty, M. Galetti, F. Smith, J. Svenning, and J. W. Terborgh. 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proc. Natl Acad. Sci. USA 113: 838–846.

McConkey, K., and W. Brockelmanm. 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. Ecology 92: 1492–1502.

Miles, L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33: 491–505.

Miller, M. F. 1995. *Acacia* seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. Afr. J. Ecol. 33: 194–210.

Mouissie, A. M., C. E. J. Van der Veen, G. F. Veen, and R. Van Diggelen. 2005. Ecological correlates of seed survival after ingestion by fallow white-tailed deer. Funct. Ecol. 19: 284–290.

Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139: 35–44.

Nassar, J., K. Stoner, L. Ávila-Cabadilla, M. do Espírito-Santo, C. Aranguren, J. A. Gonzpalez-Carcacía, J. M. Lobato-García, L. Olívio-Leite, M. Álvarez-Añorve, deMatos Brandao H., L. Dolabela-Falcao, and J. P. Rodríguez. 2013. Fruit-eating bats and birds of three seasonal tropical dry forests in the Americas. *In* A. Sánchez-Azofeifa, J. S. Powers, G. W. Fernandes, and M. Quesada (Eds.). Tropical dry forests in the Americas: Ecology, conservation, and management, pp. 173–211. CRC Press, New York.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15: 278–285.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. Trends Ecol. Evol. 23: 638–647.

O′Farrill, G., M. Galetti, and A. Campos-Arceiz. 2013. Frugivory and seed dispersal by tapirs: An insight on their ecological role. Integr. Zool. 8: 4–17.

Pakeman, R. J. 2001. Plant migration rates and seed dispersal mechanisms. J. Biogeogr. 28: 795–800.

Pakeman, R. J., G. Digneffe, and J. L. Small. 2002. Ecological correlates of endozoochory by herbivores. Funct. Ecol. 16: 296–304.

Picard, M., J. Papaïx, F. Gosselin, D. Picot, E. Bideau, and C. Baltzinger. 2015. Temporal dynamics of seed excretion by wild ungulates: Implications for plant dispersal. Ecol. Evol. 5: 2621–2632.

Pires, M. M., M. Galetti, C. I. Donatti, M. A. Pizo, R. Dirzo, and P. R. Guimarães, Jr. 2014. Reconstructing past ecological networks: The reconfiguration of seed-dispersal interactions after megafaunal extinction. Oecologia 175: 1247–1256.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Ramos-Robles, M., E. Andresen, and C. Díaz-Castelazo. 2016. Temporal changes in the structure of a plant-frugivore network are influenced by bird migration and fruit availability. PeerJ 4: e2048.

Ríos-Blanco, M. C., and J. Pérez-Torres. 2015. Dieta de las especies dominantes del ensamblaje de murciélagos frugívoros en un bosque seco tropical (Colombia). Mastozool. Neotrop. 22: 103–111.

Robertson, A. W., A. Trass, J. J. Ladley, and D. Kelly. 2006. Assessing the benefits of frugivory for seed germination: The importance of the deinhibition effect. Funct. Ecol. 20: 58–66.

Romero-Saritama, J. M., and C. Pérez-Ruíz. 2016. Rasgos morfológicos regenerativos en una comunidad de especies leñosas en un bosque seco tropical tumbesino. Rev. Biol. Trop. 64: 859–873.

Samuels, I. A., and D. J. Levey. 2005. Effects of gut passage on seed germination: Do experiments answer the questions they ask? Funct. Ecol. 19: 365–368.

Sridhara, S., K. McConkey, S. Prasad, and R. T. Corlet. 2016. Effects of frugivory and seed dispersal by large herbivores of Asia. *In* F. S. Ahrestani, and M. Sankaran (Eds.). The ecology of large herbivores in South and Southeast Asia (Vol. 225, Chapter 5), pp. 121–150. Springer, Dordrecht.

Tirira, D. 2007. Guía de campo de mamíferos del Ecuador, pp. 576. Murciélago Blanco. Publicación especial de los Mamíferos del Ecuador 6. Quito.

Traveset, A., A. W. Robertson, and J. Rodríguez-Pérez. 2007. A review on the role of endozoochory on seed germination. *In* A. J. Dennis, E. W. Schupp, R. J. Green, and D. A. Westcott (Eds.). Seed dispersal: Theory and its application in a changing world, pp. 78–103. CABI Publishing, Wallingford, UK.

Tybirk, K. 1997. Reproductive biology and evolution of the genus Acacia. Bull. Int. Gr. Study Mimosoideae 20: 45–53.

Wiles, G. J. 1980. Faeces deterioration rates of four wild ungulates in Thailand. Nat. Hist. Bull. Siam Soc. 28: 121–134.

Williams, S. C., J. S. Ward, and U. Ramakrishnan. 2008. Endozoochory by white-tailed white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface. For. Ecol. Manage. 255: 940–947.