



Consequences of tropical dry forest conversion on diaspore fate of *Enterolobium contortisiliquum* (Fabaceae)

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Abstract Habitat conversion is one of the major threats for biodiversity conservation and viability of natural populations. Thus, habitat disturbance alters distinct ecological processes, such as plant reproductive success and diaspore fate. In this study, we determined the effects of seasonally tropical dry forests (STDFs) conversion by anthropogenic disturbance by assessing diaspore fate of *Enterolobium contortisiliquum*. We compared 20 adult trees present in a STDFs preserved area and 20 adult trees present in

a human-converted area. In general, diaspore fates from both areas were similar, i.e., there was no difference in the reproductive success of trees in STDFs and human-converted area. Habitat disturbance did not affect the length or width of fruits; only fruit thickness was larger in trees of STDFs habitat. None of the biometric seed measures differed between different habitat conditions. Likewise, the number of undamaged seeds, aborted seeds, pre-dispersal predated seeds, and seed production were independent of habitat conditions. Besides, we did not observe any effect of habitat disturbance on germination percentage. However, seeds from preserved STDFs germinated faster than seeds from the human-converted area. Even though the effects of human-modified habitats on the diaspore fate have already been studied, tree species exhibit different responses to habitat conversion regarding seed predation, seed dispersal, seed germination, and seedling establishment. Overall, our results show that habitat disturbance does not affect the diaspore fate of *E. contortisiliquum*. This study also highlights the importance of remnant trees in converted landscapes as the population's connectors which maintain plant–animal mutualistic and antagonistic interactions that mitigate the effects of habitat disturbance.

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Introduction

Deforestation is the major threat to biodiversity conservation and the viability of natural populations (Saunders et al. 1991; Sala et al. 2000; Haddad et al. 2015). Biodiversity preservation in disturbed habitats requires an understanding of the effects of landscape change on community dynamics (Burkey 1993; Aguilar et al. 2012) since forest conversion may change species composition and abundance, thus altering ecological processes, such as mutualistic and antagonistic animal–plant interactions (Saunders et al. 1991; Aizen and Feinsinger 1994a; Debinski and Holt 2000; Emer et al. 2018, 2019; Marjakangas et al. 2019; Hooper and Ashton 2020). Habitat conversion by anthropogenic changes alters the optimal conditions for the long-term persistence of native plant species (Ashworth and Martí 2011; Galetti et al. 2013) because it affects animal populations that interact with in many stages of plants' life cycles (Dirzo and Miranda 1991; Aizen and Feinsinger 1994b).

Due to the intimate interactions with pollinators and seed dispersers, the reproductive success of many plant species has been negatively affected by habitat conversion (Aizen and Feinsinger 1994b; Haddad et al. 2015; Browne and Karubian, 2018; Emer et al. 2018; Hooper and Ashton 2020). For instance, habitat conversion has negative consequences for plant genetic diversity (Aguilar et al. 2006, 2008; Rosas et al. 2011; Browne and Karubian 2018), since in disturbed habitats, the abundance of pollinators decreases, and selfing increases, resulting in inbreeding depression (Aguilar et al. 2006, 2008, 2012, 2019; Eckert et al. 2009; Breed et al. 2015; Broadhurst 2015). Hence, the quantity and/or quality of progenitors are reduced (Aizen and Feinsinger 1994b; Ghazoul et al. 1998; Cascante et al. 2002; Hooper and Ashton 2020). Additionally, habitat conversion negatively affects diaspore fate by reducing fruit and seed set (Ghazoul et al. 1998; Fuchs et al. 2003; Quesada et al. 2004; Kolb 2008; Hooper and Ashton 2020), reducing seed germination (Menges 1991; Bruna 1999; Cascante et al. 2002; Ashworth and Martí 2011), and decreasing seed predation (Cascante et al. 2002; Chacoff et al. 2004; Burgos et al. 2008; Herreras-Diego et al. 2008; Mendes et al. 2016). Indeed, seed predation can be a specific antagonistic interaction, such as observed for Fabaceae family and bruchids (Coleoptera), in which about 85% of seed

predation rate is caused by this insects (Johnson 1985). Due to this strong interaction, habitat alteration may affect plant demography, since landscape changes decrease the diversity and abundance of beetle species (Didham et al. 1998). However, contradictory results were found for seed predation, and no differences in predation rates by bruchines were detected in the palm *Attalea humili* (Andreazzi et al. 2012) located in large and small Atlantic Forest remnants. Even an increase of seed predation in fragment patches in relation to continuous forests was reported in the tree species *Prunus avium* and *Viburnum lantana* (Kollmann and Buschor 2003). Altogether, these selective pressures may determine plant reproductive success and affect population recruitment (Crawley 2000).

Over the last decade, many researchers investigated the effects of habitat disturbance on diaspore fate by assessing both mutualistic and antagonistic interactions (Aizen and Feinsinger 1994a, b; Ashworth and Martí 2011; Skogen et al. 2016; Morrison and Mendenhall 2020). However, different plant species have distinct responses to habitat disturbance (Chen et al. 2017; Newbold et al. 2019), and the existing evidence do not show clear patterns for the effects of habitat disturbance on plant reproductive success (Aizen and Feinsinger 1994a, b; Costin et al. 2001; Ghazoul 2005; Ashworth and Martí 2011; Skogen et al. 2016). It has been proposed that tropical trees could be more adaptable and resilient to habitat conversion as a result of their longevity, high intra-population genetic diversity, and high rates of pollen movement (White et al. 2002; Hamrick 2004; Deacon and Cavender-Bares 2015).

Most of the studies that assessed diaspore fate response under habitat disturbance have involved evergreen species, but a better understanding is needed for trees from Seasonally Tropical Dry Forests (STDFs) (but see Aizen and Feinsinger 1994a, b; Rocha and Aguilar 2001b; Ashworth and Martí 2011; Souza-Silva et al. 2015). Despite the large tropical distribution and importance of STDFs, these ecosystems are endangered by anthropogenic activities (Murphy and Lugo 1986; Janzen 1988; Sánchez-Azofeifa et al. 2005, 2009; Espírito-Santo et al. 2009; Dupin et al. 2018), with a deforestation rate of 12% in Latin America from 1980 and 2000 (Miles et al. 2006). STDFs soils are often fertile (Murphy and Lugo 1986), and the conversion of these forests into pasture and agricultural landscapes has been increasing in the last

decades (Mass 1995; Espírito-Santo et al. 2009; Dupin et al. 2018; Clemente et al. 2020).

In this study, we assessed the effects of STDFs conversion into agricultural and pasture environments on diaspore fate of *Enterolobium contortisiliquum* tree. For this purpose, we compared fruit and seed morphometry, seed production, abortion, predation, and germination between trees from preserved and human-converted STDFs. We hypothesized that STDFs conversion would negatively affect diaspore fate, since in disturbed STDFs, individuals of *E. contortisiliquum* are under stressful environmental conditions. Thus, they would produce narrower fruits with less and smaller seeds. We also expect higher seed predation intensity and abortion percentages, and lower germination rates.

Methods

Study species

Enterolobium contortisiliquum (Vell.) Morong is a Neotropical leguminous tree frequently found in Brazilian STDFs (Oliveira-Filho 2006). Although reproductive studies about *E. contortisiliquum* do not exist, it seems that the species is pollinated by moths, hawk moths, other small nocturnal insects, and even by diurnal bees, as already registered for *E. cyclocarpum*, which has similar flower morphology (Janzen 1982; Rocha and Aguilar 2001a; Frankie et al. 2004; Hamrick and Apsit 2004). Flowering occurs during a short period, from September to October, while fruits ripen between June and July. The species has endozoochoric dispersal that occurs just after fruit ripening. Rodents, such as agoutis, are the seed dispersers (Moreira et al. 2015). Mature fruits and seeds of *E. contortisiliquum* resemble other *Enterolobium* species. Fruits are smooth, shiny, indehiscent, and deep brown, as in *E. cyclocarpum* (Janzen 1982), and seeds are hard, ovoid, and brown (Link and Costa 1995). Fruit development lasts over almost one year and seed dispersal occurs over the dry season, before the flowering period. Thus, mature fruits are resultant from the pollination of the previous year, as observed in *E. cyclocarpum* (Frankie et al. 2004).

Pre-dispersal seeds of *E. contortisiliquum* are predated by the larvae of *Merobruchus bicoloripes* (Coleoptera: Bruchidae) (Pic 1930) (Link and Costa

1995; Morandini and Viana 2009). Bruchid females oviposit on or near the fruits. When the eggs hatch, the larvae enter through the pericarp and go into the seeds, where they develop. The insect completes its life cycle consuming one or more seeds and emerges from the fruit as adult (Janzen 1969). The ingestion of *E. contortisiliquum* pods is harmful to cattle, causing photosensitivity reactions and abortion (Bonel-Raposo et al. 2008; Costa et al. 2009; Olinda et al. 2015). As a result, most farmers cut the trees near their ranches, as the fruiting period occurs during the dry season, coincident with low forage availability for cattle. Therefore, *E. contortisiliquum* is under threat due to habitat conversion and selective cutting (Moreira et al. 2015).

Study area and sampling design

The study was conducted in northern Minas Gerais State (southeastern Brazil), in the surroundings of Lapa Grande State Park (LGSP) (ca. 16°42'S, 43°56'W), a protected area with 15,000 ha. The climate in the region is characterized by marked dry winters from May to September and rainy summers, from November to March. The predominant climate is tropical semi-arid (Aw in Köppen's classification) with average rainfall ranging from 700 to 1200 mm and average temperature among 21 and 25 °C (Antunes 1994). The vegetation of LGSP is composed of cerrado and STDFs. According to Portillo-Quintero and Sánchez-Azofeifa (2010) about 52% of Brazilian STDFs have already been converted to some sort of human activity. In northern Minas Gerais, estimates indicate that 18% of STDFs has been replaced of agriculture, silviculture, and extensive cattle ranching (Rodrigues 2000; Espírito-Santo et al. 2009; Dupin et al. 2018), which has resulted in an altered matrix with scattered trees. We studied 20 reproductive trees in a preserved STDFs area (inside LGSP limits) and 20 reproductive trees in the park surroundings, which is characterized by a converted landscape of agriculture and pasture with some scattered *E. contortisiliquum* trees. We measured the height and diameter at breast height (DBH) of the 40 sampled trees. The minimum distance between *E. contortisiliquum* individuals was 5 m. In a radius of 10 m around each studied tree, we counted the individuals of *E. contortisiliquum* trees and other tree species (see Supplementary Table S1).

Fruit and seed morphometry

The study was conducted during the fruiting period (July) of 2011. On each reproductive tree, we collected between 26 and 30 mature fruits surrounding the tree crown. These fruits were produced by natural pollination in the previous year. We determined the fruit morphometrics by measuring length (in the longitudinal direction), width (in the transverse direction), and thickness of the fruit pericarp using a digital caliper (mm). After that, fruits were opened, and all seeds were extracted to assess seed morphometry, as previously described for fruits. Due to the irregular shape of aborted seeds, they were excluded from morphometric measures.

Seed production

For each fruit, we counted the number of undamaged seeds, the number of aborted seeds, the number of pre-dispersal predated seeds by bruchid beetles, and the total number of seeds produced (i.e., the sum of all previous categories). Seeds without injuries were considered potentially viable (undamaged seeds). The seeds were considered aborted when exhibited irregular shape with a brown and dry endosperm (Cascante et al. 2002). Bruchid beetle damage was identified by the characteristic hole left on seeds when adult beetle emerges (Janzen 1977).

Seed germination

To verify if the habitat disturbance affects the percentage and the time of seed germination, we collected a sample of 10 seeds per tree from each habitat condition (200 seeds per habitat). Seeds used in this experiment were undamaged, as described above. These 400 seeds were subjected to scarification by carefully sanding the seed cover to break seed dormancy. After that, seeds were placed in Petri dishes covered with a sheet of filter paper and moistened with distilled water. Then, seeds were incubated in a germination chamber (B.O.D. type) under 12 h photoperiod with controlled temperature of 25 °C on dark and 30 °C on the light. All Petri dishes were observed at 24 h intervals for 30 days and seeds were considered germinated once the radicle protrusion was observed. Mean germination time (MGT) was obtained by the equation: $MGT = \sum(n \times d)/N$,

where n is the number of seeds germinated on each day, d is the number of days from the beginning of the test, and N is the total number of seeds germinated at the end of the experiment (Ellis and Roberts 1981).

Data analyses

To test how habitat disturbance affects fruit and seed morphometrics, we used generalized linear mixed model (GLMM) with Gaussian error distribution and *lmer* function for R (*lme4* package; Bates et al. 2015). We built separate models for each response variable. Our models included habitat condition (preserved STDF or converted area) as the predictor variable with a fixed effect and sampled tree as a random effect. The response variables were (1) length, (2) width, and (3) thickness of fruits and seeds.

To determine the effect of habitat disturbance on seed production, we used GLMM models with Binomial error distribution and logit link function and *glmer* function (*lme4* package; Bates et al. 2015). Our models also included habitat condition (preserved STDF area or converted landscape) as a fixed effect and tree as a random effect. In these models, the response variables were the proportion of (1) undamaged seeds; (2) aborted seeds; (3) pre-dispersal predated seeds; and (4) seeds production.

The effect of habitat disturbance on seed germination was evaluated by comparing germination time and seed germination percentage during 30 days between habitat conditions. We calculated the mean germination time (MGT) following Labouriau (1983) for each condition. The germination speed was evaluated with a regression analysis using Weibull parametric survival distribution and survival function. The number of germinated seeds was tested through a GLM with Poisson error distribution and the response variable was the habitat condition. All analyses were performed in software R version 3.4.2 (R Development Core Team 2017).

Results

Fruit and seed morphometry

A total of 598 fruits were sampled in each habitat (1,196 in total) and 10,495 seeds were obtained in STDFs area, whereas 10,686 seeds were sampled in

human-converted habitat (21,181 seeds in total). All fruits and seeds were used for morphometric analysis (including undamaged and pre-dispersal predated seeds). Habitat condition did not affect fruit length ($X^2 = 0.10$, $df = 1$, $p = 0.75$) or fruit width ($X^2 = 2.50$, $df = 1$, $p = 0.11$). However, fruit thickness was larger in trees from preserved STDF ($X^2 = 5.40$, $df = 1$, $p = 0.02$). In contrast, none of the seeds' morphometric measures differed between habitat condition ($X^2 = 0.07$, $df = 1$, $p = 0.79$ for seed length, $X^2 = 0.81$, $df = 1$, $p = 0.37$ for seed width, and $X^2 = 0.31$, $df = 1$, $p = 0.58$ for seed thickness) (Table 1).

Seed production and seed predation

There was no difference in seed production between habitat conditions. Likewise, the number of undamaged seeds ($X^2 = 0.03$, $df = 1$, $p = 0.87$), aborted seeds ($X^2 = 1.19$, $df = 1$, $p = 0.27$), predated seeds ($X^2 = 0.51$, $df = 1$, $p = 0.48$), and total seed production ($X^2 = 0.14$, $df = 1$, $p = 0.71$) were independent of habitat condition (Table 2, Fig. 1). Trees from both habitat conditions produced an average of 18 seeds per fruit, of which 80–82% were undamaged or potentially viable seeds, 8–9% were aborted seeds, and 9–11% were predated (Fig. 1).

Seed germination

We did not observe any effect of habitat disturbance on germination percentage (an average of 85% for seeds from preserved STDF and 87% for seeds from human-converted area, $p = 0.78$). However, seeds from trees located at preserved STDFs germinated almost twice faster ($MGT = 2.4 \pm 0.85$ days), than

seeds from trees in the human-converted area ($MGT = 4.09 \pm 0.63$ days; $p = 0.003$). Thus, in preserved STDFs, 80% of seeds germinated after ca. 10 days, while in the human-converted area, seeds took ca. 17 days to germinate (Fig. 2).

Discussion

In general, our findings suggest that habitat disturbance did not affect *Enterolobium contortisiliquum* diaspore fate. Only fruit thickness was larger in trees from preserved STDFs as well as its germination speed was higher. However, the majority of studied traits did not indicate a negative effect of landscape conversion on the reproductive success of this tree species. In fact, not all tree species are impacted by land conversion in the same way (Henle et al. 2004; Winfree et al. 2011).

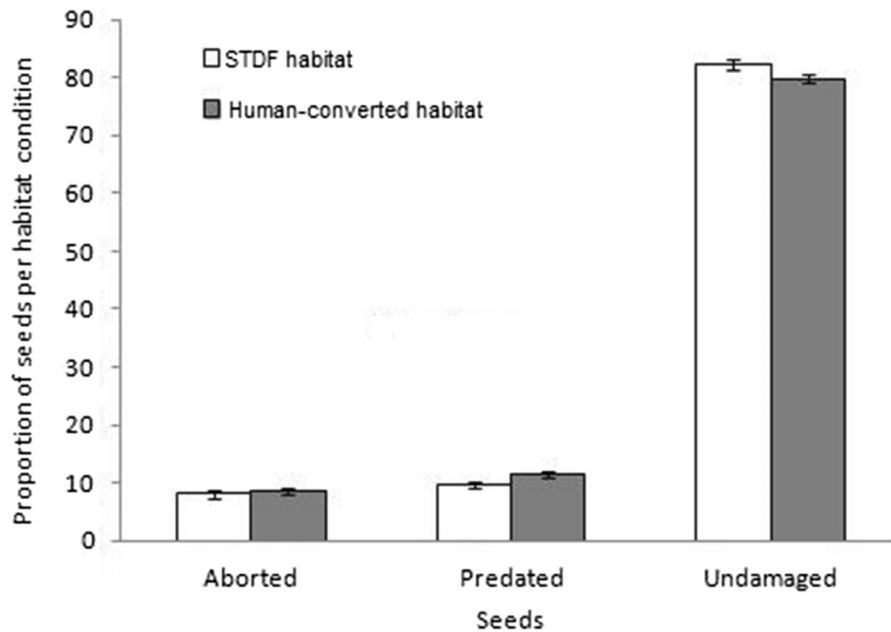
The diaspore fate influences plant dispersal and establishment (Westoby et al. 1996; Leishman et al. 2000; Moles and Westoby 2004). As seeds have morphological traits in response to the environmental conditions (Vázquez-Yanes and Orozco-Segovia 1993), we expected that fruit and seed morphometries formed in the human-converted area would be smaller and narrower. Anthropogenic habitat conversion modify local climatic conditions, and these areas become warmer and drier than natural habitats (Britter and Hanna 2003; Frishkoff et al. 2015; Senior et al. 2017). Consequently, trees in human-converted area would grow under stressful conditions when compared to trees of preserved area. However, STDFs conversion into pasture and agriculture only negatively affected fruit thickness. Thus, environmental conditions of the human-converted area (i.e., high incidence

Table 1 Morphometric measures (average \pm SE) of fruits and seeds of trees in STDF and human-converted area. Asterisk indicates significant differences between the parameters

	Fruits		Seeds	
	STDF	Human-converted area	STDF	Human-converted area
Length (mm)	67.03 \pm 0.43	67.74 \pm 0.45	12.38 \pm 0.15	12.55 \pm 0.25
Width (mm)	37.81 \pm 0.25	40.49 \pm 0.39	7.45 \pm 0.13	7.20 \pm 0.11
Thickness (mm)	13.27 \pm 0.15 *	12.13 \pm 0.14 *	5.13 \pm 0.01	5.36 \pm 0.42

Table 2 Number of undamaged, aborted, predated, and total of seeds production per fruit (average \pm SE) of trees in STDF and human-converted area

	Undamaged seeds	Aborted seeds	Predated seeds	Total of seeds
STDF	14.54 \pm 0.05	1.27 \pm 0.09	1.75 \pm 0.09	17.55 \pm 0.04
Human-converted area	14.36 \pm 0.06	1.50 \pm 0.10	2.01 \pm 0.08	17.87 \pm 0.04

**Fig. 1** Proportion of aborted seeds, predated seeds, and undamaged seeds in STDF and human-converted area. Bars represent standard error

of radiation and extremes of temperature and humidity) may not be stressors for *E. contortisiliquum*. As observed for other STDF plant species, *E. contortisiliquum* may have strategies to cope with drought through better efficiency in water use, allowing them to have physiological and morphological adjustments at high temperatures and less water availability (Pineda-García et al. 2013; Lohbeck et al. 2015).

Our results also indicated that the number of seeds per fruit of *E. contortisiliquum* was similar among habitats. If habitat disturbance affects the number of pollinia deposited in stigmas, as suggested by Aizen and Feinsinger (1994a), it would be expected more fruits and seed set in an undisturbed area. However, we did not observe any effect of habitat disturbance on seed production per fruit. This result may be related to pollinators' capacity to transfer a sufficient pollen charge to maintain the same level of seed production,

regardless of the habitat condition, as discussed below. Despite a lower density of trees in the converted habitat, trees may not suffer from pollen limitation or gene flow. Many studies highlight the ecological value of remnant trees in converted landscapes to increase population connectivity (Manning et al. 2006; Breed et al. 2011). Thus, *E. contortisiliquum* populations from both habitats may be well connected by gene flow, which promotes similar progeny.

Although we did not study pollen gene flow or progeny relatedness, our results suggest that pollination is not constrained by habitat conversion, as undamaged and aborted seeds were similar in both habitat conditions, as well as fruit and seed set. The disturbed area is surrounding the LGSP; thus, pollinators may be dispersing among patches, favoring more compatible crosses between unrelated trees. Despite the lack of knowledge on *E. contortisiliquum*

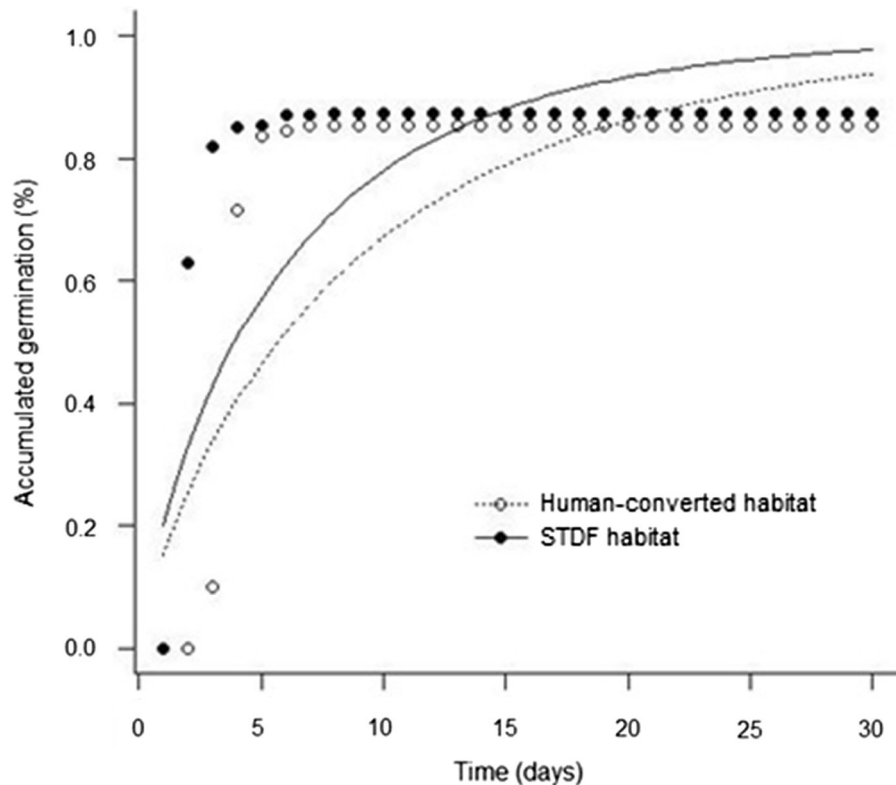


Fig. 2 Accumulated percentage of seeds germination from trees in STDF and human-converted area

pollinators, flowers are apparently pollinated by moths (Moreira et al. 2015), as observed for the congeneric species *E. cyclocarpum* (Frankie et al. 2004; Hamrick and Apsit 2004), and moths can visit many trees during a foraging route (Haber and Frankie 1989), promoting gene flow between different areas. Considering that approximately 20% of the progeny produced by the congeneric species *E. cyclocarpum* is self-fertilized (Rocha and Aguilar 2001b), an alternative explanation is that *E. contortisiliquum* would promote self-pollination, which would produce a similar number of seeds among habitats.

Seed predation of *E. contortisiliquum* was not affected by habitat disturbance, and both habitat conditions exhibited similar percentage of pre-dispersal predated seeds. It is possible that habitat disturbance did not depress *M. bicoloripes* population and/or the matrix surrounding the studied areas did not constrain predator dispersal and, consequently, maintain the same pattern of seed attack. As pointed out by Aguilar et al. (2012), the persistence of bruchid insects on fragmented habitats may be due to the tight

evolutionary relationship with Fabaceae tree species and the ability of bruchid beetles to remain nearby adult trees throughout their life cycle, despite the environmental condition. Despite fruit and seed predation is a process that affects plant reproductive success (Schupp 1988), the effects of habitat conversion on this antagonistic interaction have not been well studied (Herrerías-Diego et al. 2008), and tree species exhibit different responses (Cascante et al. 2002; Chacoff et al. 2004; Herrerías-Diego et al. 2008; Aguilar et al. 2012).

We found that the time of seed germination in *E. contortisiliquum* is affected by habitat disturbance. The mean germination time was significantly lower for seeds from trees from preserved STDFs than for seeds from trees from the human-converted area. The faster germination of seeds in the preserved habitat could be an important strategy to avoid seed viability loss due to deterioration and microorganism attack. An alternative explanation is that soil and/or humidity are different among habitats assuming that the human-modified area is warmer and drier (Britter and Hanna

2003; Frishkoff et al. 2015; Senior et al. 2017). Agreeing with our results, progeny from the congeneric species *E. cyclocarpum* trees in preserved STDFs area took less time to germinate than trees scattered in pastures (Rocha and Aguilar 2001b). Although the mean time of seed germination in the preserved habitat was almost two days faster, seeds obtained from trees of both habitat conditions showed the same germination rate. It is expected that seeds produced by scattered trees would suffer more inbreeding (Nason and Hamrick 1997) and, consequently, a reduction in germination percentage (Bruna 1999). As assumed before, it is possible that there is no pollen limitation, and pollinators could be promoting pollen flow and exogamic crosses between unrelated trees, reducing inbreeding depression and pollen limitation effects in scattered trees, which would result in a similar percentage of germination.

For many years, researchers have evaluated the effects of habitat disturbance on tree reproduction (Nason and Hamrick 1997; Herrerías-Diego et al. 2006, 2008; Aguilar et al. 2019). However, not all tropical trees species are impacted by habitat disturbance in the same way (Quesada et al. 2004; Herrerías-Diego et al. 2006; Neal et al. 2010). Despite our results were obtained in a single site and only once, we highlight the absence of negative habitat conversion effects on *E. contortisiliquum*'s diaspores fate in this study. Although, habitat disturbance may cause negative effects on plant reproduction, the long life-span of trees may make them resilient to immediate disturbance (Wilcock and Neiland 2002; Neal et al. 2010) and buffer populations against stochastic events. From a conservation biology perspective, *E. contortisiliquum* trees scattered in altered habitats of tropical dry forests may serve as important stepping stones for pollinator movement, ensuring gene flow and connecting populations, rather than being considered a living dead (Janzen 1986). Local preservation of these trees is essential to the maintenance of mutualistic and antagonistic interactions important to the biodiversity of tropical ecosystems.

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Authors' contributions PAM contributed to data curation, methodology, and writing—original draft, and review and editing. FSN was involved in methodology, formal analysis, and writing—original draft, and review and editing. JAL contributed to writing—review and editing and supervision.

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Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval This study was approved by the State Forest Institute (Instituto Estadual de Florestas – IEF/Protocol # 017/10).

Consent for participate All co-authors have read the submitted version and have agreed with the submission.

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