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Effect of Fruit Handling by Frugivores on Seed Dispersal Effectiveness

RAÍSSA SEPULVIDA

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AUTORA: RAÍSSA SEPULVIDA ALVES
ORIENTADORA: LAURENCE MARIANNE VINCIANNE CULOT
COORIENTADOR: CARLOS AUGUSTO PERES

Aprovada como parte das exigências para obtenção do Título de Mestra em ECOLOGIA E BIODIVERSIDADE, área: Biodiversidade pela Comissão Examinadora:

Profa. Dra. LAURENCE MARIANNE VINCIANNE CULOT (Participaçao Virtual)
Departamento de Biodiversidade / UNESP - Instituto de Biociências de Rio Claro - SP

Marco A. Pizo

Prof. Dr. MARCO AURELIO PIZO FERREIRA (Participaçao Virtual)
Departamento de Biodiversidade / UNESP - Instituto de Biociências de Rio Claro - SP

Alexandra Pires Fernandez

Profa. Dra. ALEXANDRA PIRES FERNANDEZ (Participaçao Virtual)
Departamento de Ciências Ambientais / UFRRJ - Universidade Federal Rural do Rio de Janeiro - Seropédica / RJ

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Therese von Bayern (Th. Von Bayer)

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RESUMO

A dispersão de sementes por animais contribui para manutenção da biodiversidade em florestas tropicais. A zoocoria é um processo importante para muitas espécies de plantas porque diminui a lacuna entre a produção de frutos e o recrutamento de plântulas. A manipulação das sementes por frugívoros (através da limpeza das sementes e remoção destas para longe do coespecífico) contribui para reduzir a mortalidade de sementes e aumentar o sucesso de germinação e recrutamento. No entanto, ainda pouco se sabe o quanto esses efeitos variam de acordo com as características dos frutos/sementes. Estudos sugerem que a limpeza da semente afeta positivamente espécies com frutos de polpa carnosa, pois a remoção da polpa reduz a atração de patógenos. A remoção da semente para longe das árvores coespecíficas auxilia as sementes a escaparem da mortalidade dependente da densidade. Esse efeito, portanto, deve ser maior em espécies submetidas a um forte *feedback* negativo da relação planta-solo. Nesse estudo, nós investigamos como a limpeza da semente e a remoção para longe do coespecífico afetam a germinação, emergência de plântulas e sobrevivência das sementes de três espécies que possuem características distintas: *Castilla ulei* (Moraceae; polpa carnosa com alta aderência e sementes com tegumento fino), *Hymenaea parvifolia* (Fabaceae; vagem lenhosa resistente, polpa farinácea e tegumento espesso) e *Byrsonima arthropoda* (Malpighiaceae; polpa carnosa revestindo um pirênio lenhoso e resistente que reveste 2-3 sementes). Nós também estimamos a variação percentual do efeito do manuseio pelo frugívoro na eficácia da dispersão de sementes (EDS – estimado como a proporção de sementes/plântulas que sobrevivem até o final do estudo) das plantas quando comparado ao sucesso reprodutivo esperado na ausência dos dispersores. Para isso, nós realizamos um experimento de campo no sudeste da Floresta Amazônica (terra firme), Mato Grosso, aplicando uma combinação de tratamentos às sementes das espécies: sementes limpas, sementes com polpa, debaixo ou longe de uma árvore coespecífica. A limpeza da semente aumentou significativamente a germinação, a emergência de plântulas e a sobrevivência da *C. ulei* enquanto a remoção das sementes para longe do coespecífico teve um efeito negativo, porém fraco, na emergência de plântulas. Nenhuma semente com polpa dessa espécie sobreviveu, assim, a limpeza das sementes por frugívoros aumentou de forma assintótica o EDS de *C. ulei*. A deposição de sementes embaixo do heterospecífico aumentou significativamente o sucesso de germinação de *H. parvifolia*, porém, de forma fraca. A limpeza da semente e a remoção não afetaram a emergência de plântulas nem a sobrevivência. Apesar do efeito positivo (porém, fraco) da remoção da semente para longe do coespecífico na germinação da *H. parvifolia*, tal efeito não foi suficiente para aumentar a sobrevivência de sementes/plântulas, a qual, na verdade, decresceu por até 25%. *B. arthropoda* não germinou durante o período de estudo e nós encontramos que a limpeza da semente diminuiu a sobrevivência da espécie, consequentemente reduzindo o EDS por até 75%. Nossos resultados sugerem que a limpeza da semente e remoção para longe do coespecífico afetam as plantas de forma diferente de acordo com o estágio de vida e com as espécies. Essa diferença na resposta pode ser explicada pelas características dos frutos e sementes. Pesquisas adicionais investigando as respostas das plantas ao manuseio pelo frugívoro de acordo com característica funcionais irá auxiliar a prever o efeito da ausência de dispersores de sementes na regeneração das florestas.

Palavras-chave: dispersão de sementes, manipulação de frutos, Janzen-Connell, floresta Amazônica.

ABSTRACT

Seed dispersal by animals is an important process for the maintenance of biodiversity in tropical forests. Zoochory is of great importance for many plant species as it increases seedling recruitment probability. Seed handling by frugivores (seed cleaning and removal away from conspecifics) has the potential to reduce seed mortality and increase germination and recruitment success. However, it is still unknown how much these effects vary according to fruit/seed traits. Indeed, we can expect that seed cleaning affects more positively fleshy-pulp fruits since this treatment reduces the pathogen infestation that is more likely to occur in such fruits. Seed removal from conspecific trees helps to escape the density-dependent mortality and its effect might thus be stronger for species suffering high negative plant-soil feedback. Here, we investigated how seed cleaning and removal away from conspecifics affect the germination, seedling emergence and survival of three species with distinct traits: *Castilla ulei* (Moraceae; fleshy pulp hardly adhered to the soft seed), *Hymenaea parvifolia* (Fabaceae; hard-wood pod, farinaceous pulp and hard seed) and *Byrsonima arthropoda* (Malpighiaceae; fleshy pulp around a hard-wood pyrene with 2-3 seeds). We also estimated how much the seed handling by frugivores changes the seed dispersal effectiveness (SDE - estimated as the proportion of seed/seedling surviving until the end of the study) of plants compared to the expected reproductive success in absence of seed dispersers. We conducted a field experiment in the southern Brazilian Amazon (*terra firme* forest), Mato Grosso, applying the combination of treatments to seed species: cleaned seeds, seeds with pulp, under and away conspecific trees. Seed cleaning significantly increased the germination, seedling emergence success and had a weak positive effect on survival of *C. ulei* while removal away from conspecifics had only a weak negative effect on seedling emergence. Since none of undispersed seeds survived, seed cleaning by frugivores increased *C. ulei* SDE asymptotically. Seed deposition under heterospecific trees significantly increased the germination success of *H. parvifolia*, but weakly. Neither removal nor seed cleaning affected seedling emergence and survival. Despite the positive (but weak) effect of seed removal away from conspecifics on *H. parvifolia* germination, it was not sufficient to positively affect seed/seedling survival, which was actually decreased by up to 25%. *B. arthropoda* did not germinate during the study period, and we found that seed cleaning decreased seed survival, consequently decreasing the SDE by up to 75%. Our results suggest that seed handling and removal from conspecifics affect the plants differently according to the life stages and the plant species. Such discrepancy may be explained by the traits of fruits and seeds and further research involving plant responses to seed handling according to functional traits would help to better predict the effect of the absence of dispersers on forest regeneration.

Keywords: seed dispersal, fruit handling, Janzen-Connell, Amazon forest.

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1. INTRODUCTION

Seed dispersal by vertebrates is an important process for the maintenance of biodiversity in tropical forests (HOWE; SMALLWOOD, 1982; STEVENSON, 2011a). In tropical rainforest, approximately 90% of plant species rely on vertebrates to disperse their seeds (JORDANO, 2000). The zoochoric dispersal is a mutualistic interaction in which the animals benefit from consuming the fruit nutrients and water and the plants gain with the dispersal of their seeds to suitable places for establishment (HOWE; SMALLWOOD, 1982). Ultimately, the seeds will be effectively dispersed if the frugivore activity not only moves them away but contributes to increasing the plant fitness (SCHUPP, 1993). Seed cleaning and removal away from conspecifics are two aspects of seed handling by frugivores that can enhance seed germination and survival. Indeed, a rich literature indicates that the escape from the vicinity of parent tree increases germination and survival probability (COMITA et al., 2014) while other studies show that seed cleaning is more determinant to enhance germination success than the removal away from conspecific trees (FRICKE et al., 2013; LEVI; PERES, 2013). However, we still know little about how the effect of both treatments varies according to plant species and whether it depends on specific fruit and seed traits.

The 'seed dispersal effectiveness (SDE)' concept, as revisited by Schupp et al. (2010), helps to understand how dispersal contributes to the overall plant recruitment and is estimated through a quality and a quantity components. Such concept can be viewed as the "dispersal effectiveness a plant receives" from its multiple agents (SCHUPP; JORDANO; GÓMEZ, 2010a). An effective dispersal enables the plants to overcome a critical bottleneck between seed and seedling recruitment (CHAMBERS; MACMAHON, 1994). The benefits plants receive from dispersal are multiple, such as colonizing new habitats, reaching suitable microsites (HOWE; SMALLWOOD, 1982), tracking climate and environmental changes (IBÁNEZ et al., 2006), promoting gene flow within and between populations (JORDANO et al., 2007), and escaping from density-depend mortality under conspecific trees (CONNELL, 1971; JANZEN, 1970). The escape benefit is an extensively studied process (COMITA et al., 2014) that affects both plant demography and community dynamics. According to the Janzen-Connell hypothesis (CONNELL, 1971; JANZEN, 1970), under parent-tree, seeds are subjected to high density-dependent mortality induced by host-specific pathogens (e.g. fungi and bacteria), seed predators (insects and rodents) and increasing intraspecific competition. Therefore, the dispersal away from parent trees enhances the *per capita* seed survival and establishment probability. It has been shown that the live soil microbiota under conspecific trees, mainly fungi pathogens, are sufficient to induce this high mortality by a process known as the negative plant-soil feedback (NPSF; KLIRONOMOS, 2002; KULMATISKI et al., 2008; MANGAN et al., 2010). The decreasing of conspecific survival and fostering of heterospecific offspring near parent trees has been recognized as an important process that modulates the relative abundance of species (LEVI et al., 2019). Fruit species are thus subjected to the distance- and density-dependent effects. However, while some zoochoric species are negatively affected by the local extinction of frugivores, others thrive relatively well (NUNEZ-ITURRI; OLSSON; HOWE, 2008). This discrepancy in the capacity of plant species to recruit without seed dispersers might be a consequence of the morphological and functional fruit/seed traits that modulate plant species responses to environmental constraints, and consequently their dependence on seed handling by frugivores.

Zoochoric seed dispersal involves the movement of seeds, their treatment in the mouth and/or the gut of frugivores, and their deposition (SCHUPP; JORDANO; GÓMEZ, 2010a; STRINGER et al., 2020). Thus, each frugivore treatment has a differential ecological contribution to the final recruitment probability and survival. First, when frugivores handle the seeds, they clean the seeds from their pulp, removing chemical inhibitors and reducing pathogen attraction (TRAVESET; VERDÚ, 2002). Secondly, the gastrointestinal passage removes the perishable exocarp from intact seeds and cleans the seed testa of the tightly adhered edible fleshy fruit pulp (LEVI; PERES, 2013). It may also contribute to mechanical and chemical scarification that interrupt the seed dormancy (BASKIN; BASKIN, 2014; TRAVESET; RODRÍGUEZ-PÉREZ; PÍAS, 2008; TRAVESET; VERDÚ, 2002). The ingestion (seed cleaning and gastrointestinal passage) by strictly frugivore primates increases the germination success by 75% and accelerates the germination time by 17% (FUZESSY et al., 2016). This fast growth enhances plant survival as the seedlings can capture resources faster and escape early from enemies. Thirdly, ingested seeds deposited in faecal matrixes can enhance their germination through a possible fertilizing effect or decrease it by the presence of microorganisms in faeces (TRAVESET; ROBERTSON; RODRÍGUEZ-PÉREZ, 2007; TRAVESET; VERDÚ, 2002) or by an increased competition when frugivore behaviour results in aggregated seed deposition (RUSSO; AUGSPURGER, 2004). Lastly, germination success and survival can increase with seed removal from the vicinity of parent-trees, where soil microbiota, chemical components and sapling density jeopardize conspecific propagules (CRAWFORD et al., 2019; MANGAN et al., 2010; MCCARTHY-NEUMANN; KOBE, 2010). As a result, seeds can benefit from or be harmed by frugivore handling along the seed dispersal process. Such interaction is a two-way road that depend on the limitations of seeds to recruit and the quality of seed handling by frugivores. By uncovering the causes of variation of plant responses to pulp removal and dispersal away from conspecifics, it would be possible to better predict the effect of the local extinction of dispersers on forest regeneration.

Aslan et al. (2019) proposed to use fruit traits to understand species vulnerabilities to seed mortality and recruitment failures and, therefore, its dependence on dispersal by frugivores. The authors argue that understanding plant characteristic that leads to germination vulnerabilities could help understanding "how much it matters if their seeds are dispersed at all" (ASLAN et al., 2019). Some studies have already associated some seeds characteristics to the plant limitation in germination and survival. Thin seed coat are less resistant to soil enemies (GARDARIN et al., 2010) while thick seed coat may protect the embryo and increase life expectancy of seeds. Moreover, thick seed coat usually result in dormancy, which also imposes germination limitation (BASKIN; BASKIN, 2001) and will require different frugivore treatments such as gut passage or deposition in adequate microsites. However, these studies do not link plant traits with seed dispersal dependence. Doing so, we can better understand the constraints underlying recruitment limitation (TERBORGH et al., 2011). Here, we proposed to estimate the effect of two frugivore treatments, seed cleaning and seed removal away from conspecifics, on the early success of three fruit species with distinct traits, under field conditions. By understanding the differential dependence of seeds on frugivores, we can best predict which treatment is indispensable for the plant early success and, therefore, what to expect in terms of plant responses in the absence of their dispersers.

In this study, we aimed to investigate how seed handling by frugivores affects the recruitment success of three plant species with distinct fruit/seed traits, under field conditions: *Castilla ulei* (Moraceae; fleshy pulp hardly adhered to the soft seed), *Hymenaea parvifolia* (Fabaceae; hard-wood pod, farinaceous pulp and hard seed) and *Byrsonima arthropoda* (Malpighiaceae; fleshy pulp around a hard-wood pyrene with 2-3 seeds) and how much these species depend on such process in early stages. To do so, we i) tested the effect of two frugivore treatments: seed cleaning and removal away from conspecifics, on germination, seedling emergence, and seed/seedling survival; ii) estimated how much each treatment changes the early plant success compared to undispersed seeds. We expected that *C. ulei* would have great increasing in germination and recruitment with seed cleaning as the species has highly adhered fleshy pulp, which attracts seed enemies and thin seed coat, which makes the embryo vulnerable to attacks. We expected that seed cleaning would have positive, but small effect on *B. arthropoda* as the species also has fleshy pulp, but seeds are protected by the pyrene. Seed removal would have secondary or null effect for these species. On the other hand, the seed removal would surpass the importance of seed cleaning for *H. parvifolia* on early success as the species has dry pulp, which is not associated with great attraction of predators and pathogens, and thick seed coat, that protects the embryo. Thus, escaping from the vicinity of conspecific would be sufficient for increasing germination and recruitment probability.

4. DISCUSSION

The three plant species we tested responded differently to the seed handling by frugivores. Such discrepancy of plant responses can be explained, at least partly, by the seed traits of species that impose differential constrains to germination, seedling emergence, and survival. Seed cleaning by frugivores have positive effect on the germination and seedling emergence of *C. ulei*, a fleshy fruit with a pulp hardly adhered to the soft seed, but it does not prevent the high rate of seed and seedling death. The deposition of *H. parvifolia* seeds, a fruit with farinaceous pulp and hard seed coat, under heterospecific trees slightly increases germination probability. However, seed cleaning combined with the removal away from conspecifics decreases the reproductive success compared to undispersed seeds. Seed cleaning by frugivores significative decreases the survival probability of *B. arthropoda*, a fleshy fruit with hard-wood pyrene containing soft seeds, indicating that seed handling by frugivores decreases the reproductive success compared to undispersed seeds.

Seed cleaning had great importance on the germination success, seedling emergence and at a lesser extent, survival of *C. ulei*. Deposition under conspecific trees had a secondary effect on the seedling emergence probability. A similar result was found for the common fleshy fruit species *Manilkara bidentata* (LEVI; PERES, 2013) and *Capsicum chacoense* (FRICKE et al., 2013), for which seed cleaning positively affected seedling recruitment. Pulp removal reduces the attraction of pathogens and predators that are accumulated under conspecific trees, especially in the case of fleshy-fruit species. *C. ulei* presents seed traits that make the species more vulnerable in early stages of development. Its soft seed coat is sensitive to desiccation (BASKIN; BASKIN, 2014). Seeds with thin seed coat are more likely to die early, probably because they are less resistant to predation and pathogens and more likely to dry (GARDARIN et al., 2010; NOTMAN; GORCHOV, 2001). The removal of the pulp helps the seeds to escape from enemies attack, thus increasing the species probability of germinate, survive and become seedlings. Fruit traits found in *C. ulei,* such as orange/yellow fruits, indehiscence, juicy pulp and high adherence of pulp were also related to high pathogen attack in an experiment with 16 Peruvian forest species (PRINGLE; ÁLVAREZ-LOAYZA; TERBORGH, 2007). Such characteristics, together with our results, indicate that the species strategy is to have seeds germinating soon after reproduction. Germination period coincides with the beginning of the rainy season in our study site. It requires that seeds have the pulp removed before reaching the ground to enable seeds to germinate fast and not be attacked by predators and pathogens when the soil is more humid.

Despite the great increasing in germination and seedling emergence probability with seed cleaning treatment, we recorded a high mortality of seedlings over the long term. This high mortality suggests that other factors, such as environmental and microsite conditions, highly limit the recruitment of new individuals, a case of life-stage conflict. Even though seedlings can emerge, they may not be able to establish and survive in the long-term due to factors different from the ones affecting germination and seedling emergence. Most seedlings in our study died during the dry season when they were found with yellow and withered leaves. Such deaths can be explained by dehydration or phyto-diseases that attacked and weaken the sprouts or, in some cases, by logs that fell on the exclosures. Experiments under field conditions include multiple uncontrolled variables, especially when there is long temporal variation. Such confounding factors may limit our predictions about the causes of seedling death. However, our results illustrate how the plant early life stages are submitted to different constraints. It is noteworthy that all seedlings that emerged and survived were from cleaned seeds. Such treatment is indispensable for seedling emergence, but it does not prevent the large mortality rate between emergence and establishment. Therefore, large amount of seeds must be cleaned to compensate such seedlings death.

The species *C. ulei* has characteristics associated with primate-dispersed species: yellow/orange colour and high-adherent fleshy-pulp. The hardly adhered pulp influences positively the decision of a frugivore to ingest the seeds to consume the pulp (STEVENSON, 2011b), which helps cleaning it. Moreover, *C. ulei* seeds are medium-sized ($\overline{X}$=8.6 mm ±1.9, N=7), which potentially increases the chances of being ingested by a wider range of bodied-sized frugivores (BUFALO; GALETTI; CULOT, 2016). Our results and inferences highly suggest that the species strongly depend on frugivore to germinate and emerge as seedlings. The genus *Castilla* is generally listed in the diet of large-bodied Ateline primates (ARROYO-RODRÍGUEZ et al., 2015; PINTO; SETZ, 2004; PRUETZ et al., 1998; STEVENSON; QUIÑONES; AHUMADA, 2000; YUMOTO, 1999). In our study site, *Lagothrix cana* and *Ateles chamek* are the most sighted frugivore vertebrates, 1.8/10km and 0.8/10km respectively (OLIVEIRA et al., 2019). We recorded *L. cana* consuming the seeds and we also recovered seeds from their faecal samples. Levi e Peres (2013) estimated that a density of 35.12 ind./km2 of *L. cana* was able to remove

71.27% of fruit production of *M. bidentata*, that has larger fruits (15.5 ± 3.2 mm) and seeds (22.3 ± 4.1 mm) than *C. ulei*. As *C. ulei* produces infructescence with multiple and medium-sized seeds, we predict that *L. cana* at FSN can also remove a high proportion of seeds from *C. ulei*'s tree. However, in a study in Colombia, dispersed seeds (collected from faeces) by *Ateles belzebuth* and *Alouatta seniculus* in the same study significantly reduced germination rate ($p<0.05$). *C. ulei* has thin seed coat, susceptible to soil enemies, thus the faecal matrix may attract a high density of pathogens and seed predators. Thus, Ateline primates have a great potential of cleaning large amount of seeds, increasing the *C. ulei* probability of germination and seedling emergence, however, more studies on gut passage and deposition within faecal matrix would be necessary to test the effect of such treatments on the final germination success of seeds with thin seed coat.

Germination of *H. parvifolia* was slightly increased by the removal away from conspecifics but not by seed cleaning. Seedling emergence and survival were not significantly affected by the treatments. Overall, seed handling by frugivores slightly decreases the reproductive success of the species. *H. parvifolia* seeds are covered by a farinaceous green pulp stocked in an indehiscent heavy and hard pod (CAMARGO et al., 2008). Seeds that fall on the soil covered by pulp are usually cleaned by fungus-cultivating ants Attini (OLIVEIRA et al., 1995), providing germination benefits to the genus *Hymenaea*. We also noticed an intense activity of ants and termites on the soil around the field exclosures. Therefore, we suggest that seeds with pulp were also rapidly cleaned by ants in our study, diminishing the importance of seed cleaning by arboreal frugivores before falling on the ground. Oliveira et al. (1995) observed that uncleaned seeds of *H. courbaril* were mostly infected by fungus, reducing seed viability. In their study, seeds completely cleaned by ants had 68% of germination success in the greenhouse; seeds partially cleaned, 53%; and seeds not cleaned at all had only 18% of germination success. These results combined with ours show that seed cleaning is an important factor to increase seeds´ early success of this species but that it can be accomplished by invertebrates once the seeds fall on the ground.

Seeds of *H. parvifolia* that did not germinate persisted in the seed bank. Seeds from leguminous trees generally have thick seed coat impermeable to water and/or gases (SILVA; CESARINO, 2016). Such characteristics prevents germination due to physical dormancy (BASKIN; BASKIN, 2001), but also prevents seed mortality due to predators and pathogens. Lewinsohn (1980), in a review of seed predation of the genus *Hymenaea*, discusses if the hard seed coat would be an evolutionary response to the high prevalence of invertebrate predators, mainly *Rhinochenus* sp. (Coleoptera: Curculionidae) and Phycitidae (Lepidoptera). These invertebrates are specialized in *Hymenaea* spp. and attack seeds still immature in the tree canopy (LEWINSOHN, 1980). Scolitids (Coleoptera: Scolytidae) and *Microscapus hymenaeae* (Coleoptera: Curculionidae) are also highly prevalent in intact fruits that fall on the soil (LEWINSOHN, 1980). Miller (1991) found that 20% of *H. parvifolia* seeds collected were infested with Curculionids. In our study, we found *Rhinochenus sp.* (Coleoptera: Curculionidae) in 1.05% of seeds (N=1895) and predation marks in 11.45% (N=1895) of screened seeds collected from the treetop. The increase of germination success under heterospecific trees indicate that seeds dispersed away are able to escape from the high prevalence of specific predators and pathogens associated with the genus *Hymenaea*, increasing germination success.

Seed hardness implies a trade-off to seeds. It protects seeds on the soil, however, it prevents germination if dormancy is not broken. The dormancy of *H. parvifolia* is overcome by mechanical or chemical scarification in laboratory conditions (SILVA; CESARINO, 2016). The mechanism whereby physical dormancy is broken in the environment is still unknown (BASKIN; BASKIN, 2001). The dormancy results in slow germination rates and a capacity to persist in seed banks. We indeed found a low germination success for *H. parvifolia* (12%), as so did Miller (1991) in an experiment conducted in a greenhouse (12%) over a longer period (345 days). Interestingly, scarified seeds in their studies had 82-100% of success. We did not investigate the effect of scarification. The passage through frugivore gut contributes to break seed dormancy by reducing water content, thinning the seed coat, or decreasing seed resistance (TRAVESET; RODRÍGUEZ-PÉREZ; PÍAS, 2008). Therefore, despite the none effect of seed cleaning in our study, seeds may have great benefit from ingestion by frugivore to overcome seed dormancy and decrease germination time and seedling establishment. This still needs to be investigated in *H. parvifolia*.

Despite the positive (but weak) effect of seed removal away from conspecifics on *H. parvifolia* germination, it was not sufficient to positively affect seed/seedling survival, which was actually decreased by up to 25%. Frugivore primates are considered the main vertebrate responsible for opening the hard fruits in the treetop and release the seeds (BASKIN; BASKIN, 2001). At FSN, *L. cana* was seen feeding on *H. parvifolia*. The individuals open the fruit, consume the pulp, and spit out most seeds cleaned and uninjured under the parent tree.

However, a few seeds, smaller ($\bar{X}$ =16.6 mm , N=6) than the ones found under trees ($\bar{X}$ =19.5 mm, N=20), were recovered from their faeces samples, indicating that they can occasionally disperse the seeds of this species endozoochorically (pers. obs.). In our study, the seed treatments we tested did not increase *H. parvifolia* SDE, suggesting that this species is not dependent on seed cleaning and removal away does not decrease mortality due to soil enemies. Other groups such as ants (Attini) may clean the seeds once they reach the soil. However, the species still benefit from removal by frugivores to release the seeds from the fruits or to bury it, which also contributes to increase germination probability due to microsite conditions and reduction of pathogens and invertebrates' attacks (ASQUITH et al., 1999) (ASQUITH et al., 1999; GORCHOV; PALMEIRIM; ASCORRA, 2004; HALLWACHS, 1986). As the seed coat is thick, seed scarification through ingestion by large animals such as Ateline primates may also contribute to reduce germination time, which needs further investigation.

We did not record any germination of *B. arthropoda* in seven months. Survival was negatively affected by seed cleaning and removal away from conspecifics did not have any significant effect on seeds. Seed cleaning decreased SDE by up to 75% while seed cleaning combined with removal away decreased SDE by up to 50%. The genus *Byrsonima* has a pyrene diaspora, where small seeds (<5 mm) are stocked in. The woody endocarp acts as a mechanical barrier that prevents seed development (CARVALHO; NASCIMENTO; MÜLLER, 1998). Therefore, we may have missed seeds that eventually germinated in the field and that we were not able to see. Carvalho et al. (1998) also found low germination rate for *B. crassifolia* (11%) tested in a greenhouse. Seeds that did not germinate were still alive. In our study, only 6.4% of seeds were alive. The genus is classified as having physiological dormancy (BASKIN; BASKIN, 2014). Seeds with such dormancy have water-permeable seed coat and require more than four weeks of incubation. Moreover, dormancy is controlled by metabolic and genetic mechanisms. These groups of seeds regulate their germination timing so that it coincides with the most favourable season for seedling establishment (Thompson, 1971 apud BASKIN; BASKIN, 2014). Season changes would be the trigger to germination. The experiment went through the rainy season and we can interpret the negative effect of seed cleaning in two ways. First, seed cleaning exposes the pyrene to water and environmental condition (seeds are water-permeable) in timing not propitious for seed germination. Seeds could have begun to germinate but ended up dying socked in the woody pyrene. Secondly, once cleaned, the pyrenes were more exposed to pathogens which can attack the seeds that present a soft coat, before being able to germinate. Such hypothesis agrees with both cleaning seeds and seeds with pulp having similar survival success under heterospecific trees in our study. We can presume that germination and survival are limited by other factors than dispersal such as local climate and physiological conditions.

B. arthropoda has similar pulp characteristics as *C. ulei*: highly adhered fleshy-pulp, which are generally assigned to the dependence on zoochoric dispersal. Cleaning seeds is sufficient to increase *C. ulei* early success. However, other seed traits such as the presence of pyrenes and dormancy are more important to limit seed survival than pulp removal for *B arthropoda*. Aslan et al. (2019) propose the use of functional groups instead of dispersal syndromes to better understand the vulnerabilities of plant species in the early stages. Dispersal syndromes are more related to the evolutionary and ecological processes underlying the interaction between plant-frugivore. In contrast, functional groups, assigned according to the plants' requirements to recruit, help to better understand the dependence of the plant on different stages of dispersal. Such a framework helps to clarify whether it matters if seeds are dispersed, into what context and with what vectors (ASLAN et al., 2019). According to *B. arthropoda* results we suggest that a group of seed/fruits traits contribute to impose limitation on seed germination and survival that frugivore treatments may not overcome, suggesting that studies should not look only on the pulp characteristics.

Our field experiments showed that the species were affected differently by seed cleaning and seed removal from conspecifics. Such response variation can be interpreted according to the seed characteristics and germination limitation as we discussed above. Comparing the SDE_{clean} (when seeds are cleaned but not removed) and SDE_{het} (when seeds are both cleaned and removed) to SDE_{null} (seeds are not cleaned either removed) help us to understand the actual magnitude and direction of the frugivore treatments on the reproduction success of the studied species.

It is important to highlight that our study tested the effect of distance-based process under population dynamic, such as how escaping from natural enemies concentrated under conspecific trees affects germination, seedling emergence and seed/seedling survival. Another different process, usually mentioned as synonym, is the long-distance dispersal under the community context (SCHUPP; JORDANO; GÓMEZ, 2010a). In this case, the long-distance dispersal contributes to connect metapopulation, colonize new habitat and promote gene flow. Therefore, even when the removal away from conspecific tree was not determinant for initial vital rates in our studies, we cannot disregard the importance of distance-depend dispersal under metapopulation and community processes. Moreover, microsite and environmental factor were not investigated in our study. Such processes highly contribute to the differential probability of seed transition to seedling and adult establishment.

In conclusion, the plant species *C. ulei*, *H. parvifolia* and *B. arthropoda* had different responses to seed cleaning and removal away from conspecifics. Indeed, we also found different responses according to plants life stages. Such responses can be better understood when we investigate the seeds/fruits characteristics. Fruit pulp, seed coat and dormancy type impose different constraints to germination and seed survival. Therefore, according to the species limitations, the seed handling by frugivores affects plant reproduction in different magnitude and in different direction. Moreover, an increased germination success due to seed handling by frugivores has low impact on the final SDE if seeds are not able to survive and recruit as seedlings. Frugivore contribution is the first filter, in long-term, seedling establishment may be more limited by climate conditions or other abiotic factors than process underlying the seed dispersal processes. Understanding such plant limitations and response to different process of frugivore handling help us to better understand the dependence of plant species on seed dispersal. Species such as *C. ulei*, which are highly dependent on large primates for dispersal, are more likely to be negatively affected by defaunation and forest degradation since such vertebrates are preferred targets of hunters and depend on intact forests. In contrast, species like *H. parvifolia*, which dispersal processes can be accomplished by animals like ants or agoutis, which are found even in disturbed habitats, are less likely to be negative affected by the absence of large seed disperser. Our study offers preliminary conclusions about how fruit and seed traits are related to specific responses to handling by frugivores. However, to clearly conclude about general patterns according to plant functional groups, it is necessary to carry out similar studies with other species belonging to the same functional groups and to other ones.

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