Effect of forest fragmentation on fruit and seed predation of the tropical dry forest tree Ceiba aesculifolia

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ABSTRACT

Forests fragmentation reduces the density of natural plant populations forming patches of the remaining individuals. One of the biotic interactions that can be affected by forest fragmentation and is poorly studied is seed predation. We determined the effects of forest fragmentation on seed and fruit predation in Ceiba aesculifolia by comparing trees in continuous forest with trees in fragmented forest. We compared the following variables: (a) frequency of fruit predation by Collie's squirrel (Sciurus colliaei) in each habitat; (b) frequency of the cotton-staining bug seed predator (Dysdercus, Orden Hemiptera) in each habitat; (c) the effect of seed predation on germination frequency and time; and (d) the effect of different life stages of Dysdercus on seed viability. In continuous habitat, 100% of the trees presented fruits with squirrel predation while only 34% of trees in fragmented habitats presented fruit predation. In continuous forest 27% of the trees contained fruits with the seed predator Dysdercus, while only 2% of the trees in fragmented forest presented fruit predation. In continuous forest 27% of the trees contained fruits with the seed predator Dysdercus, while only 2% of the trees in fragmented forest presented fruit predation. In continuous forest 27% of the trees contained fruits with the seed predator Dysdercus, while only 2% of the trees in fragmented forest presented fruit predation. The initial weight of damaged seeds was greater than seeds that were not damaged indicating that seed predators select heavier seeds to feed upon. Frequency of seed germination was affected by different life stages; pre-adults decreased germination significantly more than nymphs and adults. Seed predation significantly increased the time it took for germination to occur. Our study shows that forest fragmentation significantly affects predation patterns of squirrels and cotton-staining bugs. Reduction of natural seed predators in forest fragments may have long-term consequences on forest structure and diversity.

1. Introduction

Forest fragmentation affects many species of flora and fauna not only by eliminating their habitat but also by disrupting biotic interactions (Didham et al., 1996, 1998; Benitez-Malvido and Lemos-Albor, 2005). The effect of forest fragmentation on biotic interactions mainly has been studied in pollination systems (Aizen and Feisinger, 1994a, 1994b; Cunningham, 2000a, 2000b, Stoner et al., 2002; Dick et al., 2003; Quesada et al., 2004; Quesada and Stoner, 2004; Ghazoul, 2004, 2005). Less well studied is the effect of forest fragmentation on other biotic systems such as plant herbivory (Benitez-Malvido and Lemos-Albor, 2005; Valladares et al., 2006), plant–pathogen interactions (Gilber and Hubbell, 1996; Benitez-Malvido et al., 1999; Benitez-Malvido and Lemos-Albor, 2005), decomposition of dung or litter (Eggleton et al., 1996) mutualistic
mycorrhizal associations (Matthies et al., 1995; Didham et al., 1996), seed dispersal (Hamilton, 1999; Restrepo et al., 1999; Galetti et al., 2003; Ghazoul, 2005), and fruit and seed predation (Janzen, 1978; Sork, 1983; Adler, 1994; Cascante et al., 2002).

Seed dispersal and predation interactions in the tropics are particularly likely to be affected by forest fragmentation because many plant species are subject to animal dispersal and/or predation, and habitat disturbance tends to reduce or eliminate these vectors (Janzen, 1978; Cascante et al., 2002). Density dependent factors related to the availability and fluctuation of food resources are likely to maintain more dispersers and predators in continuous habitats (Bach, 1988; Didham et al., 1996, 1998). Therefore, habitat fragmentation may change the population dynamics of predators and dispersers affecting the spatial heterogeneity and/or survivorship of plants in fragmented habitats (Didham et al., 1996; Crawley, 2000). Few studies have evaluated the effects of forest fragmentation on fruit and seed predation. The trophic rank hypothesis, based on the species–area relationship, suggests that increased susceptibility to habitat fragmentation should be found at higher trophic levels (Kruess and Tscharntke, 1994; Holt et al., 1999). Thus, it is expected perhaps that seed predators should be more affected by habitat fragmentation. The empirical evidence, support this hypothesis, showing a reduction of seed predation in forest fragments (Janzen, 1978; Sork, 1983; Burkey, 1993; Wright and Duber, 2001; Cascante et al., 2002).

*Ceiba aesculifolia* (Order: Mavales, Family: Bombacaceae) is a tropical tree that presents high levels of seed and fruit predation by squirrels, *Sciurus colliae*, and hemipterans, *Dysdercus* sp. (Pyrhocoridae). Squirrels predate on the fruits by opening the valves of the green fruits one or two months before maturation and then eat the immature seeds. *Dysdercus* sp. enter newly opened dry fruits by introducing their proboscis through the seminal covering and sucking the seminal content (Janzen, 1976). The adults and nymphs of *Dysdercus* sp. are seed predators of other plant species of the Malvales (Janzen, 1972). In this study, we determine the effects of forest fragmentation on seed and fruit predation of *C. aesculifolia* by comparing trees in continuous forest with trees in fragmented forest. Furthermore we evaluate seed selection by different larval stages of the seed predator *Dysdercus* sp. and quantify the effect of seed predation by different larval stages on seed weight and germination.

2. Materials and methods

2.1. Study species

*C. aesculifolia* (Bombacaceae) is a Neotropical species distributed from Mexico to northern Costa Rica (Cascante-Marín, 1997). Adult trees grow up to 20 m in height and have diameters of 20–50 cm. *C. aesculifolia* has large (10–16 cm) flowers with five brown pubescent petals. Styles are on average 15 cm long and surpass the stamens by 1–2 cm. In the tropical dry forest of Mexico and Costa Rica, *C. aesculifolia* is the last species of the family to flower at the end of the dry season and all the fruit mature during the following dry season (Lobo et al., 2003; Quesada et al., 2004). *C. aesculifolia* has a predominantly outcrossing mating system. In the tropical dry forest of Mexico, two bat pollen vectors have been documented for this species, *Glossophaga soricina* and *Leptonycteris curasoae* (Quesada et al., 2004).

2.2. Study area

The study was conducted in the central Pacific coast of Mexico within and surrounding the Chamelá–Cuixmala Biosphere Reserve (ca. 19°30’N, 105°03’W). The size of Biosphere Reserve is 13,142 ha and is located between Puerto Vallarta, Jalisco and Manzanillo, Colima. The predominant vegetation type is tropical dry forest, which is characterized by a rainy season from the middle of June through October, and an extended dry season from November through May. Two main habitats have been described in this area, the upland dry forest, and “arroyo” forest which are found along the seasonally wet riverbeds (Lott, 1993). Average annual rainfall is 750 mm and average temperature is 25 °C.

2.3. Selection of trees

To examine the effects of forest fragmentation on fruit and seed predation of *C. aesculifolia*, we compared forest fragments with trees in continuous areas. Size of forest fragments are approximately 5–10 ha. Forest fragments consisted of less than two reproductive trees per hectare and were surrounded by agricultural fields or pastures. Forest cover is changed for cattle raisin and agriculture development; many of these areas are also constantly burned. Continuous forest consisted of groups of five or more reproductive individuals per hectare that were surrounded by continuous mature forest; all trees in continuous habitats were located within the Chamelá-Cuixmala Biosphere Reserve. Fifty trees of *C. aesculifolia* from fragmented habitats and 50 trees from continuous forest were studied.

2.4. Fruit predation

We determined the frequency of fruit predation in both habitat conditions by conducting weekly censuses during the fruiting period. The study was conducted in 2003. We systematically checked the 50 trees in each habitat condition to quantify the number of trees that contained fruits with predation marks of squirrels. Fruits that were predated by squirrels had characteristic incisor marks on the fruit husks which allowed them to be identified unequivocally.

2.5. Seed predation

First, we determined the effect of forest fragmentation on seed predation and then we evaluated seed selection by different larval stages and the effect of seed predation by different larval stages on seed weight and germination. The frequency of *Dysdercus* sp. (principal seed predator) in the fruits of each tree was quantified by conducting weekly censuses during the fruiting period. During each census, we recorded the presence and absence of nymphs and/or adults by checking all fruits that were found below each tree.
We conducted a laboratory experiment to determine if Dysdercus sp. is selective about the seeds attacked and to determine their effect on seed predation and seed viability. Individuals of Dysdercus sp. were placed in glass terrariums with seeds of C. aesculifolia to determine seed predation and germination. Individuals of Dysdercus sp. were grouped into three developmental stages based on age to control for any effects associated with development of the predator. These three age categories were: young nymph (body completely red), pre-adult (body red with black spots on back without wings); and adults (red body with black back and wings). Three replicates were done for each developmental stage with the corresponding control for each replicate (12 terrariums). We selected seeds from 40 trees, three fruits per tree and one seed per fruit for each terrarium and each seed was individually numbered with an indelible ink pen and weighed. We placed 120 seeds per terrarium. To obtain insects from each developmental stage, we raised them from eggs in terrariums under captivity. First, we obtained adult males and females from at least 20 different populations and allow them to mate in terrariums. Gravid females oviposited inside terrariums and eggs developed into nymphs, followed by one more nymphal instars, a pre-adult stage, and completing the life cycle as adults. The duration of each developmental stage was approximately one week. Each developmental stage used in the experiment was starved until the experiment started. In each of these 12 terrariums we randomly placed 120 seeds and 120 individuals of Dysdercus sp. Because each developmental stage of Dysdercus lasts for one week, seeds were exposed to predators for one week in each terrarium. During this week, 24 h a day, we conducted systematic observations in each terrarium every 2 h for 15 min. During each observation, for each seed we registered whether it was fed upon by Dysdercus sp. (i.e. proboscis was inserted into seminal covering).

After the one week exposure to predators, all seeds were weighed and germinated (control and experimental) in germination beds with humid sand. They were checked every day and considered germinated once the hypocotyl emerged. Seeds that did not germinate within 15 days were opened and the status of their embryos was observed under the microscope. Seeds predated by Dysdercus sp. were either hollow inside or their embryos were destroyed by the effect of the digestive enzymes that Dysdercus sp. injects while feeding (Janzen, 1972).

A generalized linear model applying the GENMOD procedure (SAS, 2000) was used to determine if the developmental stage of seed predator affects the probability of predation. The model used age class of seed predator, tree identity, and the interaction between tree identity and age class as categorical independent variables. The proportion of predated seeds was the dependent variable. The analysis used a binomial distribution and a logit link function. To control for variation associated with seed size, we used the original seed weight as a covariate in the model.

To determine if Dysdercus sp. predators are selective about the seeds they attack, we used a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used attacked seeds, predator developmental stage, tree identity, and the interaction between tree identity and age class as categorical independent variables. The original seed weight was the dependent variable. The analysis used a normal distribution.

To determine the effect predator developmental stage has on seed weight after predation, a generalized linear model applying the GENMOD procedure (SAS, 2000) was used. We first calculated the difference in seed weight before and after seeds were exposed to predators. The model of the analysis considered predator developmental stage, tree identity, and the interaction between tree identity and developmental stage as the categorical independent variables, and the difference in weight as the response variable. The analysis used a normal distribution. To control for variation associated with seed size, we used the original seed weight as a covariate in the model.

The frequency of germination after predation was evaluated using a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used predated seeds (yes or no), predator developmental stage, and the interaction between developmental stage and predated seeds as the categorical independent variables. The proportion of germinated seeds was the dependent variable. The analysis used a binomial distribution and a logit link function. To control for variation associated with seed size, we used seed weight as a covariate in the model.

Seed germination success after predation was evaluated using a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used predated seeds (yes or no), predator developmental stage and the interaction between developmental stage and seed predation as categorical independent variables. Days to seed germination was the dependent variable. The analysis used a normal distribution. To control for variation associated with seed size, we used seed weight as a covariate in the model.
fruits predated in fragmented habitats. Similarly, the frequency of the insect predator *Dysdercus* sp. was also dependent on habitat condition ($\chi^2 = 14.87$, df = 1, $p = 0.0001$). In continuous forest 27% of the trees contained fruits with predation by *Dysdercus* sp., while only 2% of the trees in fragmented forest had fruits with insect damage. No significant effects were observed for dbh or distance to nearest neighbor ($\chi^2 = 0.34$, df = 1, $p = 0.561$, $\chi^2 = 0.02$, df = 1, $p = 0.877$, respectively).

The probability of predation was significantly greater for seeds exposed to pre-adults of *Dysdercus* sp. than those exposed to nymphs or adults ($\chi^2 = 86.75$, df = 2, $p < 0.0001$; Fig. 1a). Furthermore, the probability of being predated also depended upon tree identity ($\chi^2 = 99.51$, df = 39, $p < 0.0001$), the interaction between tree identity and developmental stage ($\chi^2 = 9.38$, df = 2, $p < 0.0001$), and original seed weight ($\chi^2 = 7.5475$, df = 1, $p = 0.006$).

Seeds attacked by *Dysdercus* sp. weighed significantly more than seeds that were not selected for predation ($F = 38.43$, df = 1, $p < 0.0001$; Fig 1b). In addition, age class of seed predator ($F = 4.38$, df = 2 $p = 0.0128$), tree identity ($F = 100.62$, df = 39, $p < 0.0001$), and the interaction between tree identity and age class had a significant effect on seed selection ($F = 9.38$, df = 2 $p < 0.0001$).

**Fig. 1** – (a) Probability of seed predation by different predator developmental stage of *Dysdercus* sp. (b) The weight of seeds selected for predation by different age classes of *Dysdercus* sp. (c) The difference in seed weight before and after seed predation by predator developmental stage of *Dysdercus* sp. Bars represent standard error. Different letters represent significant differences ($p < 0.05$).
The current rates of defaunation and habitat fragmentation result in significant loss of biodiversity in fragmented habitats. For instance, the frequency of seed predation by insects was significantly affected by developmental stage and seed predation (F = 99.51, df = 39, p < 0.0001, F = 9.38, df = 2, p < 0.0001, respectively). Developmental stage had no significant effect on frequency of germination (𝜴² = 2.37, df = 2, p = 0.305), nor did the interaction between developmental stage and seed predation (𝜴² = 1.8, df = 2, p = 0.407). However, seed weight affected the frequency of seed germination (𝜴² = 27.68, df = 1, p < 0.0001), with larger seeds germinating more frequently.

The time of germination in non-attacked seeds was less than attacked seeds (1 day versus 4 days) (𝜴² = 66.9, df = 1, p < 0.0001, Fig. 2) and heavier seeds germinated significantly sooner (𝜴² = 21.33, df = 1, p < 0.0001). Developmental stage and the interaction between developmental stage and seed predation did not significantly affect the time of germination (𝜴² = 0.1, df = 2, p = 0.901, 𝜴² = 1.61, df = 2, p = 0.199, respectively).

**5. Discussion**

**5.1. Effects of forest fragmentation on seed predation**

The current rates of defaunation and habitat fragmentation are affecting drastically the interactions between animals and plants in tropical forests (Dirzo and Miranda, 1990; Turner, 1996; Wright et al., 2000; Silva and Tabarelli, 2001; Galetti, 2001; Galetti et al., 2003). Our results indicate that fruit predation of *C. aesculifolia* by the squirrel *S. colliae* and by the cotton-stainer bug *Dysdercus* sp. decrease in forest fragments. These results indicate that seed predator interactions are reduced or even eliminated in forest fragments but density dependent factors are maintained in continuous forests (Janzen, 1970, 1978; Cascante et al., 2002).

One hundred percent of the trees in continuous forest received fruit predation from squirrels, while only 37% in fragmented habitats had fruit predation. Several studies have shown that squirrels are negatively affected by forest fragmentation (Carey et al., 1992; Rodríguez and Andrén, 1999; Goheen et al., 2003) and it has been hypothesized that fragmented areas may not provide the appropriate habitat to harbor small mammal seed predators because of reduced food availability (Chiarello, 2000). Another factor that may influence the lower abundance of squirrel seed predators in fragmented areas is the greater abundance of feral animals (dogs and cats) in these habitats (Y. Herrera, M. Quesada, K. E. Stoner, Pers. Obs). Finally, reduced immigration has been identified as an important factor affecting population density of squirrels in isolated populations (Wauters et al., 1994).

Similarly, the frequency of the insect seed predator *Dysdercus* sp. was also significantly lower in fragmented habitats (2% versus 27% of trees in fragmented and continuous habitats, respectively). The populations of *Dysdercus* sp. are likely affected by density-dependent factors related to the availability of food resources within fragmented areas and the limited capacity to fly between trees that are distantly located in fragmented populations (Socha and Semek, 2003). Our results agree with some other studies that have shown less insect seed predation in fragmented compared to continuous forest (fruit predation Wright and Duber, 2001; seed predation Janzen, 1978; Burkey, 1993; Cascante et al., 2002; Francisco et al., 2002; Chacoff et al., 2004). For example, the tropical dry forest shrub *Bauhinia pauletia* and tree *Samanea saman* experience less seed predation in small forest patches and fragmented areas compared to continuous forest (Janzen, 1978; Cascante et al., 2002, respectively). Chapman et al. (2003) found reduced seed predation in forest fragments in western Uganda. Similarly, Pizo (1997) reports significantly less seed predation by both insects and small mammals in a 250 ha forest fragment compared to a 49,000 ha Reserve in the Brazilian rain forest.

**5.2. Seed selection by different larval stages and the effect of seed predation on seed weight and germination**

The probability of predation was significantly greater for seeds after seed predation exposure (F = 6.35, df = 1, p = 0.019, Fig. 1c). Seeds attacked by adults lost more biomass than seeds attacked by nymphs or pre-adults. The difference of seed weight before and after seed predation was significantly affected by tree identity and the interaction between developmental stage and seed predation (F = 39.51, df = 39, p < 0.0001, F = 3.8, df = 2, p < 0.0001, respectively).

The frequency of germination of predated seeds was significantly lower than non-predated seeds (𝜴² = 756, df = 1, p < 0.0001). Ninety-five percent of intact seeds germinated, while only 5% of attacked seeds germinated. Developmental stage had no significant effect on frequency of germination (𝜴² = 2.37, df = 2, p = 0.305), nor did the interaction between developmental stage and seed predation (𝜴² = 1.8, df = 2, p = 0.407). However, seed weight affected the frequency of seed germination (𝜴² = 27.68, df = 1, p < 0.0001), with larger seeds germinating more frequently.

The time of germination in non-attacked seeds was less than attacked seeds (1 day versus 4 days) (𝜴² = 66.9, df = 1, p < 0.0001, Fig. 2) and heavier seeds germinated significantly sooner (𝜴² = 21.33, df = 1, p < 0.0001). Developmental stage and the interaction between developmental stage and seed predation did not significantly affect the time of germination (𝜴² = 0.1, df = 2, p = 0.901, 𝜴² = 1.61, df = 2, p = 0.199, respectively).

**Fig. 2** – Time of germination after seed predation test by each predation treatment of *Dysdercus* sp. Bars represent standard error. Different letters represent significant differences.
exposed to nymphs or adults. Furthermore, Dysdercus chose significantly heavier seeds for predation. The higher incidence of seed predation observed in pre-adults may be influenced by greater metabolic needs of pre-adults before metamorphosing into adults (Derr et al., 1981). Although seeds of all sizes are subject to predation from a variety of predators while on the soil surface (Abbott and Van Heurck, 1985; Thompson et al., 1994; Meiners and Stiles, 1997; Reader, 1997; Leishman et al., 2000), only small seeds (which are consumed by invertebrates) can usually escape predation by incorporating themselves into the seed bank (Leishman et al., 2000). Maternal effects associated to seed size are also related to seed predation probability. Large seeds of specific maternal trees are more likely to be attacked by Dysdercus sp. than small seeds of other maternal trees. These effects have not been analyzed in other studies suggesting the need to understand these subtle interactions and its implications on plant regeneration.

Damaged seeds lost significantly more weight than undamaged seeds. Pre-adult and adult Dysdercus sp. reduced the biomass of seeds more than the nymphs. In Sterculia apetala, Dysdercus predated 1/4 to 3/4 of the seed weight and these seeds failed to germinate (Janzen, 1972). Seed predation can have repercussions on survival, distribution patterns, and composition of plant communities (Sallabanks and Cournay, 1992; Hammond, 1995; Benitez-Malvido, 1998; Cascante et al., 2002; Fleury and Galetti, 2004). Predation by insects reduces seed germination either by damaging the embryonic axis or by consuming the cotyledon (Schelin et al., 2004).

Our results indicate that the frequency of seed germination was significantly reduced by seed predation. Similarly, seed predation significantly increased the time of germination. Few studies have shown that plant distribution is affected by seed predation and recruitment along forest fragments (Sork, 1983). Reduction of seed viability can change the spatial heterogeneity and demography of plant species and can affect the regeneration in continuous forest fragments.

The effect of forest fragmentation on the interaction of predators of fruits and seeds has not been well studied. A high proportion of seed production is lost due to seed predators in every fruiting event and can have significant negative effects on the reproductive success of plants (Janzen, 1972, 1981; Howe, 1980; Schupp, 1988). This biotic interaction is a major ecological and evolutionary force that affects individ-

tors in every fruiting event and can have significant negative effects on plant communities (Sork, 1983). Reduction of seed viability can change the spatial heterogeneity and demography of plant species and can affect the regeneration in continuous forest fragments.

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Bacilieri et al., 1993; Burkey, 1993; Didham et al., 1996; Benitez-Malvido, 1998; Wright and Duber, 2001). The reduction or elimination of seed predators in forest fragments may negatively affect competitive interactions of plant species, thereby changing the original species composition of fragmented communities. Local exclusion or even extinction of plant species from forest fragments can eventually reduce the important biodiversity of tropical ecosystems.


