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Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest

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ARTICLE INFO

Article history:

Received 7 March 2007

Received in revised form

9 July 2007

Accepted 13 September 2007

Available online 21 December 2007

Keywords:

Astrocaryum

Coleoptera

Fragmentation

Los Tuxtlas

Palms

Pollination

ABSTRACT

Tropical forest fragmentation affects both biodiversity and plant reproductive success when small, isolated fragments sustain a reduced diversity or abundance of pollinators. Fragmentation-related effects have been poorly investigated in the case of palms, an important structural and functional component of tropical forests. We examined the relationships between fragment size and diversity and abundance of flower visitors, and palm reproduction, by quantifying the arthropod fauna associated to inflorescences of the palm *Astrocaryum mexicanum*, and its fruit set, in fragments of different size. The sample yielded a total of 228,772 arthropods (10 orders, 60 species). Coleoptera was the predominant group ($\geq 50\%$ of the species), followed by Hymenoptera (20%), while the remaining (30%) was distributed among the other eight orders. We found a predominance of pollinating insects (Coleoptera-Nitidulidae), representing 85% of all visitors. Pollinator abundance was negatively affected by fragmentation, with a 4.2-fold average difference between small (<35 ha) and large (114–700 ha) fragments. However, fruit set was relatively high (≥ 0.7) and not affected by fragmentation during three reproductive seasons. This could be explained because small fragments retained remarkably high numbers of pollinators (1191.4/inflorescence) and by the high abundance of palms (and flowers) in fragments. Further research is needed, however, to assess if fragmentation restricts pollinator movements to plants within the fragments, leading to a reduction in genetic variation of the progeny present in forest remnants.

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1. Introduction

Current patterns of land use in tropical forests (i.e., their conversion to grasslands for cattle ranching or agricultural fields) generate a landscape mosaic of fragments of different size, imbedded in a matrix of transformed lands (Dirzo, 2001; Mendoza et al., 2005; Arroyo-Rodríguez et al., 2007). Research on the biodiversity consequences of tropical fragmentation has

focused on changes in species diversity or abundance of some groups of organisms, particularly birds and mammals (e.g., Ferraz et al., 2007; Corlett, 2006; Lees and Peres, 2006) and plants (Scariot, 1999; Laurance et al., 2000; Hill and Curran, 2005; Cagnolo et al., 2006; Laurance et al., 2006). In contrast, other groups of organisms, such as insects, have received comparatively less attention (see Didham et al., 1996; Driscoll and Weir, 2005; Grimbacher et al., 2006; Vasconcelos et al.,

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doi:10.1016/j.biocon.2007.09.014

2006). This is so despite the fact that insects are critical in myriad ecological processes susceptible to be affected by fragmentation (see review in [Didham et al., 1996](#); [Tscharntke and Brandl, 2004](#); [Valladares et al., 2006](#)), including pollination ([Kearns et al., 1998](#); [Harris and Johnson, 2004](#); [Ghazoul, 2005](#); [Kremen et al., 2007](#)). It is known that more than 90% of tropical tree species require of biotic agents, particularly insects, for their pollination ([Bawa, 1990](#)). Furthermore, a large proportion of all tropical plants are self-incompatible ([Bawa, 1992](#)), or have some mechanism to avoid selfing ([Kress and Beach, 1994](#)). Thus, we could expect that in out-crossing plants remaining in isolated fragments the possibilities of receiving pollen from other compatible individuals would be low or even null, making them more vulnerable to the loss of genetic variation ([Murcia, 1996, 2002](#); [Honnay and Jacquemyn, 2007](#)). [Aguilar et al. \(2006\)](#) recently reviewed 54 publications and found that reproduction is negatively affected by habitat fragmentation, and that pollinators are crucial in these effects. However, most of the studies involved herbaceous perennial species and only a few were tropical tree species. [Lowe et al. \(2005\)](#) found that in seven out of ten studies of tropical trees there were negative consequences on seed set associated to a variety of habitat disturbances related to tree isolation. Likewise, [Aizen et al. \(2002\)](#) reviewed 25 studies involving 46 different species of plants and found that, in the case of herbaceous species, fragmentation had a negative effect on pollination and fruit or seed set in 92% and 76% of the studies, respectively. Nevertheless, most of the studies in their review involved herbaceous species from temperate ecosystems and only a minor fraction (10% of the studies) looked at species from tropical zones. In the case of trees, only three species were from tropical forests and, surprisingly, two of them showed a positive effect of fragmentation on pollination, and only one showed negative effects. While the former two species are pollinated by birds, the latter is pollinated by insects. These results are intriguing, but studies are still too few to speculate whether in the tropics insect pollination is more affected than vertebrate pollination, and whether fragmentation has limited or no negative effects on pollination.

Many important pollinators, including wasps, bees, and beetles, are of relatively small size ([Ghazoul and McLeish, 2001](#); [Listabarth, 2001](#); [Ghazoul and Shaanker, 2004](#)) and restricted capacity of movement and search range relative to the spatial configuration of the remnant forest fragments (but see [Nason et al., 1996, 1998](#); [Nason and Hamrick, 1997](#)). Many tropical insects important for tree pollination are known to experience reduced abundances within small or isolated forest fragments ([Aizen and Feinsinger, 1994](#); [Didham et al., 1996](#); [Murcia, 2002](#); [Valdivia et al., 2006](#)).

Palms, a group of floristically and structurally important plants in tropical forests, have received limited attention from the point of view of the effects of fragmentation on their reproductive biology. In their reproductive stage, palms are a diverse or abundant component of the upper and medium strata of tropical forests ([Scariot, 1999](#)), and a suite of species are also present in the understory as mature individuals. The study of the effects of fragmentation on palm reproductive biology is also important since many of them are obligate out-crossers (58% of the species) or dioecious (45% of the species) ([Murcia, 1996](#)) and many of them are of economic impor-

tance ([Vormisto, 2002](#)). Regarding their pollen vectors, [Henderson \(1986\)](#) distinguishes three pollination syndromes: cantharophily (beetle pollination), mellitophily (bee pollination), and miophily (fly pollination). Although most palms do not seem to exhibit a marked morphological fit and specialization in their flowers relative to pollinator morphology and behavior ([Uhl and Dransfield, 1987](#)), some cantharophilous species do ([Bernal and Ervik, 1996](#); [Listabarth, 1996, 2001](#); [Henderson et al., 2000](#)), and it is suggested that cantharophily is the predominant syndrome among understory palms ([Kahn and De Granville, 1992](#); [Henderson, 1995](#); [Núñez et al., 2005](#)). Given that cantharophily generally involves small-sized insects, we would expect for fragmentation to have a negative impact on pollination of understory palms ([Blanche and Cunningham, 2005](#)).

Here we quantify the community of arthropods visiting the inflorescences of the tropical palm *Astrocaryum mexicanum* Liebm. to examine to what extent fragment size affects its flower visitors and, potentially, its reproductive success. This plant is a useful model to investigate fragmentation-related changes in pollination, given that it is an abundant plant in the study site, and that a previous study ([Búrquez et al., 1987](#)) reported details of its pollination biology and the identity of the pollinators in continuous forest. We used this system to ask: (i) what are the main visitors and pollinators to the inflorescences of *A. mexicanum* in forest fragments of different size? (ii) to what extent is the abundance of the main pollinators affected by fragmentation? and, (iii) if fragmentation affects pollinator abundance, to what extent does this in turn affect fruit set?

2. Methods

2.1. Study site and selection of fragments

The area of the study site, Los Tuxtlas, is a mountainous region located in the State of Veracruz, SE Mexico ([Fig. 1a](#)), and represents the northernmost limit of tropical rainforest distribution in the Americas ([Dirzo and Miranda, 1991](#)). The predominant vegetation in the lowlands is tropical rain forest, with considerable variations along the elevation range, including cloud forest and mixed (conifer and broadleaf) forests at higher elevations. Its latitudinal position and elevation range determine the existence of remarkable combinations of species of tropical and boreal origin ([González-Soriano et al., 1997](#)). In addition to the diversity of habitats, species richness in various groups of organisms is considerable, including a total of 950 known vascular plants ([Ibarra et al., 1997](#)). Characteristics of the region's physical environment, flora, fauna and natural history are described in detail in [González-Soriano et al. \(1997\)](#).

Although the area has been occupied by humans for a long time, the most extensive conversion, mostly to grasslands for cattle ranching, has occurred in the recent decades ([Mendoza et al., 2005](#)). Rates of deforestation corresponding to the decades of the 60s–late 80s were of the order of 4.3% per year ([Dirzo and García, 1992](#)). Currently, forest remnants are restricted to the most inaccessible areas of the region and the spatial configuration of the landscape consists of a large number of small to very small fragments (<1.0 ha) with only a few extensive areas still remaining ([Mendoza et al., 2005](#)).

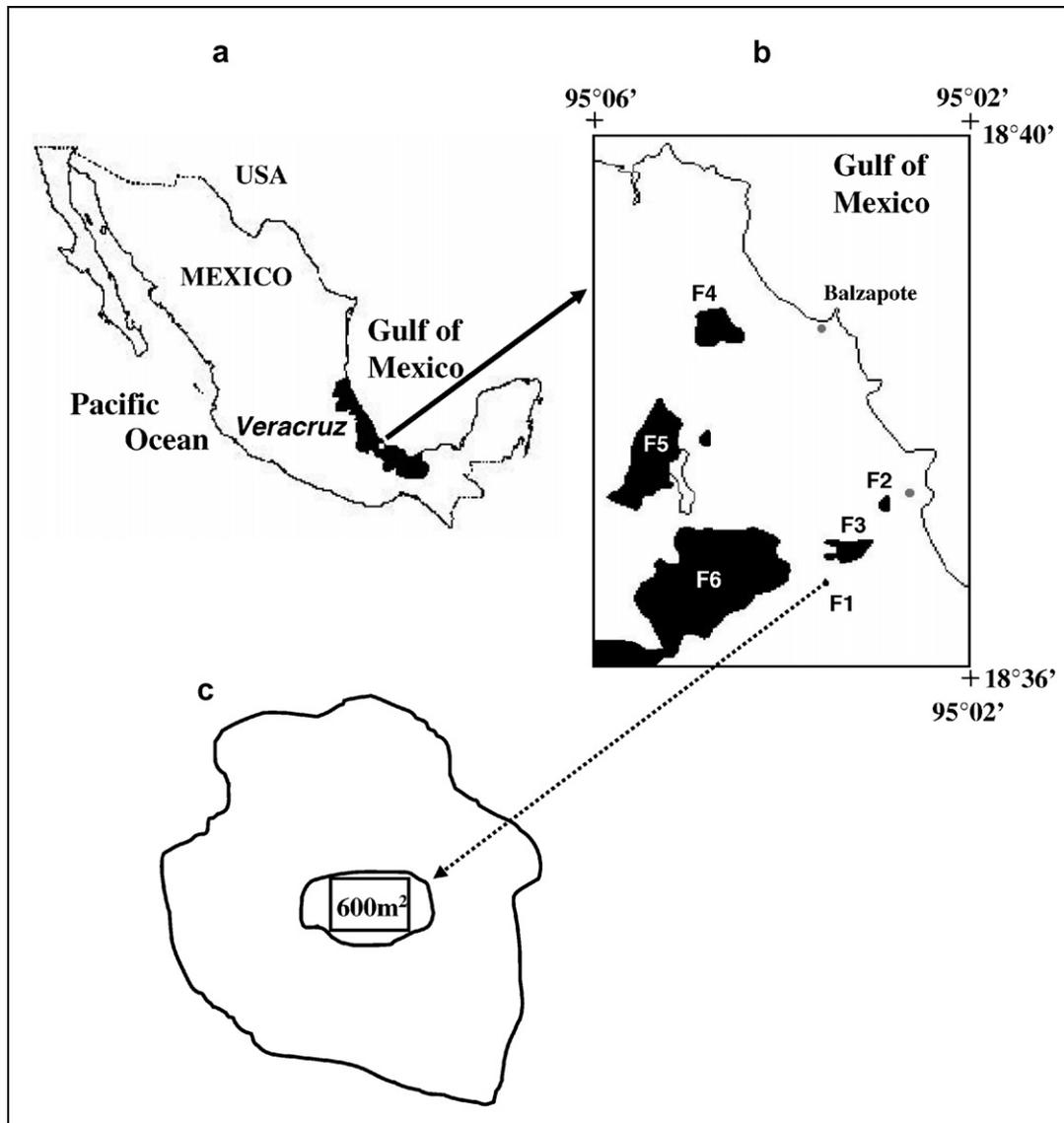


Fig. 1 – Location of the study site in the State of Veracruz, Mexico (a), including the specific location of the fragments (F1–F6) within the area of study (b) and the sampling design of plants within 600 m² permanent observation plots in the fragments (c). The drawing in C mimics a situation for smallest and second smallest fragments.

For this study we chose isolated fragments of similar age (isolation time from continuous forest), with the same vegetation type, lowland tropical rain forest, and generally similar ecological conditions (i.e., within a restricted elevation, same climate and edaphic characteristics). With these criteria, we selected five fragments of 2, 4, 19.4, 34.6, and 114.6 ha with ~20 years from excision, and an extensive tract of lowland forest (Table 1). The latter, corresponding to the Los Tuxtlas research station, extends westwards, towards the San Martin Volcano (~1600 m a.s.l.), encompassing a much larger area of relatively continuous forest, although tropical rain forest is restricted to the lowlands, representing an area of c. 700 ha. For the purposes of this study we considered this as a “large fragment” of 700 ha. Fragments were selected from direct exploration in the field and using an aerial photograph (scale 1:75,000) which was digitized using ILWIS 2.4 software to calculate the areas of each fragment (Fig. 1b).

Table 1 – The selected fragments of study in the area of Los Tuxtlas, Veracruz, Mexico

Fragment code	Area (ha)	Elevation (m a.s.l.)	Geographic location (lat.N-long.W)
F1	2.0	59	18°34'40.14"– 95°03'58.84"
F2	4.0	187	18°35'24.39"– 95°03'32.14"
F3	19.4	61	18°35'02.01"– 95°03'43.66"
F4	34.6	205	18°37'12.20"– 95°05'04.61"
F5	114.6	100	18°36'31.94"– 95°05'40.60"
F6	700.0	150–220	18°34'57.27"– 95°05'02.78"

2.2. Study system

A. mexicanum Liebm. (Arecaceae) is a monoecious palm distributed in tropical rainforest areas of Southeast Mexico,

and the only species of the genus in the country (Henderson, 1986). Its distribution in the region's altitudinal range is between 0 and 700 m a.s.l. (Fig. 1b). In the forest of Los Tuxtlas this is the most abundant species in the understory, with an average density of 1000 palms ≥ 1 m height ha^{-1} (Martínez-Ramos, 1997). The reproductive stage of *A. mexicanum* begins at about 40 years of age and lasts for more than 100 years in certain individuals, and most of the reproductive individuals belong to the height class of 2–6 m (Sarukhán, 1978; Piñero et al., 1984). The tallest individuals grow to a height of c. 8 m (Búrquez et al., 1987). Throughout the reproductive season a reproductive palm can have up to five inflorescences, each with an average of 4885 male flowers and 28 female flowers (Búrquez et al., 1987). Female flowers open synchronously on a given day, lasting until the morning of the following day, when opening of the male flowers begins. The male and female functions overlap for a short period in the same inflorescence, but at this time stigmatic receptivity is very low and the pollen is largely unviable (Búrquez et al., 1987) thus pollination requires the spatio-temporal coincidence of individuals in the two flower phases.

2.3. Insect sampling protocol

Within each fragment we established a 600 m² (30 × 20 m) permanent plot of plant observations, located in the center of each fragment (Fig. 1c). In each plot, used for a long-term demographic analysis, we located and tagged all plants of *A. mexicanum*. From these we selected a group of reproductive plants of a similar height (~age) to sample flower visitors.

Visitors to the inflorescences were collected during the peak of the flowering season (March–May) of 1999. The greatest concentration of male and female flowers per inflorescence during this period translated into the greatest availability of the reward offered by this plant (pollen grains) to flower visitors. Our sampling therefore included most visitors to flowers and not just a small sample that may not reflect the pollinator fauna. Within each plot we collected the inflorescences of 10 randomly selected palms in the female phase, and five in the male phase. With the aid of a ladder, we reached the inflorescence of each plant and using a thick-paper bag we rapidly encapsulated the inflorescence, without disturbing it, and removed it by cutting the peduncle with clippers. No visual evidence of insect escape was detected, and application of the same exact protocol insured that sampling was comparable among sites. All inflorescences were collected between 0700 and 0800 AM, the time at which we observed the most intense insect activity, consistent with observations by Búrquez et al. (1987). Upon collection, we placed a ball of cotton wool soaked in ethyl acetate in the bags with the inflorescences. The bags were transported to the laboratory for arthropod separation, quantification and individual identification. Insects, but particularly Coleoptera were the most abundant flower visitors. Sorting and identification was carried out with the assistance of Dr. S. Zaragoza (Coleopterologist, Entomology Department, Institute of Biology, UNAM).

A first approximation to describe the arthropod communities visiting the flowers of *A. mexicanum* and the possible fragmentation-related changes in the identity and composition of

the community was to sort insects by order. We calculated the number and percentage of individuals for all orders. From this we then defined the species richness and determined, based on a previous study on the pollination of *A. mexicanum* at Los Tuxtlas (Búrquez et al., 1987), and from direct observations in the field, which of them were the pollinators of this palm. Following Búrquez et al. (1987), we defined flower visitors as pollinators when, in addition to their massive, readily evident pollen loads, we observed that their behavior consisted of both collecting pollen from the flowers in the male phase and transferring it onto the receptive flowers in the female phase.

2.4. Fruit set calculation

At the fruiting peak of 1999 we collected one of the infructescences from a random sample of reproductive plants present within each of the permanent plots ($N = 10$ plants in years 1999 and 2000 and $N = 20$ in 2002, for a total of 60, 60 and 120, respectively). We estimated fruit set as the ratio of the number of fruits/number of female flowers per infructescence/inflorescence. The number of flowers per inflorescence was defined by carefully counting the female flower scars from the mature infructescences. To insure reliability of flower counting, each of the scars in the rachis of the infructescence was tallied and a mark was placed with an indelible marking to avoid repeated or missed counting. The number of fruits was counted directly from the mature infructescences. To prevent that fruits that could have fallen off the infructescences would be missing in our counting, we placed a fruit trap (a basket made of cloth mesh held with wire) directly under the inflorescence. Such traps were firmly tied to the palms' trunks. Given that this year we did not find variation in fruit set across sites the same procedure was applied on the reproductive seasons of 2000 and 2002 to assess if this result was consistent among years.

3. Results

3.1. Fauna associated to inflorescences of *A. mexicanum*

Our sampling collectively detected a remarkable abundance of arthropods: 228,772 individuals associated to all sampled inflorescences (and considering both male and female phases) of *A. mexicanum*. The vast majority of the observed animals were insects. Collectively, we found 10 orders (nine of Insecta and one of Arachnidae), 12 families and 60 species. On average, an inflorescence of *A. mexicanum* bears 2660.13 arthropods, including those present in the male and female phases of the inflorescence.

Quantification of the fauna associated to the inflorescences of *A. mexicanum* across fragments showed that, in each site, a minimum of 50% of the insect species corresponds to Coleoptera (Fig. 2a). Another important proportion corresponds to Hymenoptera (~20%), while the remaining (~30%) is distributed among two to four additional orders (Fig. 2a). The four smallest fragments (2, 4, 19.4, and 34.6 ha) had between five and six orders, while the two largest sites (114.6 and 700 ha) had four orders each. The total number of species per fragment ranged from 24 to 39, with the second smallest frag-

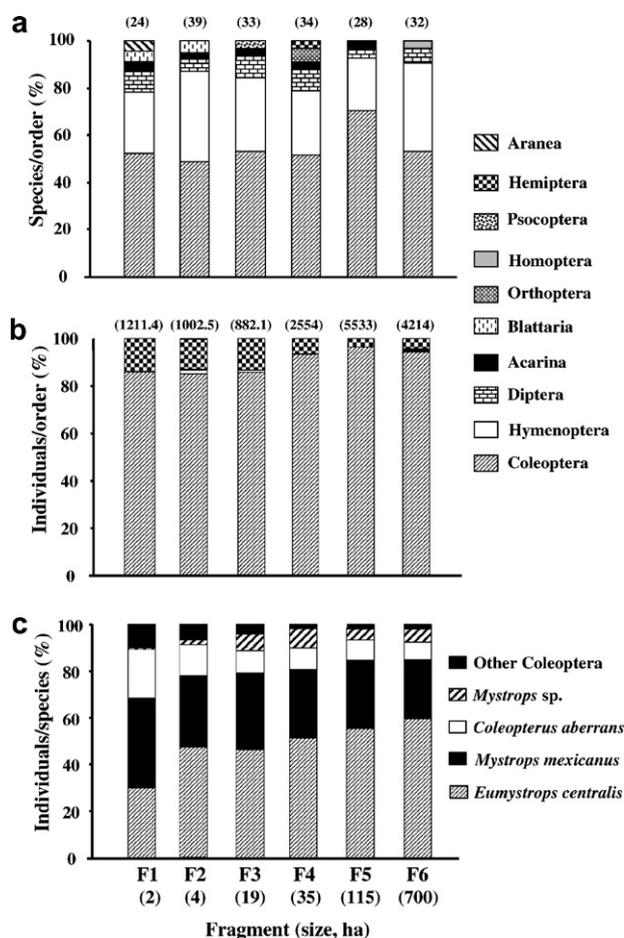


Fig. 2 – Arthropod fauna associated to the inflorescences of *Astrocarylum mexicanum*: (a) percent of species per order in each fragment, (b) abundance, as percentage of individuals per order and (c) abundance of beetles of the four species detected as the important pollinators. Numbers above the bars (in parenthesis) represent the total number of species (a) and the mean number of individuals (b) per inflorescence in each fragment.

ment (4 ha) showing the greatest number of species, 39, while the lowest number (24), was found in the smallest fragment (Fig. 2a). Apart from Coleoptera, many of the species present in the smallest fragments included visiting taxa that do not operate as pollinators.

The predominance of Coleoptera is even more noticeable when considering abundance (Fig. 2b). Overall, better than 85% of the individuals collected in each fragment were Coleoptera, with abundances of 851–5312 beetles per inflorescence in each fragment. The abundance of Coleoptera is even more marked in the three largest fragments. Hemiptera was the second most abundant group (~10%); the rest of the orders only represent a small proportion, in some cases with a single individual.

Among the Coleoptera, four species were identified as the most important pollinators, *Mystrops mexicanus*, *Coleopterus aberrans*, *Mystrops sp.* and *Eumystrops centralis*. This was determined by our direct observation of their capacity to move within an inflorescence as well as among plants, and their

pollen loads (cf. *Búrquez et al., 1987*, A. Aguirre, unpub. data), ranging from 430 to 711 pollen grains/animal. In addition, two of these four species (*E. centralis* and *M. mexicanus*) were the most abundant in all fragments, and the other two pollinators were present in abundances of 10–23% (Fig. 2c). The rest of the species of Coleoptera appeared not to be important in the pollination in this palm (lack of pollen loads and limited mobility; A. Aguirre, unpub. data) and these represented a very small proportion, of the order of up to 5–10% in all fragments. Thus, the rest of our results focus on the pollinators.

3.2. Effects of fragment size on pollinator abundance

Pollinator abundance varied in relation to fragment size (cf. Fig. 2), with a trend of reduction in abundance in the smallest fragments. The trend, however, is not linear. Instead, a threshold is insinuated, in which the three or four smallest fragments present numbers of pollinators which were considerably smaller (1270–3879 pollinators/plant) than those of the other, largest (6383–9893) fragments. With the aim of rigorously examining this trend, we ran a grouping analysis, UP-GMA (Unweighted Pair Group Method) (MVSP, version 3.1) using the total number of pollinators per inflorescence. The results, using the first divisive Euclidian distance (c. 3500), showed the definition of two major clusters: one composed of the two largest fragments (114.6 and 700 ha), which separates completely from the rest of the fragments; the second is constituted by a well defined group of fragments of 2, 4 and 19.4 ha, which in turn join the 34.6 ha fragment at a Euclidean distance of 1600. Therefore subsequently data are analyzed with two-sample comparison tests, instead of regression-type analyses.

Using this approach, the effects of fragment size on the abundance of pollinators of *A. mexicanum* become readily evident. In the case of the total number of pollinators (all four species) and lumping the data for both phases of the inflorescences, we observe a 4.2-fold reduction in the number of pollinators in the small fragments (Fig. 3a) (t -test = 4.28, $df = 4$, $P = 0.01$). The results are consistent in both phases of the inflorescences although the difference is greater in the male (an 8.8 reduction) than in the female phase (a 3.4 reduction) (data not shown). An independent analysis considering *E. centralis* in both phases of the inflorescences (Fig. 3b) showed that the mean number of these pollinators is 6-times smaller in the small fragments (t -test = 6.11, $df = 4$, $P = 0.003$); contrasts were similar in the male (an 8.9 ratio) and female (a 5.1 ratio) phases (data not shown). Finally, in *M. mexicanus* (Fig. 3c) there was a 3.6-fold reduction in abundance in the small fragments (t -test = 3.67, $df = 4$, $P = 0.02$), with a greater contrast in the male phase (a 11.4 difference) than in the female phase (a 2.7 reduction) of the inflorescences (data not shown). Given this consistent and significant reduction in the abundance of pollinators in the smaller fragments, we would expect a concordant reduction in plant reproductive success associated to fragmentation.

3.3. Effect of fragment size on fruit set

Fruit set was relatively high, at least 0.7 in all three years that we measured it (Fig. 4). In 1999, the year in which we

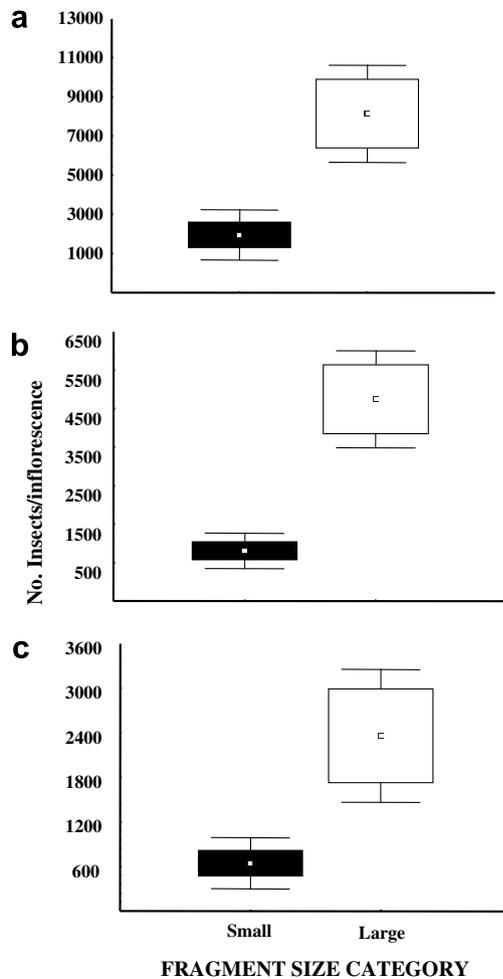


Fig. 3 – Comparisons of pollinator abundance between fragments of contrasting size (small, large) in both sexual phases of the inflorescences of *Astrocaryum mexicanum*: (a) all four pollinators, (b) *Eumystrops centralis* and (c) *Mystrops mexicanus*. Box plots represent the mean, standard error and standard deviation of four (small) and two (large) fragments.

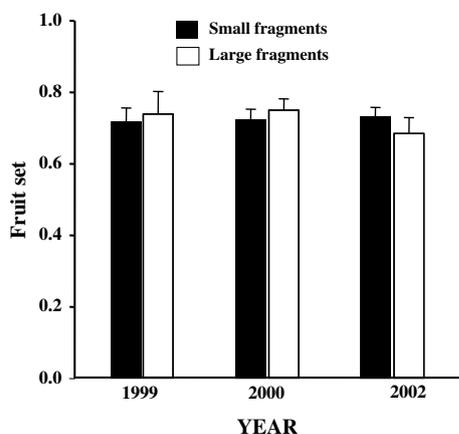


Fig. 4 – Mean fruit set of plants from the two categories of fragment size in three different years. Lines above the bars represent standard error.

measured the changes in pollinator abundance associated to fragment size, mean fruit set in small and large fragments was almost the same. When we quantified fruit set in two additional reproductive seasons, 2000 and 2002, we found remarkably consistent results and in no case were differences statistically significant (t-test, $P > 0.233$ in all three cases). In addition, we did not observe variation in the proportion of viable fruits per plant (t-test = 0.08, $P = 0.94$) and germination percentage (t test = 0.33, $P = 0.74$) across fragments.

4. Discussion

4.1. The contingent of arthropods associated to palm inflorescences

Taking into account the density of *A. mexicanum*, of c. 1000 plants ≥ 1 m height ha^{-1} (Piñero et al., 1977; Martínez-Ramos, 1997), and that in a given year the number of reproductive plants is around 300 ha^{-1} (Martínez-Ramos, 1997), our finding of an average of 2660.13 arthropods per inflorescence translates into a number of 798,039 arthropods ha^{-1} associated to this palm. This number is conservative, since some reproductive palms may produce up to five inflorescences in a given reproductive season. Using a median value of 2.0 inflorescences per reproductive palm, the abundance of arthropods associated to the inflorescences of *A. mexicanum* in Los Tuxtlas is an astonishing number of 1.596 million arthropods ha^{-1} . Furthermore, given the relatively small size of the inflorescences (only ~ 40 cm length and 24.95 ± 1.04 g dry weight), the density of arthropods is remarkable: our data suggest an animal load of 106.6 animals g^{-1} of inflorescence. These findings underscore the importance of *A. mexicanum* in particular, and of palms in general, as a resource, either trophic, or habitat, or both, for insects in tropical forests. A recent paper (Ellwood and Foster, 2004) reported an estimated abundance of 1.16 million invertebrates ha^{-1} associated to an abundant epiphytic fern (*Asplenium nidus*) in Borneo. Such striking number was used to argue that, by including the fauna of epiphytes, we can more than double the estimates of total invertebrate biomass in an entire tropical rain forest canopy. It is thus remarkable that our study yielded a similar estimate of abundance (biomass data not available) based only on the arthropod fauna associated to the inflorescences of a single, dominant palm. In addition, a salient result was the marked predominance of Coleoptera, which consistently represented c. 50% of the sampled animals in all fragments.

Species richness, totaling 60 species, is similar to that found on other palms, including *Bactris bifida*, *B. monticola* and *B. gasipaes* (Listabarth, 1996); *Geonoma irena* and *G. cuneata* (Borchsenius, 1997), *Hyospathe elegans* (Listabarth, 2001), *A. vulgare* (Consiglio and Bourne, 2001), *Attalea allenii* and *Wettinia quinaria* (Núñez et al., 2005) in natural forests, and on *Elaeis guineensis* in crop plantations (Mayfield, 2005). This data set underscores the importance of palms as reservoirs of tropical biodiversity.

Although a relatively diverse arthropod fauna visited the inflorescences of *A. mexicanum*, only a few had the appropriate attributes to function as pollinators: (i) the large amount of pollen transported on their body (range: 430 to 711 pollen grains/animal; Búrquez et al., 1987) and (ii) their activity

patterns, consisting in both collecting pollen from the flowers in the male phase, and the transfer of pollen onto the receptive flowers during the female phase (Búrquez et al., 1987; Anderson et al., 1988; Núñez et al., 2005). Such a contingent of species included those previously reported by Búrquez et al. (1987) and the two additional species (*E. centralis* and *M. mexicanus*) we detected in this study.

The contingent of non-Coleoptera taxa we observed largely corresponds to arthropods that do not seem to play a role in palm pollination (see Henderson, 1986; Búrquez et al., 1987; Listabarth, 1996). Furthermore, it is known that several of these animals can have a negative impact on the flowers. Some Orthopterans, for example, operate as flower consumers. This is the case of *Melanonotus* sp., a large phytophagous Tettigoniid that, although of low abundance, is frequently found in the inflorescences of *A. mexicanum* (R. Dirzo, unpubl. data); likewise, some species of Diptera, Apidae and Vespidae were found carrying pollen but they are unlikely to have a positive role as pollinators of *A. mexicanum* given that, in addition to their low abundance, their relatively large size (particularly in the case of wasps and bees) prevents them from reaching the female flowers at the base of the inflorescences.

4.2. Fragment size and pollinator abundance

The abundance of Coleoptera in general, and of the pollinator beetles in particular, was high in all fragments, but there was significant variation associated to fragment size. Considering either all four species of pollinators or each species individually, we detected a marked numerical reduction in the smaller fragments. These trends are consistent with those reported in other systems (see Murcia, 1996 for a review), including woody plants in Argentinean dry forest chaco (Aizen and Feinsinger, 1994), herbs in temperate forests (Jennersten, 1988) and bee visitation rates (using chemical attractants) in Amazonia (Powell and Powell, 1987). Furthermore, Wang et al. (2005) found that the abundance of the wasps responsible for the pollination of *Ficus racemosa* decreases with fragmentation, while the abundance of non-pollinating, parasitic galling wasps, increases. Such differential change resonates with our findings of a decrease in the abundance of pollinators and an increase in the abundance of non-pollinating arthropods (including phytophagous insects that damage the inflorescences, and carnivorous arthropods that prey on other visitors, including pollinators) in the smallest fragments or near the fragments' edges (Chacoff and Aizen, 2006).

A noticeable aspect of the impact of fragment size on pollinator abundance was the insinuation of a threshold. Although our resolution is limited given that we did not have sufficient fragments to represent all the size-variation across the range, in general fragments smaller than 35 ha had pollinator abundances that were 3.6- to 6.0-times lower than those of the fragments ≥ 100 ha. Reductions in pollinator abundance associated to fragmentation have been noticed in other studies with long-lived plants, including semi-tropical ecosystems (e.g., Aizen and Feinsinger, 1994; Donaldson et al., 2002; Ghazoul and McLeish, 2001), but we are not aware of other studies in which such a magnitude of fragmentation-related reduction in pollinator abundance has been detected.

4.3. Fragment size and plant reproductive success

Although the significant and consistent reduction of pollinator abundance in both phases of the inflorescences in the smallest fragments opened the possibility of an indirect negative impact of fragmentation on plant reproductive success, we found that there was no effect on the fruit set of the plants of the same study sites in the same year of the observations of pollinators. Furthermore, when we repeated the measurements of fruit set in two additional years, the results were the same. Although some studies have found evidence consistent with the expectation of negative effects of fragmentation on plant female reproductive success (seed set and/or fruit set) (Aizen and Feinsinger, 1994; Murcia, 1996; Gigord et al., 1999; Cunningham, 2000; Ghazoul and McLeish, 2001; Murren, 2002; Quesada et al., 2003; Harris and Johnson, 2004; Kolb, 2005), other researchers have reported findings similar to ours (Cascante et al., 2002; Aguilar and Galetto, 2004; Herrerias-Diego et al., 2006; Ramos and Santos, 2006). In a recent review, Ghazoul (2005) found that 21 of 51 studies analyzing the effect of patch size do not show detectable effects on pollination or other aspects of plant reproductive success.

A possible explanation for our results is that, even when pollinator reduction was substantial, the numbers of pollinators observed to be present in the plants of the small fragments were still considerably high (an average of 1191.4 pollinators, considering the four pollinator species). In addition, pollinators have considerably high pollen loads (Búrquez et al., 1987). Such pollinator abundances and pollen loads reflect the existence of several thousand pollen grains potentially available for deposition on an *A. mexicanum* inflorescence in the female phase. For example, this number is 1825 pollen grains/female flower/inflorescence, considering *Mystrops* sp. alone, the least abundant of the four pollinators. In general, male function in flowers of animal-pollinated plants needs repeated visits for the complete dispersion of pollen, while female flowers can cover all their pollen needs with a single visit (Bell, 1985; Stanton et al., 1986). Thus, since the female flower of *A. mexicanum* has only one ovule to pollinate, and there are few female flowers per inflorescence relative to male flowers (4885 male flowers: 28 female flowers; Búrquez et al., 1987), we can expect that most of the female flowers will be pollinated. These observations and the consistently high values of fruit set, suggest that our finding of a lack of effects of fragmentation on fruit set is probably due to the abundance of the remaining pollinators. This implies that fruit set could still be achieved even in the smallest fragments, although with pollen flow restricted to those plants co-occurring within the fragments. This may have genetic consequences, as we discuss below.

4.4. Implications and further work

Our result of undetectable effects of fragmentation on fruit set is significant, yet it does not necessarily imply that fragmentation has an innocuous effect on plant reproductive biology, particularly from the genetic diversity point of view. Although we have observed that pollinators can actively fly among neighboring palms in the forest understory, we have

not observed them flying over long-distances, especially not across the extensive cattle grasslands that surround the fragments. We therefore posit that most or all of the pollination and fruit set that takes place within the small fragments is likely to involve the few neighboring reproductive plants present therein. This is consistent with the fact that Eguiarte et al. (1993) found that *A. mexicanum* pollen can be dispersed only up to 20 m. In addition, these authors found that gene flow via seed dispersal is even more restricted, up to about 3 m. We therefore predict that gene flow onto small fragments is restricted and that genetic diversity of the plants that are being recruited in the small fragments is likely to be reduced. We are currently investigating the indirect effects of fragmentation on genetic diversity using genetic and ecological performance analyses of progenies of *A. mexicanum* from small and large fragments in Los Tuxtlas. Research is needed to assess if fragmentation leads to a reduction in genetic variation of the progeny present in forest remnants, even in those systems in which pollination and fruit or seed set appear not to be affected.

Acknowledgements

This work was supported by a CONACYT doctoral scholarship to AA (No. 114032). We thank Gumersindo Sánchez and Braulio Gómez for assistance in field work. Support for field work was provided by a CONACYT grant to RD. The Laboratorio de Parasitología Vegetal-UAEM and Angeles Morales provided facilities and support for the sorting of insects. S. Zaragoza (Instituto de Biología, UNAM) identified the Coleoptera and L. Quíroz (Instituto de Ecología, A.C.) and R. Ayala (Instituto de Biología, UNAM) identified the Hymenoptera. The Los Tuxtlas field station provided all necessary facilities for field work. J.C. López, E. Narbona, J. Ghazoul and E. Mendoza offered constructive comments on an earlier draft. We thank A. Búrquez for information about of the behavior of pollinators.

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