Effects of forest fragmentation on assemblages of pollinators and floral visitors to male- and female-phase inflorescences of *Astrocaryum mexicanum* (Arecaceae) in a Mexican rain forest

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Abstract: We examined the consequences of habitat fragmentation on the assemblage of floral visitors and pollinators to male- and female-phase inflorescences of the understorey dominant palm *Astrocaryum mexicanum* at the Los Tuxtlas tropical rain forest. In six forest fragments ranging from 2 to 700 ha, we collected all floral visitors, pollinators and non-pollinators, to male- and female-phase inflorescences at the time of their greatest activity. We used multivariate and mixed-effects models to explore differences in guild composition between sexual phases of inflorescences and the effects of forest fragment size on several metrics of the assemblages of floral visitors. We detected 228 786 floral visitors, grouped into 57 species, across the six forest fragments. On average, abundance and species richness of floral visitors to female-phase inflorescences were higher than to male-phase ones. Forest fragmentation had no effect on species richness but negatively affected Shannon's diversity index. Overall, the most abundant species of floral visitors were predominantly found in inflorescences of plants from the large fragments. In contrast, most of the less common species were more abundant in the smallest fragments. The abundance of pollinators (those found on inflorescences of both phases and dusted with pollen that was carried to flower stigmas), and the ratio of pollinators to other floral visitors, increased with fragment size in both sexual phases of the inflorescences but these effects were significantly stronger on male-phase inflorescences than on female-phase inflorescences. These results show that tropical forest fragmentation correlates with changes in the composition of flower visitors to a dominant palm, with a reduction in the abundance of pollinators, but that such changes co-vary with the sexual phase of the plants.

Key Words: beetles, fragmentation, floral visitors, palm, pollination, species richness

INTRODUCTION

Drivers of global environmental change such as habitat fragmentation, overexploitation, species invasions, climate change and pollution have the potential to modify plant-animal interactions (Laurance 2004, Turner 1996, Tylianakis *et al.* 2008). In particular, habitat fragmentation can affect pollination processes because pollinator mobility may be restricted across fragments embedded in the matrix of heavily transformed landscape (Didham *et al.* 1996, Kearns *et al.* 1998, Murcia 1996). Pollination is the most studied interaction in the context of land-use change in many ecosystems (Aguilar *et al.* 2006, Jennersten 1988, Steffan-Dewenter & Tscharntke 1999, Tylianakis *et al.* 2008), but no definite conclusion has been reached as to whether habitat transformation has an overall negative impact on pollination. Nearly one third of the available studies show no effects or even positive effects of habitat fragmentation on pollination and plant reproductive success (Aguilar *et al.* 2006, Tylianakis *et al.* 2008).

In tropical rain forests, over 90% of the tree species are pollinated by animals (mainly insects), and some plant-pollinator interactions have a high degree of specialization (Bawa 1990, Johnson & Steiner 2000). For instance, palm pollination is often specialized (Henderson 1986) with cantharophily (Nitidulidae and Curculionidae) being the predominant syndrome, but melittophily (e.g. *Melipona*, *Apis* and *Trigona*) and myiophily (Calliphoridae, Syrphidae and Drosophilidae) are also common (Henderson 1986). In addition many species of palm are either monoecious or dioecious and rely on biotic vectors for their pollination (Henderson 1986, Knudsen *et al.* 2001). Because many monoecious species are dichogamous it is necessary to

consider if the effects of fragmentation vary depending on the sexual phase of the inflorescences (male- and female-phase). If forest fragmentation were to decrease pollinator visitation (e.g. reduction in the abundance of pollinators or the ratio of pollinators/other floral visitors) to female-phase inflorescences, pollen may be a limiting factor and therefore a reduction in fruit set would be expected (Burd 1994) but the only study addressing this issue in a palm species found no evidence in support of this hypothesis (Aguirre & Dirzo 2008). Conversely, if pollination is affected by fragmentation mainly at the male-phase of inflorescences, pollen competition and cryptic sexual selection at the stigma are likely to be relaxed, jeopardizing the mean performance of the plants sired in forest fragments, or diminishing the genetic variation in populations in small fragments, even if fruit set is not pollen-limited as in the cantharophilus moecious herb *Dieffenbachia seguine* (Cuartas-Hernández *et al.* 2010).

The Neotropical palm *Astrocaryum mexicanum* Liebm. is a dichogamous monoecious species chiefly pollinated by beetles. This palm is the dominant understorey species at Los Tuxtlas rain forest, Mexico, and persists in forest fragments of all sizes (Arroyo-Rodríguez *et al.* 2007). Aguirre & Dirzo (2008) observed that the abundance of pollinators of *A. mexicanum* was low in small forest fragments (<35 ha) compared with that in large forest fragments (114 and 700 ha), but they found that there was no effect of forest fragment size on fruit set. Given that *A. mexicanum* is a dichogamous species it is necessary to consider if the effects of fragmentation vary depending on the sexual phase of the inflorescences (male- and female-phase), a topic not addressed by Aguirre & Dirzo (2008).

Because male flowers of *A. mexicanum* offer rewards (pollen) to floral visitors, while female flowers do not, we hypothesized that assemblages of floral visitors (pollinators and non-pollinators) to this palm would be different in female- and male- phase inflorescences. Also, since *A. mexicanum* is a shade-tolerant, mature-forest species, we also predicted that floral visitors will shift towards a more heliophilous guild of visitors with fragmentation thus decreasing the proportional representation of true pollinators. We tested these expectations by censusing floral visitors to male- and female-phase inflorescences in forest fragments and continuous forest at Los Tuxtlas.

METHODS

Study site

The study site is located in the Los Tuxtlas region of the State of Veracruz, south-eastern Mexico. The predominant vegetation in the lowlands is tropical rain forest (Dirzo & Miranda 1991). The mosaic of vegetation types along the elevation range is considerably diverse at Los Tuxtlas, ranging from tropical cloud forest and mixed forests (conifer and broadleaved) at high elevations, where several species of boreal and tropical origins coexist, to typical tropical rain forest in the lowlands, with an overwhelming predominance of species of tropical origin in all the vertical strata of the forest (González-Soriano *et al.* 1997). In Los Tuxtlas forest fragmentation is severe. Mendoza *et al.* (2005) documented that the landscape in the study area is composed of many small forest fragments and only a few large fragments: 1005 forest fragments (representing 90% of the total) with a median size of only 0.95 ha. The study was carried out in and around the Los Tuxtlas Research Station, administered by the National Autonomous University of Mexico. We selected six forest fragments (2, 4, 19.4, 34.6, 114.6 and 700 ha). The largest fragment (referred to as continuous forest) corresponds to the Los Tuxtlas Research Station, which extends westwards, towards the San Martin Volcano, encompassing a total of 1883 ha. The forest fragments were separated from the continuous forest *c.* 30 y ago, but have similar ecological and floristic compositions to those to the tropical rain forest in the research station. Further details of the sites can be found in Aguirre & Dirzo (2008).

Study species

Astrocaryum mexicanum Liebm. is the most abundant species in the understorey at the Los Tuxtlas region and its distribution is restricted to the lowlands (<700 m asl). At Los Tuxtlas, the average density of *A. mexicanum* > 1 m height is *c.* 1000 individuals ha^{-1} (Martínez-Ramos 1997). *Astrocaryum mexicanum* reaches sexual maturity around 40 y of age, and its life span is well over 100 y. Most reproductive plants are in the range of 2–6 m in height (Piñero *et al.* 1984), although some plants are up to 8 m (Búrquez *et al.* 1987). A reproductive individual can have up to five inflorescences, but has only one mature inflorescence at any one time. Each inflorescence has an average of 4885 male flowers and 28 female flowers (Búrquez *et al.* 1987). Inflorescences are dichogamous and protogynous. Female flowers are receptive in the morning, opening between 04h00–06h00 and remain functional for over 12 h. Male flowers open almost synchronously at night (after 20h00) (Búrquez *et al.* 1987). Sexual functions within an inflorescence overlap through a short period but the pollen is largely immature while most female flowers are dysfunctional, thus minimizing self-fertilization (geitonogamy). Floral visitors are abundant and diverse, but the potential pollinators are four nitidulid beetles: *Mystrops* sp., *M. mexicanus*,

Eumystrops centralis and *Coleopterus aberrans* (Aguirre & Dirzo 2008, Búrquez *et al.* 1987). Following Búrquez *et al.* (1987) we defined as pollinators those flower visitors that (1) were present in both phases of the inflorescences, (2) were observed transporting pollen on their bodies, and (3) were observed carrying pollen onto the stigmas on the female flowers.

The protocol for sampling floral visitors was reported in a previous study (Aguirre & Dirzo 2008). In sum, all reproductive plants of *A. mexicanum* were mapped in permanent plots. Within each plot we randomly selected 15 adult plants from which we collected all the floral visitors from 10 inflorescences in the female phase and in five inflorescences in the male phase. The sampling was conducted between March and May 1999 in a haphazardous fashion. All inflorescences were collected between 07h00 and 08h00, when the activity among the floral visitors to *A. mexicanum* is most intense (Aguirre & Dirzo 2008, Búrquez *et al.* 1987). In the laboratory, the floral visitors were identified to species or morphospecies level, separated and counted.

Statistical analyses

To explore the differences in the structure of the assemblages of floral visitors in the female- and male-phase inflorescences and the differences related to forest fragmentation, we used non-metric multidimensional scaling on $\log_{10}$-transformed abundances of floral visitors. An importance value index (IV) was calculated for each species of floral visitor. This index was used to include, simultaneously, the relative abundance and frequency of each flower visitors. The relative frequencies were calculated as the number of inflorescences (male or female) in which each species of floral visitor was observed divided by the sum of all the frequencies across all floral visitors. The relative abundance was calculated by dividing the abundance of each species by the overall abundance of floral visitors. IV is the sum of the two relative values, and because we sampled roughly twice the number of female inflorescences compared with male ones, calculations of IV were done separately for male and female inflorescences.

To explore the effects of forest fragment size on evenness of the community of floral visitors we used Pearson correlation analysis. To explore the effects of forest fragment size on species richness, we used mixed-effects models where sexual phase was the fixed factor and log-transformed fragment size was used as covariate, whereas fragment identity and individual palm within each fragment appeared in the random component of the model. In this way we avoided potential pseudo-replication. The same model structure was used to explore the effects of forest fragment size on pollinator abundance

and the ratio of pollinators to other floral visitors. All statistical analyses were performed with R-2.5.1 (www.R-project.org).

RESULTS

Assemblages of floral visitors

We collected 228 786 arthropod floral visitors, corresponding to 57 species (or morphospecies), from 86 inflorescences of *A. mexicanum* (30 in the male phase and 56 in the female phase) across six forest fragments. The major contingent of visitors belonged to two groups: (1) Coleoptera, which included the pollinators (*Eumystrops centralis*, *Mystrops mexicanus*, *Coleopterus aberrans* and *Mystrops* sp.) and two non-pollinators (*Enochrus* sp. and *Ciclocephala fasciolata*), and (2) Hymenoptera (*Plebeia frontalis*, *Plebeia pulchra*, *Polybia occidentalis*, *Apis mellifera*, *Trigona fulviventris*, *Pheidole* sp. 1, *Camponotus sericeiventris*, *Pachycondyla ferruginea*, *Pachycondyla villosa*, *Zacriptocerus spinosus* and *Camponotus* sp.). Beyond these two orders, other prominent visitors comprise species of Orthoptera and Diptera (Appendix 1). Abundance of floral visitors increased significantly with fragment size (F = 9.5, df = 1, 4, P = 0.04) although this relationship was not linear, particularly in female-phase inflorescences. The 10 most abundant species of floral visitor were predominately found in inflorescences from the three large fragments: their relative abundances ranged from 61% to 93% and included the three reported pollinators of *A. mexicanum*, whose relative abundances in the three large fragments ranged between 72% and 92%. In contrast, 60% of the less common species of floral visitor, excluding singletons and doubletons, were more abundant in the three small fragments and half of them had at least 70% of their abundance represented in inflorescence from the three small fragments.

On average ($\pm$SE), there were 3376 $\pm$ 409 floral visitors to female-phase inflorescences and 1324 $\pm$ 303 to male-phase inflorescences. Overall, the assemblages of floral visitors to inflorescences in the male and female phases were structurally different, as revealed by a non-parametric multidimensional scaling analysis based on the abundance of the floral visitors (Figure 1a). The robustness of this analysis was satisfactory, as suggested by the value of 8.3 for the stress parameter.

The distribution of importance values of pollinators (*E. centralis*, *M. mexicanus*, *Mystrops* sp. and *C. aberrans*) was similar in female- and male-phase inflorescences (Figure 1b) while the IVs of the other floral visitors were biased to one phase.
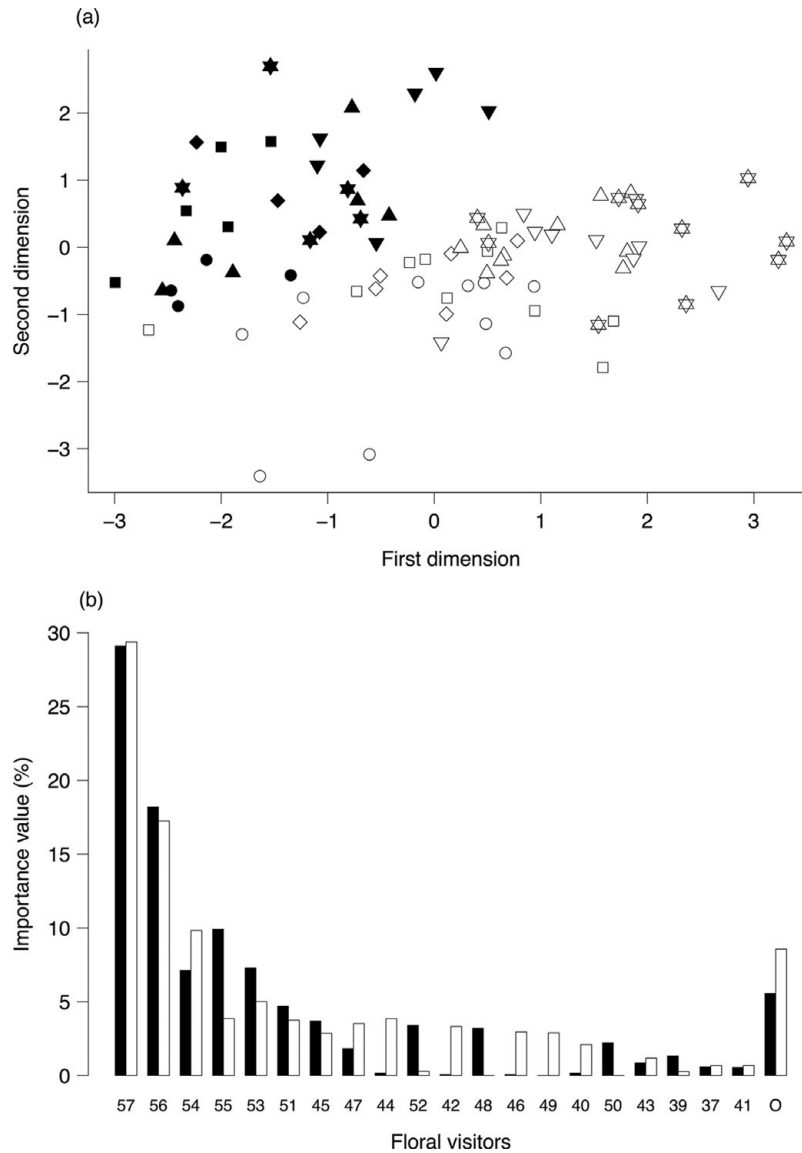
Figure 1. Assemblage of floral visitors to male-phase (black) and female-phase (white) inflorescences of *Astrocaryum mexicanum*. Non-metric multidimensional scaling based on abundance in $\log_{10}$ scale of floral visitors in six forest fragments: circles (2 ha), squares (4 ha), diamonds (19.4 ha), triangle (34.6 ha), inverted triangle (114.6 ha) and stars (700 ha) (a). Importance values of floral visitors, including the main pollinators: 57 = *Eumystrops centralis*, 56 = *Mystrops mexicanus* and 54 = *Coleopterus aberrans*. O = other floral visitors (b). For the complete list and species codes see Appendix 1.

Impact of forest fragmentation on evenness, species richness and diversity of floral visitors

The index of evenness of the community of floral visitors across fragments ranged from 0.37 to 0.51, and this index correlated negatively with the natural logarithm of forest fragment size (r = −0.82, t = 2.95, df = 4, P = 0.04). The mixed-effects model showed that the overall species richness of floral visitors to *A. mexicanum* was significantly higher (F = 10.2, df = 1, 4, P = 0.04) for inflorescences in the male phase than for female-phase inflorescences. However, the species richness of the floral visitors was unaffected by forest fragment size, either as a main effect (F = 0.03, df = 1, 4, P = 0.86) or in interaction with the sexual phase of the inflorescence (F = 0.56, df = 1, 4, P = 0.49). Consistent with this finding, Shannon's diversity index of the floral visitors was also significantly higher (F = 12.8, df = 1, 4, P < 0.023) for inflorescences in the male phase (1.60 ± 0.07) than that for female-phase inflorescences (1.37 ± 0.03). Shannon's diversity index decreased with forest fragment size (Figure 2), and this effect was significantly more pronounced in male phase inflorescences compared with female phase ones (F = 7.96, df = 1, 4, P = 0.04).
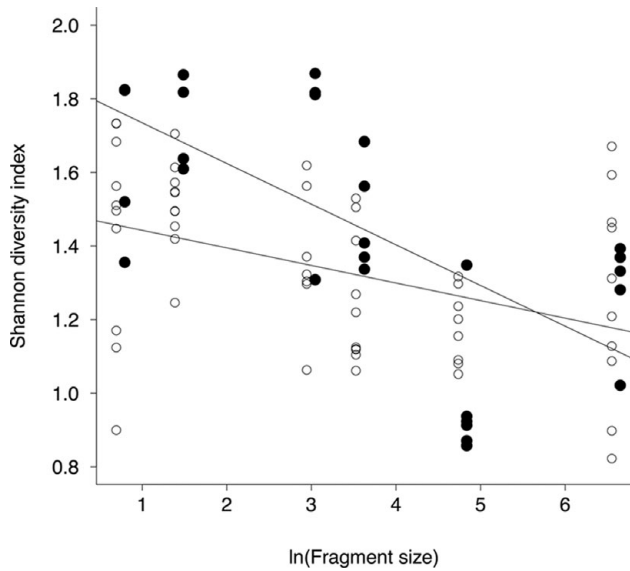
Figure 2. Forest fragment size effects on Shannon's diversity index of floral visitors in inflorescences of *Astrocaryum mexicanum* in male (black circles) and female (white circles) phases. Circles represent individual palms within each of the six forest fragments and lines are the fitted mixed effects model's predictions for each sexual phase.

Impact on pollinators of *Astrocaryum mexicanum*

Considering only those taxa that we defined as pollinators, we observed that their abundance was positively associated with forest fragment size (F = 8.69, df = 1, 4, P = 0.04, Figure 3a), but there was no significant interaction between the sexual phase of the inflorescences and the size of the forest fragments (F = 0.71, df = 1, 4, P = 0.44). The abundance of pollinators changed by over 10-fold when the smallest forest fragment (2 ha) was compared with the largest forest fragment (700 ha) in both sexual phases of the inflorescences. Nevertheless, across all the sizes of forest fragments, the abundance of pollinators in the female-phase inflorescences was higher than that in the male-phase inflorescences (F = 9.49, df = 1, 4, P = 0.03).

When we considered the ratio of the abundance of pollinators to that of other floral visitors (Figure 3b), we again observed an overall positive effect of forest fragment size (F = 12.8, df = 1, 4, P = 0.023), but the magnitude of the effect was higher in male-phase inflorescences than in female-phase inflorescences (F = 16.1, df = 1, 4, P < 0.001) and no significant effects of sex and the covariate (fragment size) as main effects were detected (F < 0.87, df = 1, 4, P > 0.354).

DISCUSSION

Our results are consistent with other studies with palms showing a great diversity of floral visitors (Ervik & Bernal 1996, Meléndez-Ramírez *et al.* 2004, Siefke & Bernal
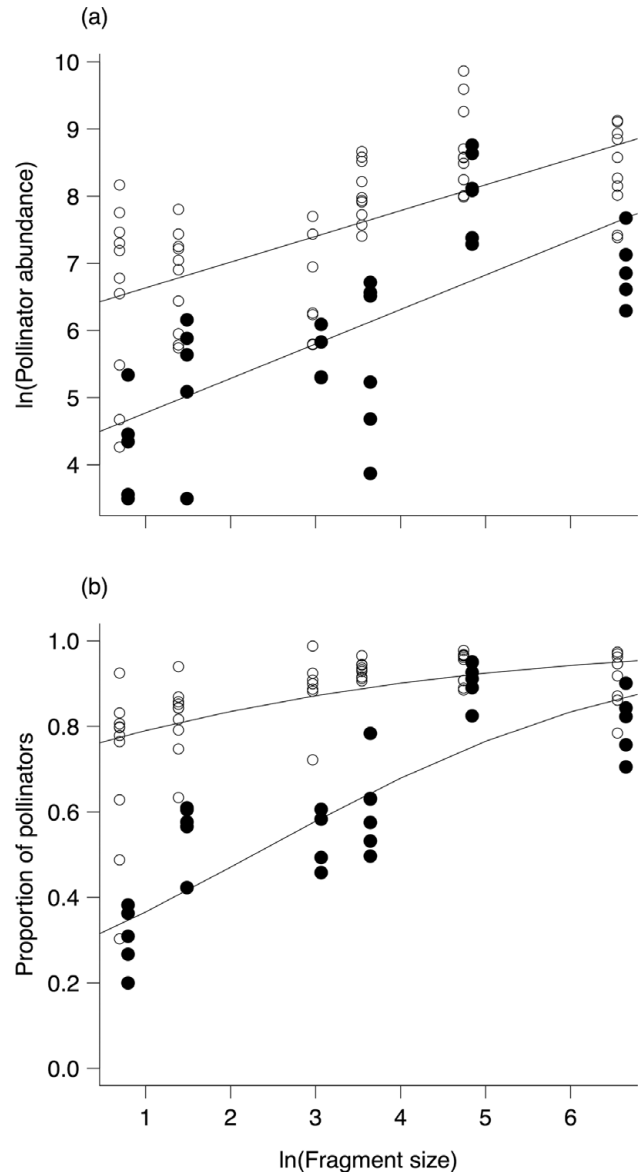

Figure 3. Forest fragment size effects on the abundance (a) and the ratio (b) of pollinators:non-pollinators visiting inflorescences to male (black circles) and female (white circles) phases. Circles represent individual palms within each of the six forest fragments and lines are the fitted mixed effects model's predictions for each sexual phase.

2004), and although variation across sexual phases regarding assemblages of floral visitors of palms have been documented with inconsistent results, no other study seems to have taken into account the effect of forest fragmentation on floral visitors of male- and female-phase inflorescences. We found higher abundance of floral visitors on male-phase inflorescences, which is consistent with reports of other palm species, including *Orbignya phalerata* (Anderson *et al.* 1988), *Euterpe precatoria* (Küchmeister *et al.* 1997), *Prestoea shultzeana* (Ervik & Feil 1997), *Wettinia quinaria, Attalea allenii* (Nuñez *et al.* 2005), *Oenocarpus bataua.* (Nuñez-Avellaneda &

Rojas-Robles 2008). In contrast, in other species (*Phytelephas seemannii, Aphandra natalia*) (Bernal & Ervik 1996, Ervik *et al.* 1999) higher abundance of floral visitors has been reported in female-phase inflorescences compared with male ones. The available evidence, including the present study, indicates an inconsistent pattern in the abundance of the non-pollinating floral visitors to inflorescences in the male and female phases of monoecious palms. However, detailed analysis of the likely subset of non-pollinating visitors has been poorly investigated. This is especially important in studies of the floral visitors to palms because their inflorescences are known to attract a large number of species of arthropods, including pollinators and many other visitors searching for food (flowers, pollen, and other floral visitors). Also, palm inflorescences can serve as mating arenas and oviposition sites (Búrquez *et al.* 1987, Consiglio & Bourne 2001, Henderson 1986, Siefke & Bernal 2004).

Considering all floral visitors, the average species richness was higher in male-phase inflorescences than in female-phase inflorescences. In other words, male inflorescences harboured a greater number of what seemed to be accessory floral visitors than did female-phase inflorescences. This finding is in agreement with the higher importance value observed in over 50 of the less important floral visitors, many of which were only found in male-phase inflorescences.

On the other hand, we found that forest fragment size was negatively correlated with the diversity (Shannon's index) of floral visitors, the abundance of pollinators and the ratio between pollinators and other floral visitors, but not with the total numbers of floral visitors. Also, these findings are in agreement with the negative correlation between forest fragment size and evenness of the community of floral visitors. Furthermore, the effect of forest fragment size on the ratio pollinators to non-pollinators was relatively small in female-phase inflorescences, varying from 4:1 in the smallest fragment to 20:1 in the largest fragment. In contrast, the ratio varied from 2:3 to 23:2 in the smallest and largest forest fragments, respectively, in the male-phase inflorescences. The effect of forest fragment size on the ratio of pollinators to non-pollinators in male-phase inflorescences resulted from a combination of a steady reduction in the abundance of pollinators as forest fragment size decreased, and the accumulation of non-pollinating visitors in small forest fragments. Male flowers of *A. mexicanum* are attractive to a large set of floral visitors, foraging for pollen without performing any pollination service for the palm (e.g. *Apis mellifera*). Because the prevalence of this kind of floral visitors was higher in small forest fragments than in large fragments, it is possible that the main threat of forest fragmentation to the pollination system of *A. mexicanum* is the increased competition (by exploitation) between non-pollinators

and pollinators in male-phase inflorescences. This finding is consistent with the reduction in diversity observed as forest fragment size increased, particularly in male-phase inflorescences.

In the smallest fragments, we observed on average 150 pollinators in male-phase inflorescences and 500 pollinators in female-phase inflorescence. Each inflorescence of *A. mexicanum* has, on average, more than 170 times more male flowers (4885) than female flowers (28), and this ratio should hold at the population level because inflorescences are dichogamous (Búrquez *et al.* 1987). Therefore, even if exploitation competition between pollinators and accessory floral visitors is high in small forest fragments, fruit set would be unlikely to be limited by pollen. This argument is supported by the results of Aguirre & Dirzo (2008), who found no effect of forest fragment size on the fruit set of *A. mexicanum* at the same study site. Nevertheless, even if pollen flow is not affected by forest fragmentation beyond a critical threshold, and thus does not limit fruit set, reduced pollen loads may relax pollen tube competition. In consequence, reduced selection pressure may operate on the siring of seeds in small forest fragments (Janse & Verhaegh 1993, Richardson & Stephenson 1992). This scenario may be more applicable to abundant plant species with many floral visitors such as *A. mexicanum*, but not necessarily to less abundant species with relatively few floral visitors. Clearly, these aspects warrant further investigation. Also, this study raises an important question as to whether the observed drop in pollinator abundance among small forest fragments occurs in other plant species, particularly those which naturally have far fewer floral visitors than *A. mexicanum* and would therefore be at greater risk of reduced pollen flow. Two other studies at Los Tuxtlas with perennial herbs showed different effects of fragmentation on pollination. Cuartas-Hernández & Nuñez-Farfán (2006) found that fragmentation negatively affects the fruit set and gene flow of *Dieffenbachia seguine*, suggesting a reduction of the populations of their main beetle pollinators (*Cyclocephala* sp. and *Erioscelis* sp.). In contrast, Suárez-Montes *et al.* (2010) found no effects of forest fragmentation on the genetic variability and gene flow of the hummingbird-pollinated *Heliconia uxpanapensis* (Heliconiaceae). As pointed above, there is not enough evidence to draw an overall conclusion of the effects of habitat fragmentation on pollination dynamics. Therefore, studies of the effects of habitat fragmentation on pollination are warranted.

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Appendix 1. List of species/morphospecies of floral visitors to male and female phase inflorescences of *Astrocaryum mexicanum* at Los Tuxtlas Veracruz, Mexico.

				Inflorescence sexual phase	
Species code	Order	Family	Species	Female	Male
30	Acaridae		sp. 40	0	14
29	Blattaria	Blattidae	sp. 53	13	0
18	Blattaria	Blattidae	sp. 11	1	3
22	Coleoptera	Cerambicidae	sp. 22	5	1
52	Coleoptera	Curculionidae	sp. 40	2493	14
4	Coleoptera	Curculionidae	sp. 24	0	1
50	Coleoptera	Curculionidae	sp. 18	878	0
47	Coleoptera	Curculionidae	sp. 5	311	147
38	Coleoptera	Curculionidae	sp. 21	32	3
23	Coleoptera	Curculionidae	sp. 7	5	1
10	Coleoptera	Curculionidae	sp. 36	1	0
45	Coleoptera	Hydrophilidae	*Enochrus* sp.	172	160
55	Coleoptera	Nitidulidae	*Coleopterus aberrans* Sharp	19894	303
56	Coleoptera	Nitidulidae	*Eumystrops centralis* Sharp	92524	20143
57	Coleoptera	Nitidulidae	*Mystrops mexicanus* Reitt.	51251	10627
53	Coleoptera	Nitidulidae	*Mystrops* sp.	9979	1647
35	Coleoptera	Nitidulidae	sp. 45	27	1
49	Coleoptera	Nitidulidae	sp. 38	0	604
32	Coleoptera	Nitidulidae	sp. 20	2	14
9	Coleoptera	Nitidulidae	sp. 34	1	0
20	Coleoptera	Nitidulidae	sp. 44	1	4
5	Coleoptera	Nitidulidae	sp. 52	0	1
39	Coleoptera	Scarabaeidae	*Cyclocephala fasciolata* Bates	37	4
51	Coleoptera	Staphylinidae	sp. 6	1120	218
41	Coleoptera	Staphylinidae	sp. 42	174	9
36	Coleoptera	Staphylinidae	sp. 47	0	28
42	Coleoptera	Staphylinidae	sp. 15	1	200
46	Coleoptera	Staphylinidae	sp. 16	1	437
7	Coleoptera	Staphylinidae	sp. 25	1	0
54	Diptera		sp. 3	9375	4629
15	Diptera		sp. 49	2	0
28	Diptera		sp. 50	2	10
6	Diptera		sp. 19	1	0
33	Hemiptera	Pyrrhocoroidae	sp. 23	22	1
3	Hemiptera		sp. 10	0	1
21	Homoptera		sp. 37	5	0
11	Homoptera		sp. 51	1	0
31	Hymenoptera	Apidae	*Apis mellifera* L.	0	16
44	Hymenoptera	Apidae	*Plebeia frontalis* Friese	2	294
40	Hymenoptera	Apidae	*Plebeia pulchra* Ayala	2	72
27	Hymenoptera	Apidae	*Trigona fulviventris* Guérin	8	3
17	Hymenoptera	Apidae	*Camponotus* sp. 3	0	4
14	Hymenoptera	Apidae	*Camponotus* sp. 41	0	2
34	Hymenoptera	Formicidae	*Camponotus* sp.	28	0
1	Hymenoptera	Formicidae	*Camponotus* sp. 2	0	1
25	Hymenoptera	Formicidae	*Camponotus sericeiventris* Guérin-Méneville	5	2
2	Hymenoptera	Formicidae	*Dolichoderus bispinosus* Olivier	1	0
26	Hymenoptera	Formicidae	*Pachycondyla* aff. *ferruginea* Smith	11	0
13	Hymenoptera	Formicidae	*Pachycondyla villosa* Fabricius	1	0
43	Hymenoptera	Formicidae	*Pheidole* sp. 1	138	86
16	Hymenoptera	Formicidae	*Pheidole* sp. 2	1	1
24	Hymenoptera	Formicidae	*Zacriptocerus* aff. *spinosus* Mayr	4	2
48	Hymenoptera	Formicidae	sp. 17	495	0
19	Hymenoptera	Formicidae	sp. 8	0	4
37	Hymenoptera	Vespidae	*Polybia occidentalis* Olivier	23	7
12	Orthoptera	Tettigonidae	sp. 54	1	0
8	Psocoptera		sp. 31	1	0