

Defoliation effects on seed dispersal and seedling recruitment in a tropical rain forest understorey palm

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Summary

1. Assessing the demographic effects of leaf area losses in perennial plants is important to determine population resilience to natural and anthropogenic disturbances. Yet, while impacts of defoliation on vital rates of adult plants have been well documented, consequences for seed dispersal and seedling recruitment have been barely explored.

2. Here, we assessed the effects of defoliation on fruit production, fruit/seed size, seed dispersal and seedling recruitment in populations of *Chamaedorea ernesti-augustii*, a tropical rain forest, understorey palm from Mesoamerica, whose leaves are exploited as a highly valuable non-timber forest product (NTFP).

3. Fruit size and seed production were quantified in mature palms that were subjected to 0% (control), 25%, 50%, 75% and 100% experimental removal of standing leaves, applied every 6 months over 2 years. Seed dispersal by birds and gravity, and seed predation by small vertebrates on the ground were also quantified. Rates of seedling recruitment were recorded in non-defoliated and 'sterile' populations (75% sustained defoliation and periodical removal of all produced fruits). Finally, a stochastic model was used to quantify the overall effect of defoliation on seedlings recruited from locally (i.e. dispersed by gravity) and immigrant produced seeds (i.e. dispersed by birds).

4. Increasing defoliation strongly reduced seed production. The probability of bird dispersal was positively correlated with fruit/seed size. Isolated (i.e. bird-dispersed) seeds endured lower predation rates than grouped (i.e. gravity-dispersed) ones. Modelling showed that seedling recruitment rate is severely reduced in highly defoliated populations due to a strong decline in the number of seedlings coming from local seed sources. Surrounding non-defoliated populations could partly compensate for this effect via seedlings coming from immigrant seeds.

5. Synthesis. Chronic and intense defoliation negatively affects seed production and dispersal, which reduces the probability of seedling recruitment. Such effects may have a profound impact on the dynamics and genetic variability of populations, which should be taken into account when considering the effects of natural defoliation and sustainability of leaf-harvesting regimes.

Key-words: *Chamaedorea ernesti-augustii*, dispersal, leaf harvesting, Mexico, non-timber forest products, plant demography, plant–animal interaction, seed fate, seed predation

Introduction

Quantifying the impacts of defoliation on plant population dynamics is important both to understand the mechanisms that determine tolerance to natural leaf losses (e.g. herbivory) and to assess the sustainability of human leaf harvesting. Several studies have documented the effects of defoliation on vital rates and population dynamics of perennial plants (e.g. Crawley 1989; Obeso 1993; Hawkes & Sullivan 2001; Ticktin *et al.* 2002; Zuidema, de Kroon & Werger 2007; Lázaro-Zermeño

et al. 2011). Overall, single defoliation events have small effects on survival, growth and reproduction (Mendoza, Piñero & Sarukhán 1987; Oyama & Mendoza 1990; Belsky *et al.* 1993) because plants can tolerate such leaf area losses through compensatory growth (McNaughton 1983; Belsky 1988; Strauss & Agrawal 1999; Stowe *et al.* 2000; Anten, Martínez-Ramos & Ackerly 2003). However, when plants are exposed to recurrent high levels of defoliation, a decline in plant's tolerance (Endress, Gorchov & Berry 2006; Martínez-Ramos, Anten & Ackerly 2009; Hernández-Barrios *et al.* 2012) and resilience (López-Toledo *et al.* 2012) occurs, negatively affecting fitness components, including seed production.

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The recruitment of seedlings in a given area is not only determined by the local production of seeds (Eriksson & Ehrlén 1983), but also by immigrant seeds dispersed into the area, seed predation and germination rates (Harper 1977). Potentially, defoliation could impact fruit and seed quality (Crawley 1989) and alter one or more of these processes. However, studies assessing demographic consequences of defoliation have generally not considered the effects on dispersal and predation of seeds (e.g. Endress, Gorchov & Noble 2004; Zuidema, de Kroon & Werger 2007; Milner-Gulland 2008; but see Berry *et al.* 2008), albeit that such effects may significantly affect population dynamics and genetic connectivity among populations (Cibrián-Jaramillo *et al.* 2009).

Leaves of understory palms of the genus *Chamaedorea* constitute one of the most important non-timber forest products (NTFP) in tropical rain forests from Mesoamerica (CEC 2003). The leaves are mostly harvested from natural populations (Endress, Gorchov & Berry 2006; Valverde, Hernández-Apolinar & Mendoza-Amaro 2006; Martínez-Ramos, Anten & Ackerly 2009; Gorchov, Gorchov & Endress 2011) and exported for the floral industry in North America and Europe (Hodel 1992; CEC 2003; Wilsey & Radachowsky 2007). Due to overharvesting, these populations may become locally extinct (Homma 1996; Kusters *et al.* 2005; Schmidt *et al.* 2011). The strong reduction in seed production and adult mortality imposed by high levels of defoliation (Martínez-Ramos, Anten & Ackerly 2009; Hernández-Barrios *et al.* 2012; López-Toledo *et al.* 2012) might be the main reasons for such loss. It has been documented for other NTFPs, such as the neotropical tree *Bertholletia excelsa* (the Brazilian nut), that overharvesting of seeds compromises the viability of natural populations (Peres *et al.* 2003).

In this study, we assess the effects of experimental defoliation on production, size, dispersal and predation of the seeds, and seedling recruitment in natural populations of the understory dioecious palm *Chamaedorea ernesti-augustii* in southeast Mexico. This palm produces single seeded fruits mostly dispersed by birds (Ibarra-Manríquez & Oyama 1992; Garwood & Bridgewater 2005). We differentiated between seedlings emerging from bird-dispersed (immigrant) seeds and those emerging from gravity-dispersed (local) ones. Local seeds tend to end up in clumps near the mother palm, while bird-dispersed ones tend to end up isolated, frequently far from the mother plant (Godoy & Jordano 2001). Using a modelling approach, we incorporated all demographic transitions followed by a seed from its production in a palm until the emergence of the seedling. This model enabled us to quantify the relative contribution of immigrant vs. local produced seeds to seedling recruitment and simulates the dynamics of seedling recruitment under different defoliation scenarios. Specifically, we aimed to test the following hypotheses: (i) seed dispersal by birds decreases under conditions of recurrent defoliation because removing leaf area causes a reduction in fruit production (Hernández-Barrios *et al.* 2012), hence a lower availability for dispersers, and defoliation could reduce the size of the fruits (birds tend to prefer higher quality, larger, fruits; Alcántara *et al.* 1997; Rey & Alcántara

2000); (ii) clumped (gravity-dispersed) seeds suffer higher predation rates than isolated (bird-dispersed) ones due to negative density-dependence effects, as predicted by Janzen-Connell hypothesis (Janzen 1970; Connell 1971; Wright 2002); (iii) highly defoliated populations exhibit low seedling recruitment rates due to reduced local seed production, reduced immigration of seeds dispersed by birds and increased seed predation; (iv) non-defoliated palms in neighbouring areas may sustain defoliated populations by functioning as a source of immigrant seeds. We discuss these hypotheses to assess the importance of seed dispersal and the conservation of healthy reproductive palms for the dynamics of populations undergoing strong defoliation regimes.

Materials and methods

STUDY SITE AND SPECIES DESCRIPTION

This study was carried out at the Lacantún Biosphere Reserve (16°27'–16°50'N, 91°10'–91°30'W), Chiapas, southeast Mexico. The topography is karstic with a rendzina soil, shallow, well drained and rich in organic matter. Mean annual precipitation is 3,500 mm, and mean monthly temperature is 27 °C (Bolaños-Citalán & Naranjo 2003). The study area was located at about 500 m asl, where dominant vegetation is tropical rain forest (Ibarra-Manríquez & Martínez-Ramos 2002).

Chamaedorea ernesti-augustii is a dioecious, long-lived understory palm (locally known as *fish-tail* palm or *xaté*), distributed across tropical forests of southern Mexico, Belize and Guatemala, and mostly found on limestone and slopes up to altitudes of 1000 m asl (Hodel 1992). Individual plants have a single stem (up to ca. 2.5 m height), possessing on average six standing bifid leaves in adult stages. Peak flowering occurs in the dry season, from March to May (Henderson, Galeano & Bernal 1995), and fruits are produced year round, peaking in the wet season (June–September). Fruits are ellipsoid 8–19 mm long and 5–18 mm wide (J. van Lent, personal observation). The single seed is surrounded by a fleshy, thin, mucilaginous mesocarp covered by a black and tough exocarp when fruits ripen. Due to the red colour of the rachises, and the black colour of the ripe fruits, it is believed that birds are the most important dispersal agent of the seeds (Galindo-González, Guevara & Sosa 2000; Garwood & Bridgewater 2005; Bridgewater 2012); on the ground, the seeds suffer predation from rodents (J. van Lent, personal observation).

Leaves of *C. ernesti-augustii* have a high value for the ornamental and flowering industry (Hodel 1992; CEC 2003). Leaf harvesters (*xateros*) usually return to the same plant once or twice a year and typically collect 30–100% of total standing leaves (Reining *et al.* 1992). *Xaté* export generated about twenty million USD in Mexico only in 1999 (Endress, Gorchov & Berry 2006), and it is one of the principal NTFPs in Mexico's tropical forests (CEC 2003).

THE MODEL

We developed a stochastic model to assess the global effects of defoliation on seedling recruitment in *C. ernesti-augustii*. We used Berkeley and Madonna modelling software ver. 8.0 (Macey, Oster & Zahnley 2000), simulating seedling recruitment at the population level in a harvested local area (0.09 ha) surrounded by a matrix of non-defoliated palm populations. The model incorporates the different transitions followed by a seed as it is produced in a palm up to the

emergence of the seedling (Fig. 1), as described in Nathan & Muller-Landau (2000). We obtained all these transition probabilities from six field experiments below described.

FIELD EXPERIMENTS

Experiment 1. Effects of defoliation on fruit production and fruit volume

In January 2006, we established two permanent plots of 50 × 50 m each. In the plots, we selected 135 female reproductive palms, which were equally distributed among five defoliation treatments: 0% (control, no leaves removed), removing every fourth (25% of total standing leaves), every other (50%), three of every four leaves (75%) or all leaves (100%). Stem length, number of leaves and leaf size (rachis length) of each experimental palm were measured. Subsequently, every 6 months over 2 years, we repeated the assigned treatment over the newly produced leaves on each experimental palm. The specifics of this experiment are detailed in Hernández-Barrios *et al.* (2012).

Over two consecutive years, we quantified total fruit production per palm by counting scars left by falling fruits in the newly produced infructescences and collecting all fruits available at each census every 3 months, during the first year, and every 6 months during the second year. Aborted fruits, discernible as withered structures that remain attached to the infructescence, were discounted. The fruits collected after the first (February 2007) and second (January 2008) experimental years were measured (width and length in mm) and weighed (in g). Fruits coming from the same mother palm were considered as a family. Then, all collected fruits were peeled removing the exocarp and mesocarp, and the width and length of the seed were measured (in mm). Fruit and seed volume (*V*) were quantified assuming an ellipsoid shape: $V = 1.25 \times \pi (D/2)^2 \times (L/2)$; here, *D* stands for the diameter (width and depth are equal) and *L* represent the longitude of the fruit or seed.

Experiment 2. Gravity and bird seed dispersal

During the fruiting season of 2010, seed catching traps (0.6 m² in size) were placed directly under the infructescences of 21 non-defoliated

female palms located in a non-harvested site. The traps were hung at about 50 cm above the ground and attached to nearby trees. Height (from the first root up to the apical meristem), number of standing leaves, fruits produced and mean fruit volume were measured for each experimental palm. Fruits were visually checked for pre-dispersal seed predation by Curculionidae beetles (J.C. Hernández-Barrios, personal observation); infested fruits attached to the palm were not removed. After 5, 61 and 90 days, we monitored the number of fruits that were still attached to palms (*F_A*), fruits falling into the trap (*F_T*), fruit scars on infructescences (*F_S*) and pre-dispersal seed predation (*F_P*), that is, fruits predated while still attached. Because experimental palms were producing new fruits during the time of monitoring, we calculated the gravity and bird seed dispersal between each census, so we used the total fruit production, split up in three measurements. We quantified gravity and bird seed dispersal using the following formulas:

$$F_G(t_n) = F_T(t_n) \times \left(1 - \frac{F_P(t_n)}{F_A(t_{n-1})}\right) \tag{eqn 1}$$

$$F_L(t_n) = F_A(t_{n-1}) - F_A(t_n) - F_G(t_n) \tag{eqn 2}$$

$$F_B(t_n) \cong F_L(t_n) \tag{eqn 3}$$

$$F_{Total} \cong F_A(t_0) + F_S(t_0) \tag{eqn 4}$$

Here, *F_G* is the number of fruits produced per palm that are gravity-dispersed after a given number of days (period *t_n*–*t_{n-1}*) with a correction for pre-dispersal seed predation (*F_P*). *F_L* is the number of fruits lost, that is, not attached nor gravity-dispersed over the time period. Following Alcántara *et al.* (1997) and Berry *et al.* (2008), we define *F_B* as the amount of fruits removed by birds over a time period and assumed to be equal to *F_L*. Finally, *F_{Total}* is the total number of fruits produced per palm in a given time period and was calculated as *F_A* + *F_S* (Alcántara *et al.* 1997).

Experiment 3. Predation of seeds on the ground

This transition was evaluated in permanent plots (30 × 30 m each) used to assess effects of defoliation on population dynamics of *C. ernesti-augustii* (Hernández-Barrios & Martínez-Ramos, in preparation). In June

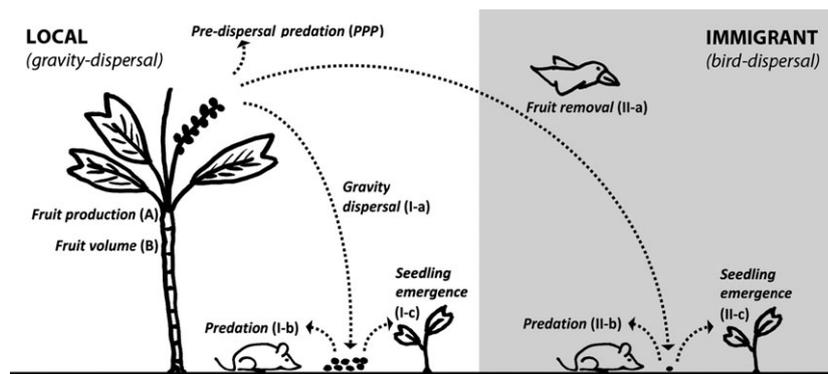


Fig. 1. Conceptual framework of transitions probabilities that a seed follows from its production on a *Chamedorea ernesti-augustii* female palm to the emergence of the seedling (recruitment); each arrow represents transition probabilities. The framework starts with the production of an *A* number of fruits (equivalent to seeds as fruits are single seeded) of size *B*. A fraction of the seeds attached to the palms are eliminated by pre-dispersal predation (*PPP*). Non-predated seeds (*1-PPP*) may follow one of two dispersal pathways, falling under the mother palm dispersed by gravity (*I-a*, clumped, local seeds) or removed and dispersed by birds (*II-a*, isolated, immigrant seeds). Each pathway follows two additional transitions: the probability of predation on the ground (*I-b*, *II-b*) and the probability of germination and seedling emergence (*I-c*, *II-c*). Then, $(1-PPP) \cdot I_a \cdot (1-I_b) \cdot I_c$ and $(1-PPP) \cdot II_a \cdot (1-II_b) \cdot II_c$ determine the probability that a newly produced seed reaches the seedling stage for gravity and bird-dispersal pathways, respectively. See text for further explanation and experiments conducted to quantify the different transitions probability values.

2007, two plots were established for each of the two treatments: a non-defoliated population (control, 0% defoliation) and a strongly defoliated, reproductively sterile population. We established the latter condition by applying 75% defoliation (biannually over 2 years, following the same protocol as described above) on female palms and removing periodically all fruits that might still be produced (hereafter, we will refer to this treatment as sterile plots). Distance between control and sterile plots was about 100 m. To quantify the total number of fruits produced per plot per year, every 6 months from June 2007 to January 2010, all infructescences produced in the plots were registered and tagged, and the fruits and scars on all infructescences were counted.

To quantify seed predation on the ground, in January 2010, ripe fruits were gathered from areas more than 3 km from the experimental plots. Fruits (hereafter, we will refer to fruits and seeds as the same experimental unit) were visually checked for rot and fungi damage; infested fruits were excluded to avoid any bias in fruit preference by predators (Mendoza & Dirzo 2007). We measured the volume of each of 192 fruits selected; each fruit was then drilled (traversing the seed) to tie one end of a fishing nylon string (10 m long), labelled with a plastic tag (3 × 5 cm), as indicated in other studies (Forget & Cuijpers 2008; Ruiz 2008; Yi & Zhang 2008). As this test was not aimed at estimating germination, the damage of the embryo due to drilling was unimportant (Forget *et al.* 2005). The experimental fruits were placed on the forest floor the next day, dividing them in the following treatments (two levels per treatment): presence/absence of nearby fruit-bearing palms (fruits in control vs. in sterile plots), fruit density (isolated fruits vs. fruits in groups of eight) and seeds with pulp vs. seeds without pulp (manually peeled off). For each combination of factors (e.g. sterile-grouped-with pulp), there were eight tagged fruits assigned to each of the eight different treatments with three repetitions (24 fruits × 8 treatments = 192 fruits); all treatments were randomly placed across the two sterile and two control plots, more than three metres apart from each other.

We monitored the tagged seeds after 2, 7, 63 and 92 days. For every seed, we recorded whether it was moved (and the distance), taken to a burrow, lost, or whether the tag was removed. Because the fate of lost seeds was unknown, those seeds were not included in the analysis. Following Notman & Villegas (2005), we assumed that seeds that were chewed off from the tag were predated and that all others were secondarily dispersed. Remaining seeds were visually tested for viability (looking for fungus presence, rotten inside or insect damage). We tested the influence of fruit tagging on seed removal by placing one group with eight untagged fruits, one group with four tagged fruits and four untagged fruits, and eight isolated untagged fruits; these treatments were established on control plots with two replicas each. Also, within control plots, we placed one group of eight fruits and eight isolated fruits within cages of wire metallic mesh (1 cm aperture), to compare seed predation by vertebrates and insects. Additionally, we assessed whether drilling affected susceptibility of the seeds to infection. Following Xiao, Jansen & Zhang (2006), we visually tested whether drilled seeds were more susceptible to infection.

Experiment 4. Seed rain estimation

We placed 20 seed traps uniformly at each of two control and two sterile plots (80 in total). Each trap had a sampling area of 0.125 m² and was suspended at 1 m above ground to limit seed predation in the traps by vertebrates or insects. The trap had a cone-inverted shape, with a single pole and a foldable metal cross on top with fine netting attached underneath. Traps were monitored after 56 and

85 days. On control plots, traps were placed at distances larger than 2 m from fruiting palms to limit the chance of catching fruits dispersed by gravity. For sterile plots, this was unnecessary, as there was no local fruit production. This design was comparable to that of Berry *et al.* (2008).

Experiment 5. Seedling emergence

To assess seed germination probability, on November 2008, a sample of 223 seeds was obtained from more than 10 non-defoliated palms located outside our permanent plots. These seeds were put to germinate on the ground, equally divided among three randomly chosen spots within our permanent plots. The seeds were protected from vertebrate predators by a wire mesh cage (1 × 1 m and 0.3 m height). All germinated and non-germinated seeds were counted on December 2009.

Experiment 6. Seedling recruitment

Within each of the control and sterile permanent plots, seedling recruitment was estimated in nine subplots (4 × 4 m each). All seedlings present at the initial census were registered and tagged; subsequently, all new recruits were registered and tagged every 6 months over 2 years (2007 and 2008).

MODEL CALIBRATION

The model predicts yearly seedling production on a local population within an area of a given size. We used the size (900 m²) of our control and sterile plots (experiment 3 and 4) as our area to be modelled. To feed the model, we used mean fruit volume obtained from experiment 1 and yearly fruit production recorded in the control plots (experiment 3). Gravity and bird seed-dispersal probabilities for pathways *I* and *II* (Fig. 1) were estimated using the percentage of fruits removed from the infructescences [bird-removed probability (*BRP*)] obtained dividing formulae (2) by formulae (4) above described the probability of gravity dispersal was defined as $1 - BRP$. We assumed that all fruits removed by birds were dispersed; this assumption was tested comparing the observed bird dispersal (seed rain, experiment 5) with that estimated from the model (*BRP*). Predation rates on the ground for seeds in groups on control plots were used to calculate seed predation probability for gravity-dispersed seeds (*I-b*, Fig. 1), while predation rates for bird-dispersed seeds (*II-b*, Fig. 1) were estimated from the predation probability of isolated seeds deposited on the sterile and control plots. Finally, we assumed that seedling emergence probability (*I-c* and *II-c*, Fig. 1) was the same for gravity and bird-dispersed seeds, and it was obtained from the above-described germination tests. Further studies are needed to verify this assumption.

The model was constructed to simulate time intervals (runs) equivalent to 1 year, each run resulting in the amount of 'local seedlings' (i.e. those emerging from gravity-dispersed seeds) and 'immigrant seedlings' (i.e. those emerging from bird-dispersed seeds) recruited per unit area. At each run, the model started with a fixed fruit production value for a given year and defoliation regime. As shown in the results, *BRP* was positively related to fruit volume. Therefore, in the next modelling step, fruit volume was randomly selected from the population mean and standard deviation recorded in the field for the same year. Subsequently, the model randomly selects a value from empirical means and variances for the different seed transition probabilities. The model was iterated ($t = 50$) until the values of seedling recruitment stabilized. This procedure was repeated 1000 times, and

the stabilized values of all simulations were used to calculate a mean and standard deviation of the yearly seedling recruitment rate.

Finally, we used Macey, Oster & Zahnley (2000) modelling routines to perform a sensitivity analysis to assess the impact of changes in model parameters [fruit volume (thus indirectly *BRP*), fruit production, and seed predation and germination probabilities of local and immigrant seeds] on seedling recruitment (model's variable, *V*).

$$S(x) = \frac{V_2(x * \Delta) - V_1(x)}{\Delta} \quad \text{eqn 5}$$

Here, sensitivity (S_x) is calculated as the difference between a model run (V_2) in which a parameter x was modified by a relative change parameter (Δ) and a run without such change (V_1), divided by Δ (eqn 5). We set Δ at 10%.

SIMULATIONS OF DEFOLIATION SCENARIOS

After calibration, we used the stochastic model to assess the effects of four hypothetical defoliation scenarios on seedling recruitment and on the proportion of local and immigrant seedlings. Commercial leaf harvesting in *C. ernesti-augustii* generally involves at least two leaf-harvesting events per palm every year and the removal of more than 50% of standing leaves per palm every defoliation event (Bridgewater *et al.* 2006; J. C. Hernández-Barrios, personal observation). Based on this, we simulated scenarios where a small palm population (in 900 m²), undisturbed (*c*, control treatment) or 75% defoliated (*df*, sterile treatment), was surrounded by a forest matrix containing either undisturbed or 75% defoliated palm populations, which could or could not act as a source of immigrant seeds, respectively.

We tested the model by comparing the results of *c+c* and *df+c* scenarios with the observed seedling recruitment rates in the control plots and sterile plots. As our experimental plots corresponded to a scenario where the surroundings were not defoliated, the observed seedling recruitment rates could only be compared with the model scenarios with undisturbed surroundings (*df+c*). Additionally, as germination generally takes a year (see below), seedling recruitment rate in a given year is the result of the amount of fruits and fruit sizes produced in the previous year. Therefore, the model prediction for year n is compared with the observed seedling recruitment rate for year $n + 1$.

Results

FIELD EXPERIMENTS

Effects of defoliation on fruit quality

Repeated-measures ANOVA indicated that fruit production per palm (log-transformed) differed between defoliation treatments ($F_{3,56} = 4.358$; $P < 0.01$), between years ($F_{1,56} = 17.023$; $P = 0.0001$) and that these factors also interacted ($F_{1,56} = 4.270$; $P < 0.01$). Plants that were defoliated $\geq 50\%$ had very low fruit production, especially during the second year of sustained defoliation where palms subjected to 100% defoliation did not produce any fruit at all (Fig. 2).

Fruit volume and seed volume were tightly related within the different defoliation treatments ($R^2 = 71\text{--}90\%$; $P < 0.0001$). A nested ANOVA (fruit volume was nested in plant family to avoid pseudo-replication) showed that there were no significant effects of defoliation treatment on fruit

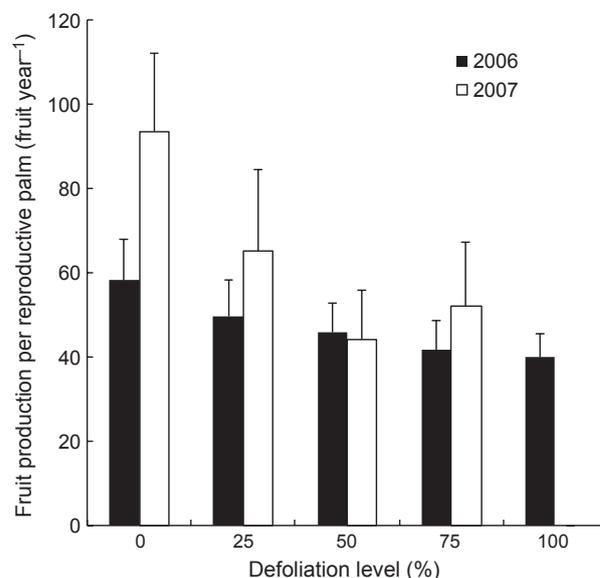


Fig. 2. Effects of experimental defoliation treatments (control, 0%; 25%; 50%; 75%; and 100% of leaves removed every 6 months during 2 years) on fruit production per reproductive *Chamedorea ernesti-augustii* palms. Error bars represent one standard error, while the zero value in brackets indicates that no fruits were produced in the 100% defoliation treatment.

volume after the first year of defoliation; fruit volume was significantly different only between plant families ($F_{17,258} = 23.369$, $P < 0.0001$). In the second year after defoliation, the number of fruits produced by palms was very low in the most intensive defoliation levels (50%, 75%); when lumping these categories, we found again only a family effect ($F_{16,329} = 25.8$, $P < 0.0001$).

Gravity and bird seed dispersal

After 90 days, a mean (\pm SE) of 10.3% (± 2.9) of the produced seeds were gravity-dispersed and 20.5% (± 5.6) were bird-removed, while 66.4% (± 7.1) were still attached to the palms. Extrapolating these fractions by assuming all seeds to ultimately have one of the above fates, we get 37% (± 8.1) of the seeds were gravity-dispersed and 63% (± 8.1) bird-removed. Pre-dispersal predation accounted for 2.9% ($\pm 2.8\%$). A forward multiple regression analysis showed that fruit volume was the only measured palm trait that significantly affected inter-palm variation in the probability of fruit removal (angular transformed). Probability of fruit removal increased with fruit volume ($R^2 = 0.43$; $P = 0.002$; Fig. 3).

Seed predation

Fruit tagging did not affect removal rates significantly ($P = 0.16$). However, untagged fruits were removed before tagged ones. Drilling of the seeds increased the infection probability by fungi, as none of the undrilled seeds ($N = 48$) were infected in comparison with 27% of the drilled ones ($N = 44$). Vertebrates (mostly rodents) were the main cause of seed predation, as caged fruits showed no signs of

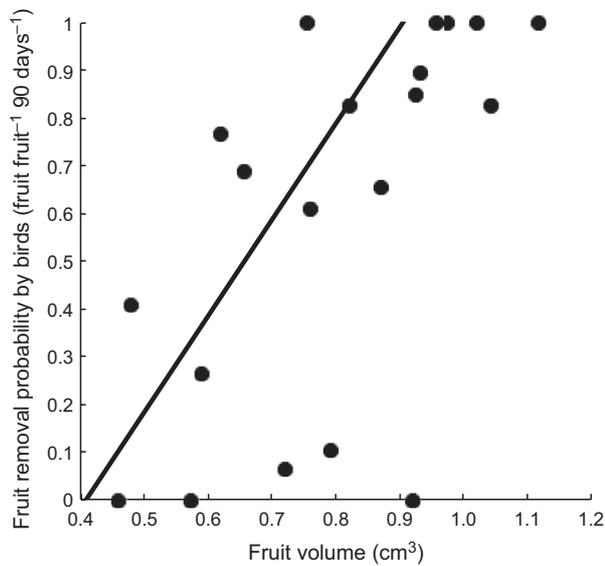


Fig. 3. Fruit removal probability as a function of fruit size in *Chamaedorea ernesti-augustii* palms in southeast Mexico. The line is the best-adjusted regression model for the relationship between the probability of removal of fruits by birds after 90 days and fruit volume ($R^2 = 0.43$; $P = 0.002$).

predation by insects. Two-thirds (63.2%) of the seeds were predated on the ground after 90 days and 13.7% were lost (Fig. 4a). In addition, 26.8% of all seeds were secondarily dispersed over a mean distance of 1.5 m (± 0.14). Predation and secondary dispersal rates were highest during the first 7 days; hereafter, these rates strongly decreased, approaching zero at the end of the observed period (Fig. 4b). Seed predation rate was not significantly influenced by fruit pulp presence ($P = 0.56$; *Wald Stat.* = 0.34) or by fruit volume ($P = 0.87$; *Wald Stat.* = 0.027). However, seed density did influence predation rates; seeds in groups had higher predation rates than isolated ones, and this effect depended significantly on the presence of fruit-bearing palms (*Wald Stat.* = 5.34; $P = 0.02$). Isolated seeds on control plots (with fruit-bearing palms) had significantly lower predation rates than isolated seeds in sterile plots (Fig. 4c).

Seedling emergence and recruitment

Eighty two per cent (± 0.7 SE) of the seeds germinated after 13 months. The mean number of seedlings recorded at the beginning of the defoliation experiment (i.e. those recruited in 2006) was 215.5 (± 46.1 in 900 m²) all treatments considered. After 2 years of sustained defoliation, the total number of recruited seedlings per treatment per year was 234 ± 91 for the control treatment and 160 ± 33 for the sterile plots, respectively.

MODEL CALIBRATION AND VALIDATION

Table 1 shows transition probabilities used to parameterize and calibrate the stochastic model. Defoliation impacted fruit production and indirectly predation rates on the ground.

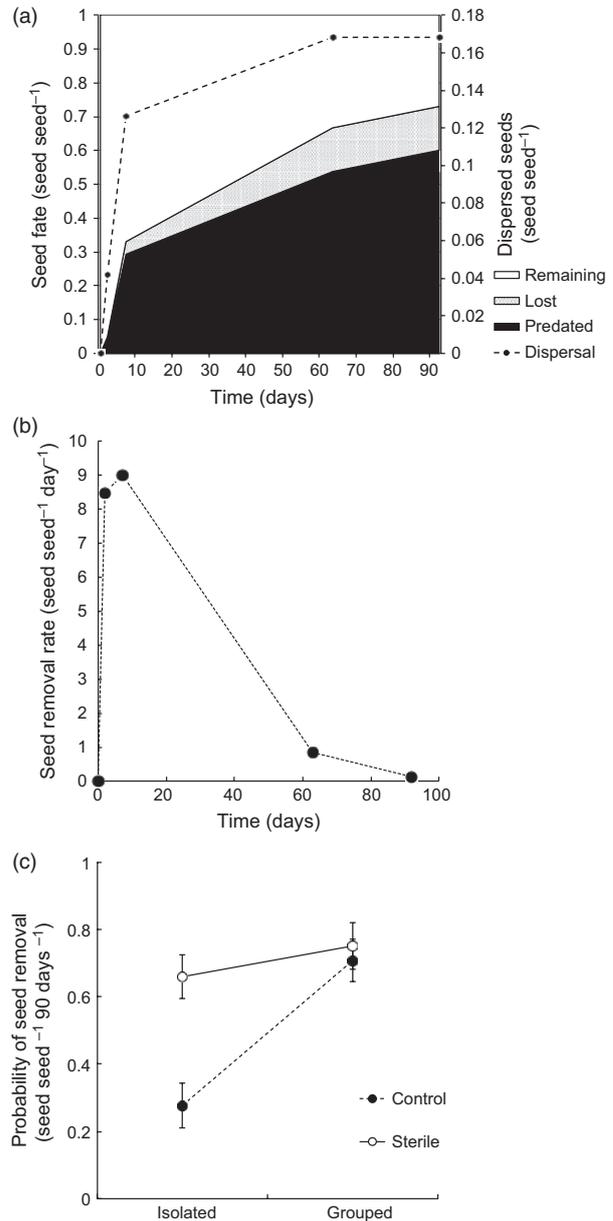


Fig. 4. Components of the dynamics of *Chamaedorea ernesti-augustii* seeds on the forest floor in southeast Mexico. (a) Fractions of seeds remained viable, predated, lost and secondarily dispersed over time; (b) daily seed removal rate as a function of time since seed deposition; (c) effect of seed density (isolated vs. grouped) and the presence/absence of fruit-bearing palms nearby (fruits on control vs. sterile plots) on predation rates on the ground by small vertebrates in *C. ernesti-augustii* palm populations in southeast Mexico. Vertical lines indicate one standard error.

Additionally, fruit volume differed between years, and this influenced the bird and gravity seed-dispersal probabilities. The model assumption that the proportion of fruits removed corresponds to the probability of seed dispersal by birds was supported moderately well by our seed rain experiment. In the total sampling area (10 m²), seed traps did catch two fruits, equivalent to 0.86 seeds m⁻² year⁻¹. Mean bird seed-dispersal probability calculated from annual fruit production and fruit removal rates for two consecutive years (2007 and

Table 1. Transition probability values that *Chamaedorea ernesti-augustii* seeds follow from their production on a palm until the emergence of the seedling. See Fig. 1 for schematic explanation of transitions. We assumed that fruit removal was equivalent to bird removal probability (*BRP*)

Key	Transition	Probability values
I-a	Seed dispersal by gravity	$1 - BRP$
I-b	Seed predation on the ground	0.71 ± 0.07
I-c	Seedling emergence	0.82 ± 0.03
II-a	Fruit removal	$BRP = 1.25 * \text{fruit volume} - 0.4$
II-b	Seed predation on the ground	Control plot: 0.28 ± 0.07 Sterile plot: 0.66 ± 0.07
II-c	Seedling emergence	0.82 ± 0.03
PP	Pre-dispersal predation	0.029 ± 0.028

2008) ranged between 0.7 and 0.6 seeds $\text{m}^{-2} \text{year}^{-1}$, respectively. Model estimates for seedling recruitment rates (for years 2007 and 2008) matched those recorded in the field (Fig. 5). Seedling recruitment rates recorded in the control plots during 2007 were quite similar to that predicted by the model (in Fig. 5a). One year after treatment initiation, seedling recruitment observed in the sterile plots decreased with respect to the control treatment; this change was simulated by the model but to a lesser degree (Fig. 5b).

Sensitivity analysis showed that the modelled recruitment rate was much more sensitive to changes in fruit volume, and thus to bird and gravity seed-dispersal probabilities, than to changes in fruit production (Table 2). Additionally, seedling recruitment was more sensitive to changes in predation and germination probabilities of local (gravity-dispersed) seeds than in the same probabilities of immigrant (bird-dispersed) seeds.

SIMULATED DEFOLIATION SCENARIOS AND SEEDLING RECRUITMENT

Model results indicate that seed dispersal by birds (immigrant seeds) is the major source for seedling recruitment under all simulated scenarios (Fig. 5). The importance of immigrant seeds increased after 2 years of sustained defoliation (year 2009). Thus, the model predicted that all recruited seedlings would come from immigration in the absence of locally produced seeds (*df+c* scenario, Fig. 5c). Furthermore, under the absence of external seed sources seedling recruitment collapsed, as simulated by the *c+df* and *df+df* scenarios (Fig. 5c).

Discussion

Overall, our study shows that intensive and recurrent defoliation had a negative impact on seedling recruitment. This effect was due to a direct negative effect of defoliation on fruit production and an indirect effect through a reduction in seed dispersal by birds and an increased seed predation on the ground. We know of no other study documenting the

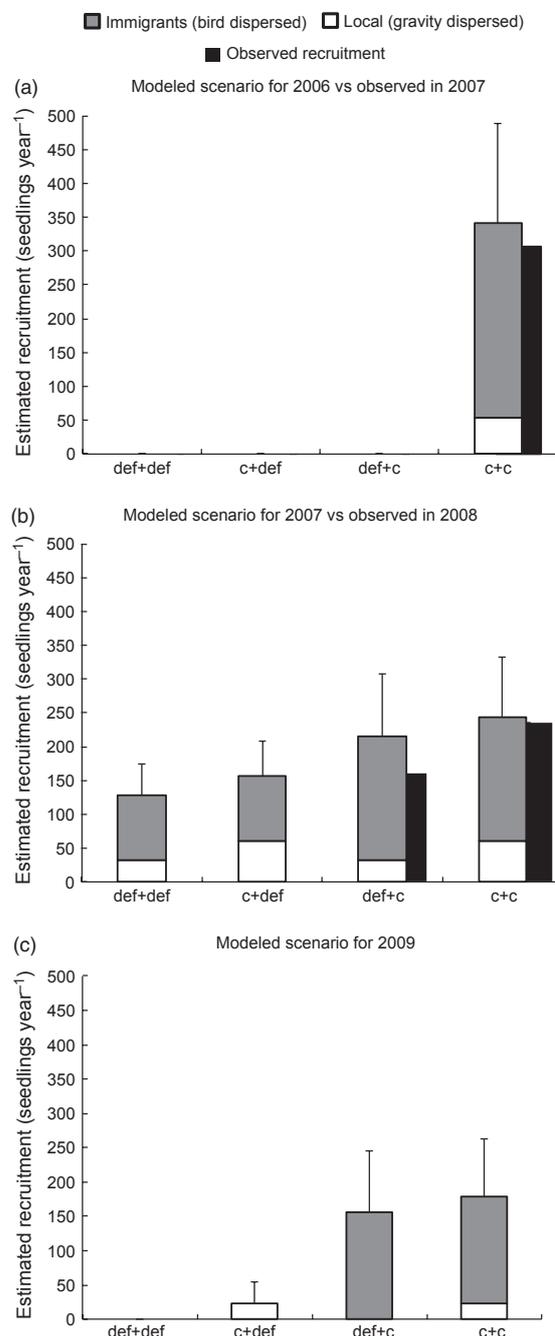


Fig. 5. Results of stochastic modelling of the global effects of defoliation on seedling recruitment in *Chamaedorea ernesti-augustii* in southern Mexico. Result of (a) model predictions for 2006, compared with observed recruitment rate in 2007; (b) model predictions 2007 and observed seedling recruitment rate in 2008; and (c) model predictions for 2009. Abbreviations on the x-axis indicate modelled scenarios as follows: defoliated plot surrounded with defoliated area (def-def), control plots surrounded with defoliated area (c-def), defoliated plots surrounded with control area (def-c); control plots surrounded with control area (c-c). Black bars represent observations from the field; dark grey and white bars represent model predictions.

integrated effects of defoliation on different components of the reproductive biology and demography of a plant species (but see Berry *et al.* 2008). Our stochastic modelling (Fig. 1)

Table 2. Results of the sensitivity analysis (S_x) performed to assess the importance of changes in model's parameters (x) for seedling recruitment. Sensitivity of bird and gravity dispersal probabilities is tested indirectly via the sensitivity for changes in fruit volume. Sensitivity with respect to changes in probabilities of seed predation and seed germination (seedling emergence) was tested both within the local pathway (I, seeds dispersed by gravity) and the immigration pathway (II, seeds dispersed by birds; see Fig. 1). Parameters that more strongly affect seedling recruitment are indicated by larger S_x values. See Materials and methods section for sensitivity calculation protocol

Key	Parameter (x)	Sensitivity factor (S_x)
A	Fruit production	9
B	Fruit volume	3332
I-b	Seed predation on the ground	3638
I-c	Seedling emergence	3265
II-b	Seed predation on the ground	1432
II-c	Seedling emergence	372

showed that seed dispersal by birds plays a major role on seedling recruitment in *C. ernesti-augustii* and that strong defoliation regimes can hinder regenerative potential if there are no external seed sources in the neighbourhood of exploited populations. However, plant reproductive behaviour is known to vary across individuals, time and spatial scales (Clark *et al.* 1999; Nathan & Muller-Landau 2000). Despite the fact that we relied only on a single fruiting season and a small local (plot) scale for describing the seed to seedling transition, we believe that our approach is sufficiently robust to infer the implications of intensive defoliation regimes on the reproductive biology and demography of a long-lived understorey tropical rain forest plant as below discussed.

INFLUENCE OF DEFOLIATION ON FRUIT PRODUCTION AND FRUIT SIZE

Hernández-Barrios *et al.* (2012) showed that 2 years of intense and repeated defoliation reduced the probability of reproduction by 80% in *C. ernesti-augustii* palms. Similar effects have been reported for *Chamaedorea elegans* (Anten, Martínez-Ramos & Ackerly 2003; Martínez-Ramos, Anten & Ackerly 2009; López-Toledo *et al.* 2012), *C. radialis* (Endress, Gorchov & Berry 2006) and *C. oblongata* (Hernández-Barrios *et al.* 2012). Other studies have also documented that defoliation reduces reproduction in several species with a wide array of life histories (Crawley 1989; Obeso 1993). Such negative effects on reproduction may even persist for several years after defoliation treatments are stopped as was shown for *C. elegans* palms (López-Toledo *et al.* 2012). Such plant responses may be the result of compensatory mechanisms that enable plants to counteract the loss of leaf area through reallocation of resources devoted to reproduction towards the production of new leaves (Marquis, Newell & Villegas 1997; Anten, Martínez-Ramos & Ackerly 2003; Eyles, Pinkard & Mohammed 2009). Compensatory mechanisms explain why fruit production of our *C. ernesti-augustii*

experimental palms reduced when sustained defoliation level was high (Fig. 2). Thus, a severe reduction in seed production constitutes an immediate demographic effect caused by chronic and intensive defoliation levels (> 50%) in *C. ernesti-augustii* populations.

Fruit size is a plastic trait that can be influenced by environmental factors such as nutrient and light availability (Pato & Obeso 2012). We expected that increased levels of defoliation would reduce fruit size because plants with smaller leaf areas capture less light, which in turn may limit the production of high quality (bigger) fruits. Our results do not support this hypothesis, as fruit/seed volume was independent of defoliation treatments. Because we evaluated the hypothesis by analysing the defoliation effects over the first 2 years (although the fruit sample was insufficient for the more intensive treatments for the second year), we cannot rule out the possibility that reductions in seed size will emerge later, when stored resources become exhausted as more defoliation events occur. Studies for tropical (Rockwood 1973) and non-tropical plant species (e.g. Crawley 1989; Koptur, Smith & Lawton 2005; Yuan *et al.* 2005) have documented that defoliation reduces fruit/seed size.

INFLUENCE OF FRUIT SIZE ON SEED DISPERSAL AND SEED PREDATION

Although fruit dispersal by frugivorous birds was not directly documented in our study, the assumption that birds are the primary dispersal agent is very likely as fruits of *C. ernesti-augustii* present an evident bird-dispersal syndrome (fleshy black fruits on an infructescence with vivid red colour; Hodel 1992; Machado, Lopes & Sazima 2005; Garwood & Bridgewater 2005). This syndrome has also been documented in the understorey tropical palm *Geonoma pauciflora* whose seeds are effectively dispersed by frugivorous birds (Pizo & Almeida-Neto 2009).

Our estimation of the percentage of fruits removed on the palm (> 60%) suggests that frugivorous animals may play a major role in the active dispersal ability of *C. ernesti-augustii*. There is evidence that seed removal by birds increases with fruit availability (crop size), as has been documented for the understorey palm *G. pauciflora* (Pizo & Almeida-Neto 2009). This positive relationship has two important implications for our study. First, because we quantified fruit removal when relatively large numbers of fruits were still on the palms, it is possible that our fruit removal level was overestimated. Second, as defoliation reduced fruit production, it is quite likely that losses of leaf area can also reduce the ability of the palms to disperse their seeds. Besides fruit crop size, fruit quality could also have consequences for dispersal as fruit removal rates were positively correlated with fruit size, as has also been shown in olive trees (Alcántara *et al.* 1997; Rey & Alcántara 2000). However, this effect is believed to be less important than crop size (Pizo & Almeida-Neto 2009).

The fact that isolated seeds (mimicking bird-dispersed seeds) suffered lower predation rates (most likely by rodents) on the ground, than grouped seeds (mimicking gravity-dispersed seeds), indicates the importance of the frugivore-plant

interaction for the palm's fitness. This result also points to the existence of a density-dependent seed predation mechanism in our study system, in line with the Janzen–Connell hypothesis (Janzen 1970; Connell 1971). We showed these density-dependent effects to be stronger on sites with fruiting palms (control plots) compared with 'sterile plots'. The fact that isolated seeds in the control plots suffered three times lower predation rates than in sterile plots could indicate that predators are satiated at sites with high availability of seeds, as proposed in other studies (Wolff 1996; Xiao, Zhang & Wang 2005; but see Ims 1990; Hulme 1998; and Shibata *et al.* 2002).

It should be noted, however, that not all seeds removed by rodents are eaten, some might be cached and forgotten, or some might be partly eaten and remain viable (Forget & Milleron 1991). Furthermore, there is evidence that rodent predators may act as secondary dispersal agents, increasing seedling recruitment (Jansen, Bongers & Hemerik 2004). In our experiment, about 14% of the tagged fruits were not located. Although the fate of these fruits is unknown, including or excluding this fraction did not affect our conclusions regarding the effects of defoliation on seedling recruitment. Furthermore, our estimated seed predation level (70%) is consistent with others studies (e.g. Obeso & Fernández-Calvo 2002). Levels of predation and secondary dispersal of seeds by rodents, which are similar to our estimates (20% dispersed at distances greater than one metre), were reported for a set of tree species in Costa Rica (Wenny 2005).

POPULATION CONSEQUENCES OF DEFOLIATION ON SEEDLING RECRUITMENT

Our study clearly points to a key role for immigrant seeds for recruitment in populations subjected to intense defoliation such as commonly applied in leaf harvesting. Even under no defoliation scenarios, where palms suffer leaf losses due to canopy falling debris and herbivory, bird seed dispersal is expected to be important because it compensates the higher predation rates suffered by gravity-dispersed seeds.

Lack of local seed sources due to low fecundity, limited seed dispersal and clumping, can have lasting impacts on plant population dynamics (Clark *et al.* 1999). The results from our model suggest that the negative consequences of defoliation on fruit availability and seed dispersal by birds may negatively affect *C. ernesti-augustii* populations by reducing seedling recruitment from immigrant seeds, if defoliation happens over a large area as often the case with leaf harvesting. The importance of immigration has been highlighted in studies analysing metapopulation dynamics of plant species (e.g. Cipollini, Wallace-Senft & Whigham 1994; Husband & Barrett 1996; Valverde & Silvertown 1997; Alexander *et al.* 2012). The source-sink paradigm (Pulliam 1988; Eriksson 1996; Husband & Barrett 1996; Hull, Morzillo & Wiens 2011), in which expanding populations found in high quality habitats (sources) provide a flux of individuals to declining populations found in low quality habitats (sinks), can be applied to *Chamaedorea* species as shown by Berry

et al. (2008). In our case, non-defoliated (healthy) populations play the role of seed sources, and the intensively defoliated populations, the role of sinks, persistence of the harvested populations depending on the flux of immigrating seeds from the sources. It might be noted, however, that loss of migration (dispersion) may have higher demographic consequences in spatially clumped populations, which is the case for *C. ernesti-augustii* in our area where it forms clumps of about 0.5 ha, separated by 0.5 or more kilometres (J.C. Hernández-Barrios, personal observations).

Our modelled scenarios and empirical data support the above idea. The presence of fruiting palms, playing the role of sources, enabled the recruitment of seedlings from immigrant seeds in the heavy defoliated plots (sinks), which was neatly exemplified by our modelled 'df+c' scenario (harvested patches surrounded by non-defoliated populations). Our model also helped to explain the recruitment of seedlings on the sterile plots, characterized by an absence of local seed production. The mean annual recruitment rate of seedlings produced by immigrant seeds estimated by our model (209 ± 68 in 900 m^2) was comparable to that observed in the sterile plots (160 ± 33 SE). Also, the estimated seedling recruitment in the sterile plots, using our seed rain ($0.86 \text{ seeds m}^2 \text{ year}^{-1}$), seed survival to predation ($0.44 \text{ seeds seeds}^{-1}$) and seed germination ($0.82 \text{ seeds seeds}^{-1}$) data, was within the same order of magnitude ($279 \text{ seedlings } 900 \text{ m}^{-2} \text{ year}^{-1}$). In our sensitivity analysis, seedling recruitment was more sensitive to changes in dispersal probabilities, than to changes in predation and germination probabilities of immigrant seeds. Such results indicate that our modelling analysis could be improved by having better estimates of fruit removal by birds (that was estimated for a time shorter than the total fruiting period) and seed germination (that we assumed to be the same for immigrant and local seeds).

Overall, our results emphasize the importance of immigration for seedling recruitment in the studied palm populations. In *C. radicalis*, immigrant seeds from undisturbed populations proved their importance for the maintenance of populations that were subjected to heavy browsing by donkeys (Berry *et al.* 2008). In the understory palm *Astrocaryum mexicanum*, immigrant seeds dispersed from forest patches with higher fruit production increased seedling recruitment where seed predation rates were lower (Martínez-Ramos & Álvarez-Buylla 1995). Garnier, Deville & Lecomte (2006) simulated that when fecundity declines to zero immigration of seeds from outside permits the persistence of weed populations. It would seem inappropriate to emphasize the importance of seed production and dispersal for population dynamics of a long-lived species, such as *C. ernesti-augustii*, when matrix-modelling studies have shown that fecundity is relatively unimportant for population growth in such species (Silvertown *et al.* 1993; Franco & Silvertown 2004). However, we simulated scenarios with high levels of defoliation that reduced fruit production near zero, where strong negative demographic consequences may emerge. For example, in the Brazil, nut tree (*B. excelsa*), chronic and severe seed harvesting regimes generate a long-lasting lack of recruitment in the population (Peres *et al.* 2003).

Seed movement by animals is critical for the spatial structuring of plant populations (e.g. López-Toledo *et al.* 2013). Seed dispersal is also of paramount relevance for the genetic diversity and connectivity of populations (Álvarez-Buylla *et al.* 1996; Soons & Ozinga 2005; Soons *et al.* 2005; Cole, White & Nair 2007; Honnay *et al.* 2009). The reduction in seed dispersal due to impoverished fruit/seed quality (abundance and size) caused by high levels of chronic defoliation may produce the loss of genetic connectivity. *C. ernesti-augustii* populations in Belize suffer increasing inbreeding depression and the risk of genetic drift, likely due to the loss of connectivity due to high leaf-harvesting regimes (Cibrián-Jaramillo *et al.* 2009). A formal metapopulation analysis, encompassing different time-spatial scales and the demographic and genetic effects of dispersal limitations imposed by leaf-harvesting regimes, could provide an integral assessment of the ecological effects of intense and sustained defoliation in natural populations of this species.

Conclusion

Recurrent and intense leaf area losses in *C. ernesti-augustii* have strong effects on mutualistic (e.g. seed dispersal by birds) and antagonistic (e.g. seed predation by small vertebrates) biotic interactions, leading to a decrease in the dispersal of the seeds and in the recruitment rate of seedlings. Such effects may have strong negative consequences for the demography and genetic diversity of palm populations. Several tropical rain forest plants depend on animals for the dispersal of the seeds and suffer recurrent leaf area losses by hits from falling canopy debris (Martínez-Ramos *et al.* 1988; Clark & Clark 1991) or from herbivores (Coley & Barone 1996). The defoliation effects documented here for *C. ernesti-augustii* might apply to other plant species, especially to other commercially harvested *Chamaedorea* species. The defoliation consequences for seed dispersal and seedling recruitment should be taken into account when determining the long-term sustainability of palm leaf-harvesting regimes (Jongejans, Skarpaas & Shea 2008).

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