Ecology of palm populations and communities in a fragmented tropical landscape

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Abstract

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Dramatic declines in the global forested area in recent decades have been particularly severe in tropical areas. Tropical forests have been heavily impacted by a range of human activities including conversion to agriculture, hunting, and timber extraction. Deforestation has led to extensive habitat fragmentation, and most tropical forests are now embedded in human-modified landscapes comprising a mosaic of land-cover types. The consequences of these changes for biodiversity and species interactions are an area of active research interest.

In this thesis, I assess whether remnants of rainforest conserve species and interactions within a fragmented tropical landscape in tropical Mexico, and compare data from fragments with data from nearby protected and continuous rainforests. I focus on palms (Arecaceae), an ecologically and economically important plant family of tropical and subtropical regions, and investigate responses to fragmentation at the population and community level, as well as interactions with mutualists (pollinators) and antagonists (pathogens and herbivores).

I found evidence that management practices within fragments affects palm populations: palm abundances were lower in unprotected forest fragments than in those protected from human activities such as wood and timber extraction,

extraction of plants and hunting and poaching. Community composition did not differ significantly between these protected and unprotected fragments. Edge effects were also apparent in forest fragments: changes in palm abundances and palm diversity were most pronounced within 100 m of the forest edge, and these edge effects were similar in both protected and unprotected fragments.

For one focal palm species, *Geonoma interrupta,* pollination and fruit production, and the likely consequences for demography, were investigated in detail. Reproductive success was significantly lower in fragments than in continuous forest. Native bees were the most frequent visitors and likely pollen vectors. Experimental exclusion of natural enemies in a field significantly increased seedling survival of two palm species. However, the effect of excluding enemies did not differ significantly between the forest edge and interior of a fragmented forest.

The results presented in this thesis should be valuable in informing conservation and management strategies to conserve viable populations of rainforest palms. They show that the full effects of habitat fragmentation on palm distributions, diversity and abundance are best understood by taking into account biotic interactions and human management practices.

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Chapter 1. General introduction

With a current global population of 7.7 billion, expected to increase to nearly 10 billion by 2050 (UN 2019), humans are imposing an unprecedented strain on the world's natural resources. Recent discoveries of single-use plastic at the bottom of the world's deepest ocean trench at 10,898 m (Chiba *et al.* 2018), illustrate that the influence of the human species extends to all corners of the planet (Sanderson *et al.* 2002). This immense human impact has led some people to propose that we have entered a new geological epoch: the Anthropocene (Crutzen 2002, Steffen *et al.* 2007, Dirzo *et al.* 2014, Monastersky 2015). The growing demands for energy, food and other natural resources are impacting all corners of the planet, with forests among the most threatened ecosystems.

Much of the world's human population benefits either directly or indirectly from the biodiversity that forests contain. It has been estimated that at least 1.25 billion people have lifestyles that make them forest-dependent (FAO 2016). However, global forested area declined by 129 million ha (3.1 %) between 1990 and 2015 due to deforestation (FAO 2016). Alarmingly, over a shorter period (2010-2015), tropical forests have seen the highest decrease in area with an estimated 7 million ha of forest lost per year (FAO 2016).

Land-use change and deforestation

Over the past decades deforestation in tropical systems has received particular attention (Skole & Tucker 1993, FAO 2016). The causes and extent of deforestation differ between locations (FAO 2016), but globally tropical forests have lost more

than half of their original area due to human activities (Skole & Tucker 1993, Pimm & Raven 2000, Lewis 2006). In a recent review about human impacts on tropical forests it was proposed that after three biodiversity impoverishment phases, humanity is now on the verge of entering a fourth phase: global simplification of biodiversity (Lewis *et al.* 2015). This extreme scenario is defined mainly as the loss of species across landscapes through the combined effects of rapid change in climate, isolation of populations in fragmented landscapes (increasing the risk of extinctions), intensive competition with alien species and accumulative disturbances, such as logging and fires. Despite covering only about 10 per cent of the planet's surface, tropical forests contain more that 50 per cent of earth's biodiversity and they are highly important in regulating global processes such as climate, water cycling and carbon storage (Lewis *et al.* 2015). Consequently, the documented rapid decline of continuous forest area in many tropical regions has the potential to alter ecosystem processes and functions (Tabarelli *et al.* 1999).

To account for the needs of the growing human population, large areas of previously forested land have been converted to agricultural use. Globally, ~83% of all available farmland is used for pasture and fodder crops (like corn and soy) (Poore & Nemecek 2018). In the tropics over only five years (2010-2015), the area of agricultural land increased by 6 million hectares per year (FAO 2016). In Latin America, commercial agriculture accounts for almost 70% of deforestation (FAO 2016). In the Amazon region, cattle ranching, soybean farming and oil-palm plantations have been major drivers of deforestation since 1990 (FAO 2016). In fact, in most Neotropical countries the major threats to forests come from industrial drivers such as logging, oil-palm plantations and extensive cattle and soy farming (Lowman *et al.* 2013). In tropical areas of Mexico, abandoned pastures

that were recovering for decades have been recently transformed into oil-palm plantations (Gerardo Ceron, pers. obs.). Logging is among the primary drivers of biodiversity loss, with the potential to alter the capacity of forests to maintain important ecosystem services (Millennium Ecosystem Assessment (Program) 2005, Laurance *et al.* 2012, Haddad *et al.* 2015). It was estimated that between 2000 and 2005 tropical forests lost about one-fifth of their cover due to logging (Asner *et al.* 2009). Since many tree species in tropical forests tend to be rare (ter Steege *et al.* 2013), forest loss of this magnitude has the potential to push some tree species towards the brink of extinction.

Consequences of habitat loss: deforestation, logging and defaunation

Destruction of forest habitats leads to fragmentation of once continuous forest landscapes. Although there is evidence that remnant fragments can support a high diversity of species (Arroyo-Rodríguez *et al.* 2009, Hernández-Ruedas *et al.* 2014), the role of forest fragments in sustaining high levels of biodiversity in the longer term and in maintaining important ecosystem processes is still far from well known.

Forest fragmentation can affect biodiversity by changing physical factors such as water, wind, radiation, evaporation, and nutrient availability. These changes – which can be particularly strong near the fragment edge – can have negative consequences for the remnant species within fragments, particularly species adapted to the conditions in the forest interior. Edge effects can reach up to 500 m inside some fragments. The most evident effects are typically found within 200 m from edges (Laurance 1991), although the extent of the edge effect zone depends on the variable measured (i.e. temperature, humidity, invasive species).

This implies that even relatively large fragments, up to 1000 ha in size, may be entirely influenced by edge effects (Laurance 1991).

Even if species can endure the changing environmental conditions caused by edge effects, fragmentation of once continuous forests can still pose a threat to their survival. Fragmentation can also lead to loss of diversity by making populations smaller (and therefore more prone to extinction) and more isolated from each other (making recolonisation less likely if populations go locally extinct (Hanski 1998, 1999)). If individuals in fragments are reproductively isolated, this could also lead to a suite of consequences, such as inbreeding or unsuccessful transfer of gametes and potentially decreased in offspring production (Nonaka *et al.* 2019), which could eventually influence community structure. Following predictions from island biogeography and metapopulation theory, we may also expect the diversity to be positively correlated with the size of the fragments, if fragments are too small to sustain populations large enough to be viable in the long term (Hanski 1998, Hanski *et al.* 2013).

Logging through clear-cutting and timber extraction (including targeted logging of individuals of selected tree species) is also thought to pose a threat to forest diversity because of its potential to reduce the genetic diversity of tree populations (Finkeldey & Ziehe 2004). Selective logging targets valuable timber species, usually applying a minimum stem diameter for extraction (Putz *et al.* 2008). Selective logging therefore tends to remove the largest tree individuals within a population, which are also the ones that frequently have the largest seed set. In practice, felling schemes may not take the reproductive output of individual trees within the population into account, and as a result trees are often removed before they reach an optimal reproductive stage (Jalonen *et al.* 2014). Even if tree

individuals are left at the selectively logged forest site, the regeneration process might be compromised if there are few opportunities for successful regeneration (e.g. tree densities are too low to allow successful pollination (Jalonen *et al.* 2014)). In this context, tropical tree species might be particularly sensitive, since compared to temperate species, they are usually present at lower densities. As a majority of tropical tree species require cross fertilization to produce seeds (Alvarez-Buylla *et al.* 1996), this could potentially make tropical tree species particularly likely to suffer from reproductive problems following selective logging (Finkeldey & Ziehe 2004).

By creating new access to areas of forests, fragmentation aids in the process of extensive overhunting of animal populations and this is spreading rapidly across tropical forests. In the Neotropics large herbivores, including peccaries, tapirs, deer and large rodents, are among the most hunted species (Redford 1992, Wright & Duber 2001). For instance, the white-lipped peccary (*Tayassu pecari*) has been extirpated from over 21 per cent of its historical range from Southern Mexico to South America (Altrichter *et al.* 2012). This strong human pressure over mammals has led to their decrease in population size or local extinction, a phenomenon known as defaunation (Dirzo & Miranda 1991, Redford 1992). Direct and indirect species interactions, such as pollination, seed dispersal, seed predation, herbivory and trampling of seedlings, may be severely altered in defaunated forests. In the absence of predation and dispersal of seeds, large seeds tend to accumulate underneath their parent trees, which may change the spatial distribution of individuals and the community composition of the forest.

This thesis will concentrate on one particular aspect of the tropical biodiversity crisis, the impacts of fragmentation and land-use change on the diversity and reproductive ecology of palms. In the remainder of this General Introduction I introduce the biology of palms, discuss my specific research questions, and describe the forested landscape in Mexico where my research took place.

Palms as a focal taxon

The palm family (Arecaceae), with more than 2400 species worldwide (Govaerts *et al.* 2019) represents a key component of tropical and subtropical regions. In the Neotropics, palms are a conspicuous and distinctive element of the vegetation with approximately 500 species documented in the region (Henderson 1986). In Mexico there are more than 100 species from 22 genera (Quero 1992a). In Chiapas (the region in which the work presented here took place; see below) there are 40 species of palms, contributing to the local and regional biodiversity (Martínez *et al.* 1994, Meave *et al.* 2008).

Palms are also an important ecological and structural element in tropical vegetation (Quero 1992b). Mexican palms can be found at different strata in tropical forests, with species ranging from 30 cm to ~30 m in height. Some species of the genera *Attalea* and *Sabal* can be important elements of the canopy layer of primary evergreen rainforest, while *Astrocaryum*, *Chamaedorea*, *Bactris*, *Reinhardtia* and *Geonoma* occur in the lower strata of rainforest and other types of tropical forests.

Inflorescences, fruits and seeds from palms are often available all year round, representing an important food source for vertebrates and invertebrates to

exploit when other resources are scarce (Brewer 2001, Beck 2006, Barfod *et al.* 2011). For example, some species like *Astrocaryum mexicanum* can reach densities up to *c.* 1000 individuals/ha (Martínez-Ramos 1997), and approximately half of these individuals produce fruits.

The prevalent pollination mode of palms is by insects (Henderson 1986, Barfod *et al.* 2011). Although most palms do not seem to have a morphological flower specialization towards particular types of insect pollinators, some understorey cantharophilous species do, suggesting that beetle pollination is predominant (Henderson 1995, Núñez *et al.* 2005). Beetles are the most common visitors to palm flowers, followed by honeybees, stingless bees and flies (Barfod *et al.* 2011). Despite their importance in tropical forest, studies of the effects of fragmentation on the reproductive biology of palms are still limited. In a review of 90 published studies of palm pollination, the authors mentioned only two study cases documenting the effects of fragmentation on pollination mechanisms in palms (Barfod *et al.* 2011). Since about 58 percent of palms are obligated out-crossers and 45 per cent are dioecious, the study of the effects of fragmentation becomes relevant (Murcia 1996).

Palms are one of the plant families most exploited by humans, along with Poaceae and Fabaceae. Even without considering the most economically important species, date palm (*Phoenix dactylifera*), oil palm (*Elaeis guineensis*) and coconut (*Cocos nucifera*), palms occupy an important historical role in human history (FAO 2010). For many centuries, humans have used palms for different purposes such as food, medicine, fuel, materials, ornaments among others (de la Torre *et al.* 2009, Rico García-Amado *et al.* 2013). For example, Mayans used leaves from the species *Thrinax radiata* for thatching and broom manufacturing, and in present times this

species is used in the building industry (Calvo-Irabién *et al.* 2009). In fact, palm leaves represent an important non-timber forest product in the tropics, but excessive extraction can promote structural and physiological changes in the affected individuals (Lopez-Toledo *et al.* 2018). The utilization of palms, as a whole or in parts, can have negative effects at the population and individual level, impacting survival, growth and reproduction (Ticktin 2004, Lopez-Toledo *et al.* 2018). The resulting changes in palm communities could have impacts on both the forest structure and its associated fauna.

A handful of published studies have explored the relationship between palms and edge effects, demonstrating that palm species richness can be negatively affected by edge effects and by forest fragment size (Benítez-Malvido 1998, Benítez-Malvido & Martínez-Ramos 2003). Nonetheless, these studies only considered palm seedling communities.

The responses of palms to anthropogenic effects appear to be context dependent (Eiserhardt *et al.* 2011). For example, in the tropical rainforest of Los Tuxtlas, Mexico, the fragmentation process has led to more frequent gap formation in smaller fragments allowing more light to reach the understorey (Dirzo *et al.* 1992). More light has allowed the palm *Astrocaryum mexicanum* to increase its seed production. The increasing light levels has also allowed younger palms to grow faster and reach maturity sooner, while older palms suffer from exposure to sunlight and die (Ezcurra 2016). Through fragmentation and an increased light availability the demography of *A. mexicanum* has changed, its life span shortened, it reached the reproductive stage earlier, and its fecundity increased (Ezcurra 2016). Changes in palms can also be triggered by the loss of ecological interactions (Galetti & Dirzo 2013, Galetti *et al.* 2013, Carvalho *et al.* 2016). For instance,

defaunation (i.e. the contemporary decrease in abundance or extinction of animals caused by human activities) has caused a reduction in seed size and allelic frequency of the palm *Euterpe edulis* in forest fragments from which large seed predators have been lost; in areas where large avian frugivores are absent palm populations have smaller seeds and are 1.5 times more similar genetically than populations in pristine forests with an intact vertebrate fauna (Galetti *et al.* 2013, Carvalho *et al.* 2016). In Chiapas, seed dispersal of palms is carried out by a wide range of mammals, such as collared and white-lipped peccaries, tapir, agoutis, squirrels and howler and spider monkeys; but also by birds such as the scarlet macaw (Cerón-Marínez pers. obs.). Altered habitats can bring rapid changes to the evolutionary trajectory of palms.

Scope and structure of thesis

Despite the abundance and ecological importance of palms in tropical forests, our knowledge about how palm communities respond to forest fragmentation is still limited. As a key part of my thesis research, I conducted surveys of palm communities to assess whether forest fragmentation generates shifts in the diversity, species composition, and spatial structure of these plants. More specifically, I investigated how palm communities change across a human modified landscape in Chiapas, Mexico, and how palms respond to the abiotic and biotic conditions created by forest fragmentation. The study is based on observational and experimental studies conducted in a fragmented forest landscape in the southeastern state of Chiapas, Mexico.

In Chapter 2, I present data from palm surveys conducted in four different forest types (three types of fragmented forest differing in their degree of human

influence and a continuous, protected forest). I analyzed the recorded abundance, diversity and community composition of palms inside these four site types, along with environmental variables (forest cover in a 500m square, canopy cover, slope and elevation). I expected that the local abundance and diversity of palms would be positively associated with the amount of forest cover in the surrounding landscape.

In Chapter 3, I evaluate the extent that forest edge effects impact communities of palms. I compare abundance and diversity of palms in plots along 500-m transects from the edge to the forest interior to evaluate how far any edge effects extend. I also investigate if there were differences between study sites located in two landscape types (forest fragments *versus* continuous forest).

In Chapter 4, I investigate the effects that fragmentation has on the reproductive success of the palm *Geonoma interrupta*. I gathered information about flower phenology and the main flower visitors and if they transport the pollen of *G. interrupta*. I also excluded flower visitors in order to investigate the capacity of *G. interrupta* to self-fertilize. Finally I assessed the reproductive outcome of the palm, measured as the number of fruits produced. I conducted this research in a continuous and in fragmented forest landscape.

In Chapter 5, I assess the role that natural enemies play in the germination and establishment of palms. In this chapter I provide results of a field experiment, including physical and chemical exclusion of insects, fungal pathogens and ground-dwelling vertebrates. I also assess if habitat type (forest edge and forest interior) and the exclusion of natural enemies interact and influence seed germination and seedling survival of two palm species.

Chapter 6 is a general discussion of all four data chapters. Here I highlight the main conclusions of the work and possible implications. I also suggest potential future directions that would inform and complement what we have learned in this thesis.

Study area

The Greater Lacandona Ecosystem in southeast Mexico also includes parts of Guatemala, making it one of the largest areas of tropical rainforest in Mesoamerica (16°14.71' N, 90°56.23' W). The climate is warm and humid, with a mean annual temperature of 24°C. The annual rainfall varies from 2000 to 3500 mm (O'Brien 1998) and most precipitation occurs during the wet season from May to December with a relatively dry period from January to April. The main vegetation type is evergreen and semi-evergreen rainforest (De Jong *et al.* 2000).

This area is one of the most diverse ecosystems in Mexico, containing the highest mammal richness in the country (Medellín 1994). It also contains between 10 and 19 per cent of all vascular plant species in the country (Martínez *et al.* 1994). A list of species in the Arecaceae family recorded in the Lacandona region is presented in the Table 1. Seven Natural Protected Areas safeguard this particular ecosystem, of which Montes Azules Biosphere Reserve (MABR) is the largest, comprising a total of 331,200 ha, representing 34.6 percent of the Greater Lacandona Ecosystem (PMRBMA 2000).

Most of the fieldwork took place in the non-protected landscape of Marquez de Comillas region (MCR; approx. 93,300 ha), where fragmentation of previously continuous forest started over 40 years ago. Cornfields, cattle ranches and more recently oil-palm plantations surround the remaining forest patches. Comparative

studies took place in the adjacent continuous protected forest of Montes Azules Biosphere Reserve (MABR).

Table 1. List of species from the Arecaceae family registered in the Lacandona region (Martínez *et al.* 1994). Life form: U= understory; C: canopy; CL: climbing. RC: ∗ included in the Mexican list of threatened species (SEMARNAT 2010).

No.	Species	LF	RC
1	*Acoelorrhaphe wrightii*	U	
2	*Acrocomia mexicana*	C	
3	*Astrocaryum mexicanum*	U	
4	*Attalea butyracea* (Mutis ex L.f.) Wess.Boer	C	
5	*Attalea cohune* Mart.	C	
6	*Attalea rostrata* Oerst.	C	
7	*Bactris baculifera*	U	
8	*Bactris major* Jacq.	U	∗
9	*Bactris mexicana* Mart.	U	
10	*Chamaedorea adscendens* (Dammer) Burret	U	
11	*Chamaedorea arenbergiana* H.Wendl.	U	∗
12	*Chamaedorea cataractarum* Mart.	U	∗
13	*Chamaedorea elatior* Mart.	U	∗
14	*Chamaedorea elegans* Mart.	U	
15	*Chamaedorea ernesti-augusti* H.Wendl.	U	∗
16	*Chamaedorea geonomiformis* H.Wendl.	U	∗
17	*Chamaedorea neurochlamys* Burret	U	
18	*Chamaedorea nubium* Standl. & Steyerm.	U	∗
19	*Chamaedorea oblongata* Mart.	U	
20	*Chamaedorea simplex* Burret	U	∗
21	*Chamaedorea tepejilote* Liebm.	U	
22	*Chrysophila argentea* Bartlett	C	∗
23	*Cryosophila stauracantha* (Heynh.) R. Evans	U	
24	*Desmoncus ferox* Bartlett	CL	
25	*Desmoncus quasillarius* Bartlett	CL	
26	*Desmoncus uaxactunensis* Bartlett.	CL	

27	*Gaussia gomez-pompae* Quero	C	*
28	*Gaussia maya* Quero	C	*
29	*Geonoma binervia* Oerst.	U	
30	*Geonoma interrupta* (Ruiz & Pav.) Mart.	U	*
31	*Geonoma mexicana Liebm.*	U	
32	*Geonoma oxycarpa* Mart.	U	*
33	*Geonoma seleri* Burret	U	
34	*Reinhardtia gracilis* H.Wendl.	U	*
35	*Reinhardtia simplex* H.Wendl.	U	
36	*Sabal mauritiiformis* (H. Karst.) Griseb. & H. Wendl.	C	
37	*Sabal mexicana* Mart.	C	
38	*Schippia concolor* Burret	U	

Chapter 2. Local forest attributes impact palm communities in a fragmented rainforest

Introduction

Human activities transform continuous forest landscapes into a complex matrix of land-cover types, particularly in tropical areas (Gibson *et al.* 2011). Agriculture, cattle ranching and selective logging are among some of the causes that reduce the amount of forest cover. This habitat loss poses threats to the remaining species and leads to loss of biodiversity (Murcia 1995, Gibson *et al.* 2011). Given that a large proportion of tropical rainforest biodiversity occurs in fragments (Gibson *et al.* 2011), understanding their effectiveness in maintaining its diversity is crucial.

The size of a fragment can be an important factor determining its value as a reservoir of forest diversity. Although relatively small fragments can play an important role in harboring the remaining species there is still debate about their conservation value (Ferraz *et al.* 2003, Hernández-Ruedas *et al.* 2014). Inside small fragments populations of plants and other taxa tend to be small. As a consequence, these populations may be more prone to local extinctions (for example through small population processes such as environmental and demographic stochasticity and inbreeding (Simberloff 2009, Nonaka *et al.* 2019). Connectivity is another essential component in fragmented landscapes. If fragments are well-connected (close to other fragments), the flux of individuals through the landscape might facilitate the long-term persistence of populations with positive effects on biodiversity (Matesanz *et al.* 2015). On the contrary, if fragments are isolated from each other, biodiversity might suffer, for example if

recolonizations are not possible following extinctions within individual fragments.

Human intervention does not necessarily stop after fragmentation, as local people often use the remnant forest patches in a variety of ways that degrades the remaining forest (Lewis *et al.* 2015). Hunting, selective logging and extraction of plant-based products (such as firewood) are among the activities that further impoverish the remnant forest patches. Occasionally, fragments are declared as communal reserves, sometimes incentivised by socioeconomic factors and by governmental payments for ecosystem services (Lewis *et al.* 2015). The effects of management history and current land use on patterns of diversity in fragmented forest landscapes are often not known.

Palms form an important part of the tropical forest food web. Since palms can reach high local densities (Martínez-Ramos 1997) and since inflorescences, fruits and seeds of palms are often available all year around, palms represent an important food source for vertebrates and invertebrates to exploit when other resources are scarce (Brewer 2001, Beck 2006, Barfod *et al.* 2011). Previous studies have shown that palm species richness can be negatively affected by edge effects and by forest fragmentation (Benítez-Malvido 1998, Benítez-Malvido & Martínez-Ramos 2003, Baez & Balslev 2007, Browne & Karubian 2016). However, these studies only considered the palm seedling community. Despite the abundance and ecological importance of palms in tropical forests, our knowledge about how palm communities respond to forest fragmentation is still limited. Since changes in palm communities could have potential impacts on both the forest structure and its associated fauna, understanding the responses of palms to forest fragmentation is important.

Here we examine the effects of fragmentation and local land use on the diversity of native palm assemblages in a human-modified forest landscape in the State of Chiapas, Southeast Mexico. We asked whether the level of protection provided by local communities contributes to the conservation of palm diversity. In order to achieve our aim, we recorded abundance, size-distribution and diversity of palms in forest remnants that are either protected and managed by local communities or unprotected. For comparison, we documented palm assemblages within a continuous forested area protected by the federal government. We predicted that the local abundance and diversity of palms would be positively associated with the degree of protection they receive but also with amount of forest cover in the surrounding landscape. Larger remnants of forest may allow for more species to survive in the long term and may also be associated with lower anthropogenic impacts (e.g. less logging and less impact on seed dispersers and other species interacting with palms). As habitat loss and fragmentation do not always result in discrete forest patches, but rather in a complex and heterogeneous matrix of different land cover types, we focused on the effects that landscape structure could have on palm abundance, demography and diversity.

Methods

Study area

The study was conducted in the Greater Lacandona Ecosystem, southeast Mexico (Figure 1A). This ecosystem includes parts of Guatemala, making it one of the largest areas of tropical rainforest in Mesoamerica (16°14.71' N, 90°56.23' W). Although it has lost two-thirds of its original 1,500,000 ha area over the past ~40

years through anthropogenic activities (Mendoza & Dirzo 1999, De Jong *et al.* 2000), the Greater Lacandona Ecosystem remains an important area in terms of biodiversity conservation.

The climate of the Greater Lacandona area is warm and humid, with a mean annual temperature of 24°C. The average (SE) annual rainfall is 3187±447 mm (O'Brien 1998) and most precipitation falls during the wet season (May to December). The period from January to April is relatively dry. The main vegetation type in the area is evergreen and semi-evergreen rainforest (De Jong *et al.* 2000).

The Greater Lacandona area is one of the most diverse ecosystems in Mexico, having the highest mammal richness in the country including viable populations of jaguar (*Panthera onca*), white-lipped peccary (*Tayassu pecari*) and tapir (*Tapirus bairdii*) (Medellín 1994). Between 10% and 19% of all vascular plant species in the country occur in the Lacandona region, including 38 species of palms (Martínez *et al.* 1994). Seven Natural Protected Areas safeguard the Lacandona region. Of these, Montes Azules Biosphere Reserve (MABR) is the largest, comprising a total of 331,200 ha of the Greater Lacandona Ecosystem (PMRBMA 2000).

Fieldwork took place within the non-protected landscape of Marquez de Comillas region (MCR; approx. 93,300 ha, adjacent to the MABR), where fragmentation of previously continuous forest started over 40 years ago. Settlements, crops, cattle pasture and more recently oil-palm plantations surround the remaining rainforest. In this particular landscape, the deforestation process has not created isolated forest patches, but rather an intricate configuration of different land covers. Even though, hereafter we call our study

sites *fragments*, we are aware that there is a degree of connectivity among the remaining forest (Figure 1A).

Specific study sites

Potential study sites were selected prior to fieldwork using satellite images from 2015, freely available from Bing maps (www.bing.com/maps). All sites were restricted, as much as possible, to lowlands (ranging from 137 to 218 metres above sea level) and flat areas (Table S1). We surveyed four forest types: 1) fragments adjacent to human settlements; 2) unprotected fragments further away from settlements; 3) communal reserves; and 4) sites inside MABR (a continuous and protected forest). ***Forest fragments adjacent to human settlements*** are relatively undisturbed areas, although there are some sporadic activities (e.g. firewood collection and extraction of non-woody plants). One of the major purposes of these patches is to function as a catchment area, a source of fresh water. Local authorities prohibit hunting. These fragments were on average (±SE) 210±8 m away from the settlements. ***Unprotected fragments further away from settlements***, on average (±SE) 2633±107 m away from the settlements, were also included in our study. Common activities in these patches include wood and timber extraction, extraction of plants and hunting and poaching. ***Communal reserves*** are relatively large areas of forest that have been conserved by local communities. This practice is incentivised by payments received from the federal government to provide compensation for ecosystem services provided by the forest. Constantly monitored by authorities, all access and activities inside these reserves are restricted. Ecotourism and research are the main activities inside the communal reserves, but the frequency of visitors is

low. These reserves were on average (±SE) 2833±296 m away from the settlements. The ***sites in the continuous protected forest area*** were all located ~1000 m away from the closest edge (the Lacantún river) within the MABR (Figure 1A).

When selecting study sites, we took care not to confound site type with spatial location within the landscape (e.g. sites representing different types were interspersed as much as possible). After scouting the potential study sites and gaining access permits from landowners, we were able to include, across the fragmented landscape of MCR, six fragments adjacent to human settlements; six unprotected patches of similar size but far from settlements, and six communal reserves. In addition to the 18 sites in the fragmented MCR landscape we included five control sites within the protected rainforest area of MABR (Figure 1), making a grand total of 23 surveyed sites.

Study system: Palms

The Arecaceae family represents a key component of Neotropical vegetation with approximately 500 species (Henderson 1986). In Mexico alone there are more than 100 species representing 22 genera (Quero 1992a), and of these nearly 40 % occur in the region of Chiapas (Martínez *et al.* 1994, Meave *et al.* 2008). In addition to forming an important part of the tropical forest plant diversity, palms are important ecological and structural elements in the tropical forest vegetation (Quero 1992b). Some species in the genera *Attalea* and *Sabal* are important elements of the canopy of primary evergreen rainforest, while species in genera such as *Astrocaryum*, *Chamaedorea*, *Bactris*, *Reinhardtia* and *Geonoma* occur at lower strata in rainforests. The prevalent pollination mode of

palms is by insects (Henderson 1986, Barfod *et al.* 2011). Although most palms do not seem to have a morphological flower specialization, some understorey cantharophilous species do, suggesting that beetle pollination is predominant (Henderson 1995, Núñez *et al.* 2005). Beetles are the most common visitors to palm flowers, followed by honeybees and stingless bees and flies (Chapter 4 of this thesis, Barfod et al., 2011). In Chiapas, seed dispersal is mainly carried out by mammals, such as collared and white-lipped peccaries (*Peccari tajacu* and *Tayassu pecari*), tapir (*Tapirus bairdii*), agouti (*Dasyprocta punctata*), squirrels (*Sciurus* spp.) and howler (*Alouata pigra*) and spider monkey (*Ateles geoffroyi*); but also by birds such as the scarlet macaw (*Ara macao*)(Cerón-Martínez pers. obs.).

Field surveys of palms and study plots

Data were collected during the dry season (January-April) of 2016. To document the palm community at each site we set up a series of six 25 x 4 m plots (0.06 ha of forest surveyed per site). The six plots were arranged according to the layout presented in Figure 1B. Within each plot, all adult (individual with past or present reproductive parts) and juvenile (pinnate leaves without signs of reproduction) palm individuals were recorded and identified to species level (where necessary, morphospecies codes were used). Some palms can grow clonal stems and to avoid errors based on misjudgement in the context of the analysis on total abundance (see below), we counted every clonal stem as a separate individual. On every juvenile and adult palm we measured height and basal stem diameter. For some species with juvenile individuals that do not develop an early stem, but rather present a rosette arrangement of leaves near

the ground (e.g. *Attalea* and *Geonoma*), it was not possible to measure basal stem diameter.

Within each 25 x 4 m plot, the number of seedlings (singled-leaved individuals) was counted in ten systematically located sub-plots of 5 × 2 m (Figure 1B). Identifying seedlings to species presents various challenges; therefore we could only identify and group them at genus level. We identified palm species with the aid of two experienced parabiologists and identification keys for Mexico (Quero & Pérez-Farrera 2010). Cerón-Martínez measured variables (related to size and reproduction) for all palm species within each plot at all sites.

At each plot, canopy cover was estimated from photographs taken with a camera Nikon (Model Coolpix S2900), with NIKKOR lens with 5x optical zoom and a focal length of 4.6-23.0 mm (angle of view equivalent to that of 26–130 mm lens in 35mm), at 100 cm from the ground at the plot centre. We followed the method proposed by Beckschäfer (2015) for non-hemispherical photographs to estimate the light availability at each plot. Images were processed using ImageJ 1.50i (Schneider *et al.* 2012). Elevation measurements (metres above sea level) were taken using a GPS, and slope was calculated with the aid of a clinometer. All data were recorded at the plot level.

Forest cover

Using satellite images from March 2016 obtained from the Copernicus Open Access Hub (https://scihub.copernicus.eu/dhus/#/home), we characterized the forest cover within a 500m square from the center of each of our study sites. Cloud cover on the satellite images was <2%. We used SNAP 5 to process

satellite images and calculate the normalized difference vegetation index (https://step.esa.int/main/doc/tutorials/snap-tutorials). We used the Semi-Automatic Classification Plugin (Congedo 2016) for QGIS to obtain the forest cover for the wider landscape surrounding the centre of each site. This forest cover was verified with the information obtained during data collection. We followed Olofsson et al. (2014) to classify the spectral signatures of our regions of interest (ROI) and used a systematic selection over a random selection because we performed field verifications of the ROI assignments. Forest cover classification was improved with reclassification of wrongly assigned pixels based on data taken from the field. Accuracy was assessed by comparing three different classification algorithms from the Semi-Automatic Classification Plugin (Olofsson *et al.* 2014, Congedo 2016). The overall accuracy of land cover type was 73%.

Statistical analysis

All analyses were performed using R version 3.3.3 (R Core Team 2017). Palm abundance, (overall, and separately for individual life stages, i.e. seedlings, juveniles and adults), diversity (Simpson's D for pooled juveniles and adults and separately for juveniles and adults) and community composition were analysed in separate models.

We analysed how site type and environmental variables influence the abundance of palms using generalized linear mixed-effects models (GLMMs) with a negative binomial distribution using the *glmmADMB* (Skaug *et al.* 2016) package. The total abundance of palms was modelled as a function of site type (continuous forest, communal reserve, settlement or small fragment), forest

cover (in a 500m square), canopy cover, slope and elevation. Site ID was included as a random effect to account for non-independence of plots within individual study sites. A full model including all interactions was initially assessed, but since none of the interactions were significant they were dropped. The best model was selected based on Akaike Information Criterion (AIC) using the "*dredge*" function in the *MuMIn* package (Bartoń 2019). All explanatory variables were standardized before the analyses (centred and divided by standard deviation). Multicollinearity was detected for the explanatory variable canopy cover; the variance inflation factor was higher than three, so we removed it from the analyses (Zuur *et al.* 2010). We compared differences among site types with a Tukey post hoc test using the *glht* function, with Holm correction, in the *multcomp* package (Hothorn *et al.* 2008). Initially, we analysed all life stages and all species combined, but we also conducted separate analyses for total abundances of adults, juveniles and seedlings using the same approach. Using the approach described above, we also modelled the total abundance of each of four palm species that occurred in a minimum of three sites within each of the four site types (Table 2): *Bactris mexicana*, *Desmoncus orthacanthos*, *Chamaedorea tepejilote* and *C. neurochlamys*.

Differences in palm diversity among sites were analysed using a linear mixed effects model (using the *glmmADMB* package with a normal error distribution) in which plot-specific palm diversity was modelled as a function of site type (continuous, communal reserve, settlement and small fragments), forest cover (in a 500m square), slope and elevation. As a measure of diversity, we used the effective number of individuals, obtained by calculating the inverse Simpson's dominance index of diversity, for juveniles and adults pooled and for

juveniles and adults separately, using the *vegan* package (Oksanen *et al.* 2017). Prior to analysis, the diversity index was log-transformed to improve normality of residuals.

To assess if the species composition of palm assemblages are different among the four site types, (continuous, communal reserve, settlement and small fragments) we used the *manyglm* function from the package *mvabund* (Wang *et al.* 2012) for a multivariate analysis. This approach fits a separate GLM to each species using a common set of explanatory variables (Wang *et al.* 2012). Data were visualized with a two-dimensional non-metric multidimensional scaling (NMDS) ordination plot using Bray-Curtis dissimilarity metrics to display the distances between plots. These analyses were performed using the *vegan* package (Oksanen *et al.* 2017).

Results

Overall patterns in abundance, richness and species composition

We recorded 13,147 palm individuals representing 19 palm species across the 23 study sites. Twelve species were recorded within the continuous forest (n = 5 sites) and 17 species in the fragmented landscape (n=18 sites). The average number of individuals (±SE) per site was 572±119 (all life stages pooled); while adult stems averaged 126±26, juvenile stems 69±14 and seedlings 376±78 individuals. The five most abundant species (based on numbers of adult and juveniles) were *Chamaedorea tepejilote* (885), *Bactris mexicana* (823), *B. major* (757), *Reinhardtia simplex* (535) and *Desmoncus orthacanthos* (507). None of the species was recorded in all sites, but *B. mexicana* and *D. orthacanthos* were present in the majority of sites (21 out of 23 sites; Table 1).

Abundance

Overall, site type was the only significant variable in the analyses on the abundance of palms. The total abundance of palms (adults, juveniles and seedlings combined) was significantly higher in the continuous forest sites than in the communal reserves and non-protected patches (Table 3). Although not statistically significant, there was a trend for sites close to settlements to have lower palm abundances than sites in the continuous forest (Table 3). A similar pattern was seen when data were analysed separately for adults, juveniles and seedlings: Palm abundances tended to be higher at the continuous forest sites than other site types (negative coefficient values for all other site types; Table 3). Across all life stages (adults, juveniles and seedlings) palm abundances were significantly lower at non-protected fragment sites than at continuous forest sites. There was also significantly lower seedling abundance in both communal reserves and non-protected fragment sites than in continuous forest sites (Table 3).

For two of the four palm species for which species-specific analyses were conducted, abundances were significantly affected by site type. Of these, *D. orthacanthos* had significantly higher abundances in the communal reserve sites than in the continuous forest sites (Table 3). *Chamaedorea tepejilote* was the only species significantly *less* abundant in the three fragmented site types compared to the continuous forest sites (Table 3). For this species, there were also some marginally non-significant effects of forest cover and elevation, with more individuals at sites with low forest cover and at lower elevations (Table 3).

Diversity

There were no significant differences in palm diversity (Simpson's *D*) between site types (Table 4).

Community composition

The palm assemblages associated with the four site types were not significantly different from each other in terms of species composition (Table 5). This result was supported by the NMDS, which showed that sites clustered together (Figure 3).

Discussion

Our results showed that the total abundance of palms in the southern Lacandona forest area differed only between the MABR and the non-protected fragmented sites. *Only communal reserves* and *fragments adjacent to human settlements* presented a relative degree of protection compared to the *sites in the continuous protected forest area.* This indicates that the studied fragments that are relatively protected by locals can harbour similar abundances of palms to the protected and continuous forest. Although the *unprotected fragments further away from settlements* presented the lowest abundance of all study sites, the only significant differences were against the values in continuous forest sites. The relevance of maintaining routine inspections of the remnant patches of forest was also supported by the lack of differences in diversity and community composition among all site types. The continuous forest sites provide a baseline for comparisons and give us an indication about the impact of anthropogenic

activities on palm assemblages. Palm abundances were indeed lower in some of the human-modified sites than in the continuous forest sites.

Among the more human-modified sites we studied, communal reserves represent the highest protection relative to other types of fragments. While patches adjacent to settlements are not subjected to exploitation, the non-protected fragments, which are distant from settlements, showed signs of unsupervised human activities (such as cattle presence and/or extraction of timber and non-timber products). Among all sites, the non-protected fragments presented the lowest total palm abundance, as well as the lowest adult and seedling abundances. Evidence of recent palm harvesting and cattle activity (personal observations) suggests that these patches are more prone to suffer from anthropogenic effects. This could be one explanation for why the non-protected patches had the lowest palm abundances (a pattern detected across all studied life stages). Plant abundances and diversity can be linked to the level of human activity. For example, studies from South America indicate that many plant species can disappear from small fragments (Silva & Tabarelli 2000). Complex cascading effects, derived from human activities, can have consequences for the seedling community. In an African rainforest, forests protected from hunting had significantly higher numbers of seedlings compared to forests without protection (Effiom *et al.* 2013) – a pattern that was likely caused by a loss of primates. Under a constant human pressure, the unprotected fragments could be unable to maintain key biological processes.

The landscape matrix can be a determinant of the ability of a fragment to maintain its biodiversity, especially if surrounded by a complex structure of pasture or croplands (Murcia 1995). The altered abiotic conditions near forest

edges that can extend toward the fragment interior may contribute to the changes in biological processes. Lower abundance can be related to those edge effects reaching far inside the forest patches (Chapter 3 of this thesis). For instance, many palm species are associated with the kind of light conditions that an open canopy provides (Siebert 2000, Svenning 2001). Dominance from one or few species that rapidly benefited from disturbance can also be associated to alterations created by fragmentation (Santos *et al.* 2012). For example, populations of *Desmoncus orthacanthos* grow significantly greater under high light environments. The distribution of this palm covers a wide range of forest, climatic and edaphic conditions, but its population recovers faster under high-light conditions, even after human impacts, from small-scale harvesting (for handicrafts and basketry) to some large-scale disturbances, such as deforestation and fragmentation (Siebert 2000). This can produce less diverse plant communities, i.e. where a few species of relatively high abundance dominate numerically.

We are aware that all the studied fragmented sites present, to some extent, some degree of connectivity to other remnants of forest; therefore, because we are not studying entirely isolated fragments, we were expecting that forest cover would be a better predictor of the current conditions of the palm communities. Canopy cover could provide some degree of protection from the surrounding matrix (Murcia 1995). But surprisingly, among the explanatory variables, forest cover (in a 500m square) was a poor indicator of palm abundance, diversity and community composition. Similar results were found in other studies, where at a landscape level, forest cover was not associated with species richness nor abundance of palms (Browne & Karubian 2016), nor plant diversity of species of

trees, shrubs, lianas, palms, and herbs (Arroyo-Rodríguez *et al.* 2009). Finally, we are also aware that forest cover and site type may be expected to covary. Caution is called for when interpreting the trends of palm responses to fragmentation.

Since topographic variation (elevation and slope), from flat to hilly areas, has been linked to changes in overall palm abundance (Eiserhardt *et al.* 2011, Browne & Karubian 2016), we chose sites that were as homogeneous as possible. By standardising topographic variables we sought to investigate the role of other predictor variables, such as site type, in explaining variation in palm abundance, diversity and composition. In our landscape study, communal reserves had the most contrasting topographic variation but without a significant effect on palm abundance. As expected, we did not find topography to be a significant factor explaining abundance, diversity and community composition in palms. We are aware that by incorporating a more heterogeneous topography (higher and steeper sites), these results could change. There is evidence that the relationship between topography and abundance of palms seems to depend on the study area (geographical location). There are assemblages of palms that are more abundant on steeper slopes (>24 degrees) and crests in Costa Rica (Clark *et al.* 1995) and the central Amazonian forest (Kahn & de Castro 1985), while abundances decrease with elevation in the southern Amazonian forest (Salm *et al.* 2007) but increase in lower lands (<100 m.a.s.l.) of Costa Rica (Lieberman *et al.* 1996). Inundation can have a strong effect on palm diversity, as documented for western Amazonian palm species (Kristiansen *et al.* 2009). Although we avoided sites prone to flooding/inundation, we cannot rule out the possibility that historical regimes of inundation may have shaped the distribution of palms in the southern region of the Lacandona forest.

The Mexican Government places five out of the 19 species we recorded in a risk category; *Chamaedorea elatior, C. ernesti-augusti, Cryosophila stauracantha* and *Geonoma interrupta* are threatened, and *B. major* is subject to special protection (SEMARNAT 2010). Both *Chamaedorea* species were found only in forest fragments. Our findings showed that remnants of forest can harbour at least one palm species listed under a risk category. Preserving forest patches, regardless of their size, becomes a relevant topic of discussion for maintaining not only the regional palm diversity, but also preserve those species that may be at risk of local extinction.

Tables and figures

Table 1. Mean (±SE) species richness, abundance and diversity (Simpson's D) of palms across 23 sites from the Lacandona rainforest in southwest Chiapas, Mexico. Abundance* was calculated using the total number of stems. Species richness and diversity for seedlings were not included because some taxa were not identified to species level.

Variable	Site type	Overall	Adults	Juveniles	Seedlings
Number of species	All sites pooled (n=23)	6.4±0.4	4.2±0.3	5.6±0.3	-
	Continuous (n=5)	7.2±0.7	4.4±0.4	6.6±0.5	-
	Communal reserve (n=6)	7.3±0.9	4.3±0.6	6.5±0.8	-
	Non-protected (n=6)	6.1±0.8	4.3±0.8	5±0.5	-
	Settlement (n=6)	5.3±0.4	3.7±0.6	4.7±0.3	-
Abundance	All sites pooled	25±4	5±1	3±0.3	16±3
	Continuous	215±52	37±19	21±1	157±22
	Communal reserve	78±19	20±5	10±3	48±19
	Non-protected	50±14	11±6	8±2	31±7
	Settlement	89±17	24±10	12±3	52±9
Diversity	All sites pooled	3.26±0.28	3.11±0.22	3.34±0.26	-
	Continuous	3.74±0.86	2.89±0.38	4.04±0.68	-
	Communal reserve	3.22±0.35	3.43±0.37	3.67±0.56	-
	Non-protected	3.4±0.34	3.06±0.51	3.12±0.32	-
	Settlement	2.77±0.58	3.03±0.43	2.65±0.31	-

* Abundance is expressed in individuals per hectare.

Table 2. Combined numbers of individuals (adults and juveniles) of the 19 palm species recorded across the 23 sites, grouped by site type. Seedlings were not included in this summary since for some taxa seedlings could not be identified to species level. The column 'Occupancy' indicates the number of sites (out of 23) in which the species was observed. * Species included in a species-specific analysis (see Table 3).

Species	Continuous					Communal Reserves						Non-protected						Settlement						Occupancy
	1	2	3	4	5	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	
Attalea butyracea	3	1	8	-	7	6	-	-	-	-	-	-	8	-	-	-	-	-	-	-	6	-	-	7
Attalea cohume	-	-	-	-	-	-	-	-	-	-	71	-	-	-	-	-	-	-	-	-	-	-	-	1
Bactris major	-	-	4	2	-	-	18	-	-	-	3	-	8	-	-	-	-	-	-	22	36	-	-	7
Bactris mexicana	22	14	9	7	6	6	3	8	14	21	4	5	12	2	11	5	7	23	14	-	-	14	5	21*
Chamaedorea elatior	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	1
Chamaedorea elegans	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2
Chamaedorea ernesti-augusti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1
Chamaedorea neurochlamys	5	2	2	-	46	1	-	-	22	6	13	-	1	7	1	-	12	-	33	-	-	36	43	15*
Chamaedorea oblongata	-	-	-	-	12	-	-	-	5	-	1	-	2	-	-	-	-	-	-	-	-	-	-	4
Chamaedorea pinnatifrons	18	-	-	-	-	21	-	5	1	42	10	4	-	3	26	-	2	3	34	4	-	21	6	15
Chamaedorea tepejilote	20	45	21	85	34	-	-	3	1	6	1	-	71	-	1	1	13	-	1	1	60	-	69	17*
Cryosophila stauracantha	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Desmoncus orthacanthos	8	3	8	-	19	8	19	18	7	13	1	4	4	4	13	3	8	11	8	-	1	6	10	21*
Euterpe precatoria	-	-	-	-	-	4	-	-	-	1	-	-	-	12	-	-	-	1	4	-	-	18	-	6
Geonoma interrupta	-	-	-	-	-	-	-	-	-	17	-	-	-	-	-	-	3	-	18	-	-	-	-	3
Geonoma pinnatifrons	-	21	21	6	-	3	-	-	2	5	-	1	1	-	-	-	2	-	-	-	-	-	-	9
Geonoma undata	6	4	36	7	-	4	-	-	2	15	-	-	6	1	-	-	32	3	-	6	-	-	-	12
Reinhardtia simplex	8	39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Sabal mexicana	-	-	-	-	-	-	-	10	23	-	19	-	-	-	-	-	-	-	-	-	1	-	-	4

Table 3. Results from GLMMs with a negative binomial distribution assessing the effects of the explanatory variables site type (continuous, communal reserve, settlement and non-protected patches), forest cover (in a 500m square), slope and elevation on the response variables total palm abundance, adults, juveniles, seedlings and four palm species that occurred in a minimum of three sites within each of the four site types (for the latter only adults and juveniles were included in the models, as seedling identification could not be achieved to species level). For each response variable, the best model was selected based on Akaike Information Criterion using the "*dredge*" function in R. The column 'Post hoc' provides results from Tukey post hoc test assessing differences between site types. Treatments sharing letters are not significantly different.

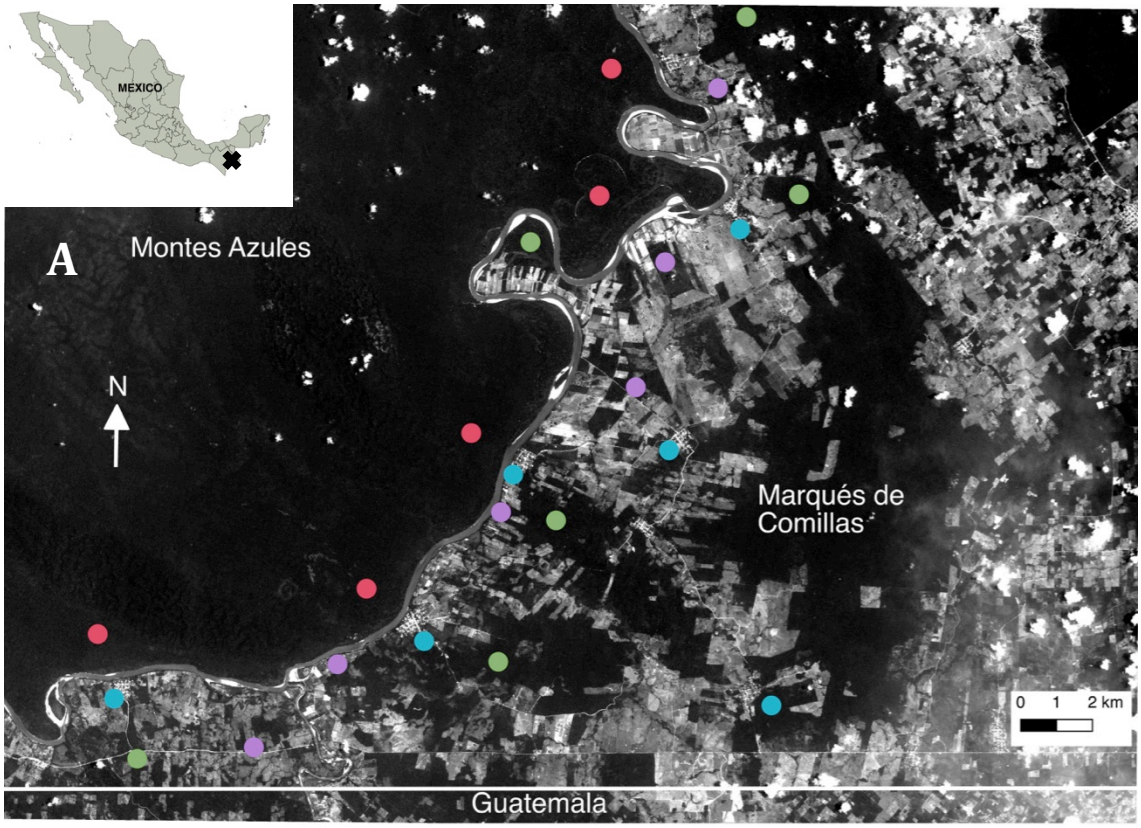
Response		Estimate	SE	z value	*P*	Post hoc
Total abundance	Continuous (Intercept)	6.819	0.256	26.62	<0.001***	a
	Communal Reserve	-0.826	0.347	-2.38	0.017*	ab
	Settlement	-0.631	0.347	-1.82	0.069	ab
	Non-protected	-1.367	0.348	-3.93	<0.001***	b
Adults	Continuous (Intercept)	5.265	0.471	11.19	<0.001***	a
	Communal Reserve	-0.224	0.504	-0.44	0.656	ab
	Settlement	-1.213	0.766	-1.58	0.113	ab
	Non-protected	-2.147	0.704	-3.05	0.002**	b
	Forest cover	-0.606	0.315	-1.92	0.054	-
Juveniles	Continuous (Intercept)	4.644	0.252	18.45	<0.001***	a
	Communal Reserve	-0.556	0.343	-1.62	0.105	a
	Settlement	-0.340	0.342	-1	0.319	a
	Non-protected	-0.819	0.344	-2.38	0.017*	a
Seedlings	Continuous (Intercept)	6.664	0.311	21.41	<0.001***	a
	Communal Reserve	-1.003	0.422	-2.38	0.017*	ab
	Settlement	-0.913	0.422	-2.16	0.031*	ab
	Non-protected	-1.439	0.422	-3.41	<0.001***	b
Bactris mexicana	Continuous (Intercept)	3.440	0.472	7.29	<0.001***	a
	Communal Reserve	0.313	0.638	0.49	0.62	a
	Settlement	0.232	0.638	0.36	0.72	a
	Non-protected	-0.067	0.639	-0.11	0.92	a
Desmoncus orthacanthos	Continuous (Intercept)	2.501	0.427	5.87	<0.001***	a
	Communal Reserve	1.387	0.569	2.44	0.01*	a
	Settlement	0.064	0.577	0.11	0.91	a
	Non-protected	0.024	0.577	0.04	0.97	a
Chamaedorea tepejilote	Continuous (Intercept)	5.334	1.257	4.24	<0.001***	a
	Communal Reserve	-3.819	1.353	-2.82	0.004**	b
	Settlement	-6.385	2.498	-2.56	0.011*	b
	Non-protected	-5.413	2.050	-2.64	0.008**	b
	Forest cover	-1.889	1.005	-1.88	0.06	-
	Elevation	-0.892	0.493	-1.81	0.07	-
Chamaedorea neurochlamys	Continuous (Intercept)	-0.229	1.245	-0.18	0.85	a
	Communal Reserve	-0.092	1.297	-0.07	0.94	a
	Settlement	2.573	1.940	1.33	0.18	a
	Non-protected	1.090	1.821	0.6	0.55	a
	Forest cover	1.382	0.858	1.61	0.11	-

Table 4. Coefficient estimates and SE from a GLMM assessing the effects of site type (continuous, communal reserve, settlement and non-protected patches) on the log-transformed Simpson's diversity index. The best model was selected based on Akaike Information Criterion using the "dredge" function in R.

Response		Estimate	SE	z value	*P*
Adults and juveniles pooled	Continuous (Intercept)	1.268	0.268	4.73	<0.001***
	Communal Reserve	-0.385	0.386	-1.00	0.32
	Settlement	-0.449	0.387	-1.16	0.25
	Non-protected	-0.231	0.382	-0.61	0.54
	Slope	0.147	0.135	1.09	0.28
Adults	Continuous (Intercept)	0.952	0.295	3.23	0.001**
	Communal Reserve	0.092	0.392	0.24	0.81
	Settlement	-0.089	0.396	-0.23	0.82
	Non-protected	-0.103	0.409	-0.25	0.79
	Elevation	0.158	0.137	1.15	0.24
Juveniles	Continuous (Intercept)	1.383	0.242	5.71	<0.001***
	Communal Reserve	-0.312	0.352	-0.89	0.37
	Settlement	-0.671	0.376	-1.78	0.07
	Non-protected	-0.501	0.368	-1.36	0.17
	Elevation	0.217	0.132	1.64	0.10

Table 5. Results from a negative binomial GLM on palm community composition from four different site types (continuous, communal reserve, settlement and non-protected patches) and explanatory variables (forest cover (in a 500m square), slope and elevation). P-values were calculated using 999 resampling iterations. Degrees of freedom (Df).

Variable	Residual Df	Df difference	Deviance	*P-value*
Site type	19	3	83.1	0.08
Forest cover	18	1	23.86	0.36
Elevation	17	1	51.46	0.10
Slope	15	1	35.99	0.43



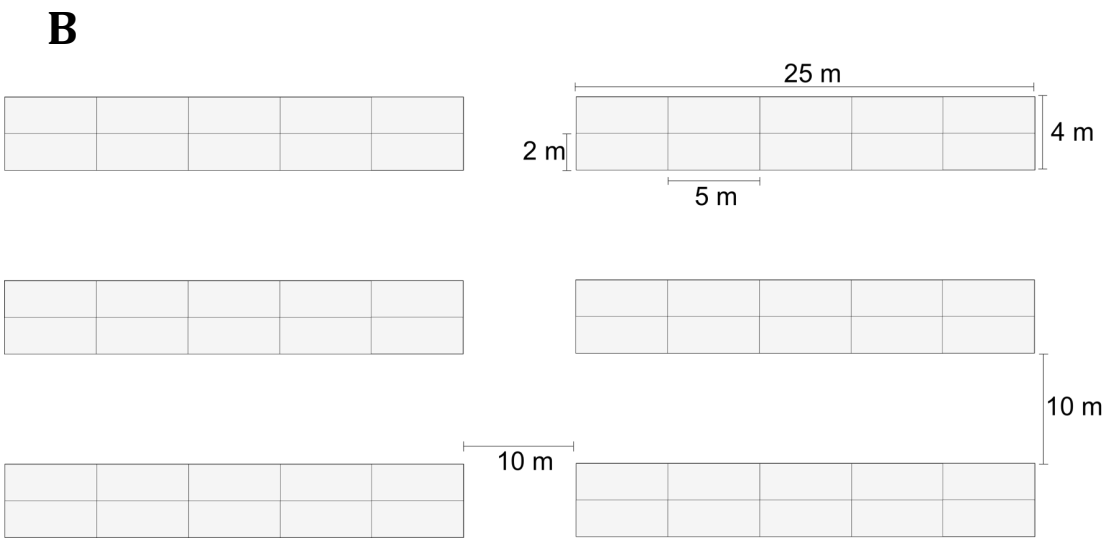


Figure 1. A) Map showing the study area located in southeast Chiapas, Mexico. Study sites are shown as coloured dots (red: continuous and protected forest within the MABR; green: communal reserves; blue: fragments next to human settlements; purple: non-protected patches). B) Spatial arrangement of the six plots used in the palm community survey at each of the 23 study sites. Each plot was divided into ten subplots that were used to survey the seedling community.

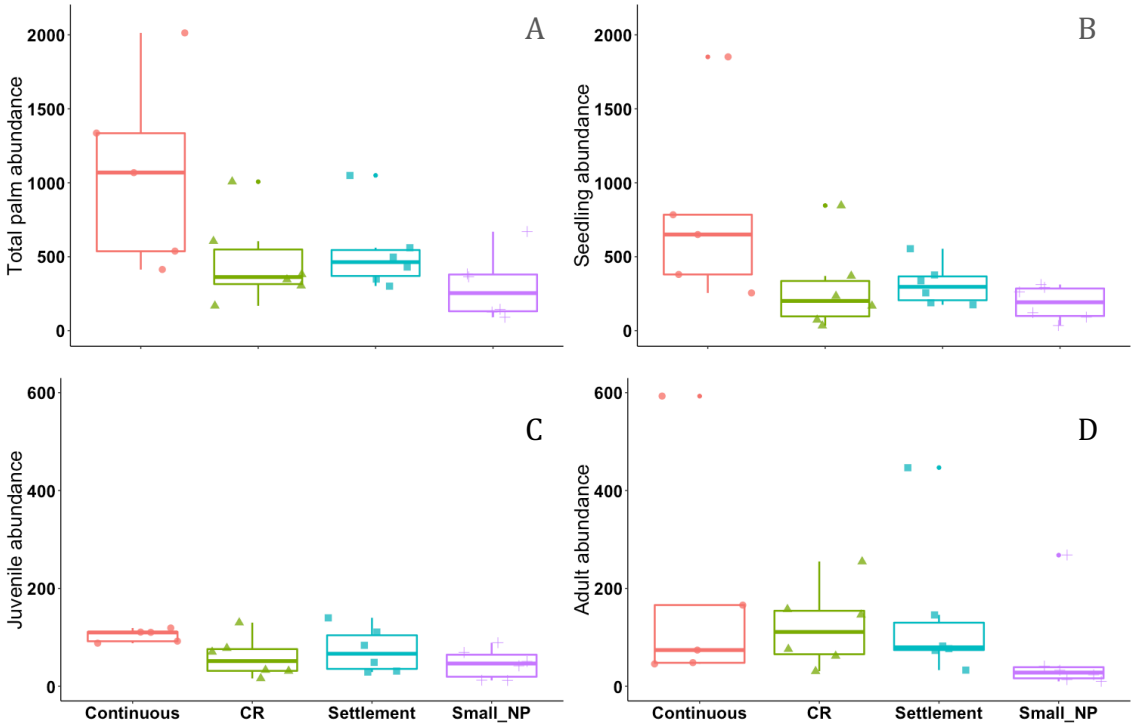


Figure 2. (A) Total palm abundance, and abundance of (B) seedlings, (C) juveniles and (D) adult palms in transects in four different types of forests (continuous, communal reserves (CR), settlements and small non-protected patches) in the southeast of Chiapas, Mexico. Boxes show the median and upper and lower inter-quartile ranges. Colour coding corresponds to Figure 1.

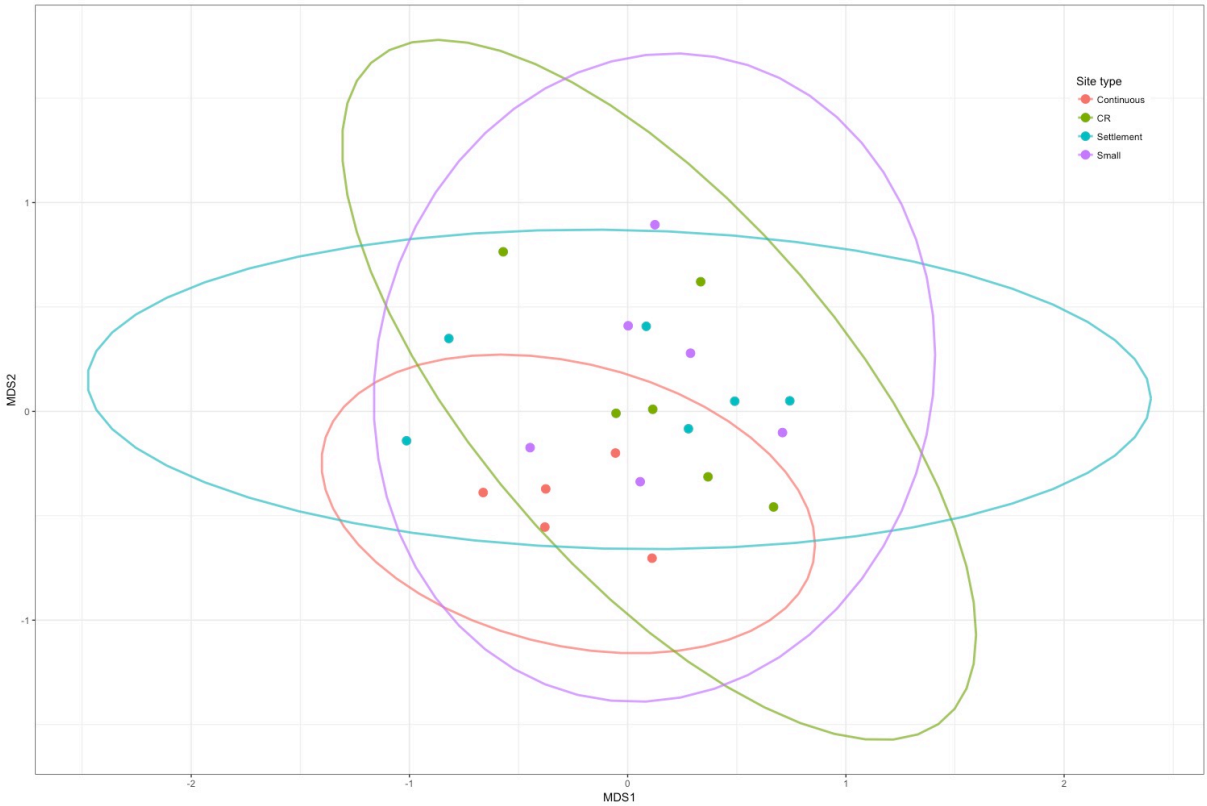


Figure 3. Non-metric multidimensional scaling (NMDS) ordination plot based on Bray-Curtis) between assemblages of palms in four different types of forests (continuous, communal reserves (CR), settlements and small non-protected patches) based on palm total abundances. Points closer together have more similar species composition. Ellipses represent 95% confidence intervals around the centroid. Stress = 0.18. Colour coding corresponds to Figure 1.

Supplementary information

Table S1. Mean and range of the explanatory variables used as covariates in the analyses to determine their influence on abundance, diversity and community composition of palms from continuous and fragmented forests in the southeast of Chiapas, Mexico. Metres above sea level (m.a.s.l.).

Variable	Continuous	Communal Reserve	Settlement	Non-protected
Forest cover (%)	100	95.55 (87.3-100)	50.56 (23.4-92.6)	58.39 (35.8-81.3)
Elevation (m.a.s.l.)	157 (138-181)	172.2 (148-214)	165.3 (141-182)	175.3 (144-201)
Slope (˚)	0.4 (0-1)	2.6 (0-8)	2.7 (0-6)	3.1 (0-8)

Chapter 3. Edge effects in fragmented palm communities of the Lacandona rainforest

Introduction

It is widely recognized that deforestation poses a serious threat to tropical forests, dramatically altering landscapes particularly by means of habitat loss and fragmentation. In some areas, the remaining forest is comprised entirely of fragments. The success of these fragments in preserving the original forest diversity may depend factors such as fragment size and isolation, as well as on how sensitive species are to the altered environmental conditions in the edge zones created by fragmentation (Arroyo-Rodríguez *et al.* 2009, Laurance *et al.* 2012, Hernández-Ruedas *et al.* 2014).

Research has demonstrated that fragmented forests often have an altered species composition when compared with areas in the forest interior (Fleury & Galetti 2004, Sfair *et al.* 2016). Such changes have been documented in many taxa, including fungi (Ruete *et al.* 2016), beetles (Magura *et al.* 2017), birds (Lamb *et al.* 2016) and mammals (Rosa *et al.* 2018)). There are several potential mechanisms that could result in changes in diversity patterns following fragmentation. For example, fragmentation can lead to loss of biodiversity by making populations smaller (and therefore more prone to extinction (Matthies *et al.* 2004) and can make populations more exposed to human activities such as hunting. The more isolated from each other fragments are, the less likely it is for recolonisation to happen if species go locally extinct (Hanski 1999).

A major consequence of fragmentation is the creation of new habitat edges. These man-made edges impact the dynamics of many species by changing both abiotic conditions, such as humidity, wind, radiation, evaporation and nutrient availability (Murcia 1995, Benítez-Malvido 1998, Harper *et al.* 2005), and biotic conditions, such as vegetation structure and ecological interactions (Murcia 1995). These changes – which can be particularly strong near the edges – can have negative consequences for the remnant species within fragments, particularly species adapted to the conditions in the forest interior. It has been shown that edge effects can reach up to 500 m into the interior of fragments (Ewers & Didham 2008). Nevertheless, the most evident effects are typically found within 200 m from edges (Laurance 1991), although the spatial extent of the edge effect zone may depend on the variable measured (i.e. temperature, humidity, invasive species). This implies that even relatively big fragments, up to 1000 ha, may be entirely influenced by edge effects (Laurance 1991). Considering that an estimated 70% of the total remaining global forest area can be found within 1km from an edge (Haddad *et al.* 2015), a considerable proportion of the global forest area are likely to experience some kind of edge effects.

While there are many studies of edge effects in areas subject to anthropogenic habitat fragmentation, relatively few studies have considered how forest species respond to natural edges. Natural edges are formed by natural processes, such as geological and hydrological events, and are maintained without human intervention. Whether forest edges are created and maintained by natural *versus* anthropogenic activities can dictate the biotic and abiotic components of the forest near the edges (Magura *et al.* 2017). In tropical

areas many natural forest edges are found adjacent to water bodies such as rivers and lakes. Such forest edges can serve as a reference point for studies of edge zones in anthropogenically fragmented forest landscapes and contribute to the understanding of generalised ecological patterns related to edge effects (Harper & Macdonald 2001).

Despite the vast literature on edge effects in forest landscapes (Murcia 1995, Ewers & Didham 2008, Magura *et al.* 2017), most studies assessing edge effects on plants have focused on woody plants while other groups, e.g. palms, have received less attention (Hernández-Ruedas et al., 2014, but see Baez & Balslev 2007, Browne & Karubian 2016 and Campbell *et al.* 2017). Previous research has shown that palm species richness can be negatively affected by human-created edge effects and by forest fragment size (Benítez-Malvido 1998, Benítez-Malvido & Martínez-Ramos 2003). Nonetheless, since these studies only considered the palm seedling community, the influence of edge effects on larger size classes of palms is largely unknown. Since changes in palm communities could have impacts on both the forest structure and its associated fauna, understanding how palm communities respond to forest fragmentation is important.

Here we assessed the effects of both man-made and natural edges (up to 500 m to the interior of forests) on palm communities within a fragmented forest landscape and a continuous and protected tropical rainforest in Southeast Mexico. The region has been under strong human influence for more than 40 years, making it an ideal site to understand how anthropogenic forest fragmentation influences the abundance, diversity and community composition of palms. We aimed to answer, how: a) the overall abundance; b) the abundance

of adults, juveniles and seedlings; c) the aboveground biomass; and d) the diversity and community composition of palms change with distance from the forest edge (from 0 to 500 m) and differs between study sites located in two landscape types (forest fragments *versus* continuous forest). We hypothesised that the changes in physical and environmental factors associated with forest fragmentation will generate changes in the composition and diversity of palm communities. We predicted that total palm abundance, diversity and biomass would be higher in the continuous and protected forest than in the fragmented forest landscape, and would increase with distance from the edge in both landscape types. In relation to the community composition of palms, we predicted significant differences between the two forest types given that individual palm species may respond differently to the changes in biotic and abiotic conditions associated with fragmentation (e.g. the climbing palm *Desmoncus orthacanthus* may benefit from the conditions that the new edge provides due to its positive association with forest gap formation).

Methods

Study system: Palms

The Arecaceae family represents a key component of Neotropical vegetation with approximately 500 species (Henderson 1986). In Mexico there are more than 100 species from 22 genera (Quero 1992a). The Chiapas region, in which this study was conducted, contains nearly 40 % of the Arecaceae species present in the country (Martínez *et al.* 1994, Meave *et al.* 2008). Palms form an important ecological and structural element in tropical vegetation (Quero 1992b). Inflorescences, fruits and seeds from palms are often available all year round and

represent an important food source for vertebrates and invertebrates to exploit when other resources are scarce (Brewer 2001, Beck 2006, Barfod *et al.* 2011). The prevalent pollination mode of palms is by insects (Henderson 1986, Barfod *et al.* 2011). Although most palms do not seem to have a morphological flower specialization, some understorey cantharophilous species do, suggesting that beetle pollination is predominant (Henderson 1995, Núñez *et al.* 2005). Among the most common visitors of palm flowers are beetles, honeybees and stingless bees and flies (Barfod *et al.* 2011). In the region, seed dispersal is carried out by a wide range of animals, including mammals (such as peccaries, tapir, agouties, squirrels and, howler and spider monkeys), and birds (such as the scarlet macaw, doves and Lesson's motmot (Cerón-Martínez pers. obs.)).

In Mexico, wild populations of palms have been exploited for commercial purposes. From the 1950s to 1990s palms have been overexploited without regulations, and with legal protection starting from the 1090s (Rico García-Amado *et al.* 2013). In Chiapas, palms are traditionally used for food, construction, decoration, medicine, trade, handcraft among others (Cortés *et al.* 2018). In our study area, we found some evidence of palm extraction, particularly from *Chamaedorea, Bactris, Geonoma* and *Euterpe precatoria.*

Study area

The study was conducted at the Greater Lacandona Ecosystem, southeast Mexico (Figure 1a). The Greater Lacandona Ecosystem also includes parts of Guatemala, making it one of the largest areas of tropical rainforest in Mesoamerica (16°14.71' N, 90°56.23' W). Despite its importance in terms of conservation, this ecosystem has lost two-thirds of its original 1,500,000 ha in the past ~40 years,

primarily by anthropogenic activities (Mendoza & Dirzo 1999, De Jong *et al.* 2000).

The climate of the Lacandona ecosystem is warm and humid, with a mean annual temperature of 24°C. The annual rainfall varies from 2000 to 3500 mm (O'Brien 1998) and most precipitation falls during the wet season from May to December. The period from January to April is relatively dry. The main vegetation type is evergreen and semi-evergreen rainforest (De Jong *et al.* 2000).

The Greater Lacandona area is one of the largest rainforest remnants and the most diverse ecosystems in Mexico, containing the highest mammal richness in the country. It contains viable populations of jaguar (*Panthera onca*), white-lipped peccary (*Tayassu pecari*) and tapir (*Tapirus bairdii*) (Medellín 1994). It also contains between 10 and 19 per cent of all vascular plant species in the country, including 38 species of palms (Martínez *et al.* 1994). Seven Natural Protected Areas safeguard the Greater Lacandona area. Of these, Montes Azules Biosphere Reserve (MABR) is the largest, comprising a total of 331,200 ha or 34.6% of the Greater Lacandona Ecosystem (PMRBMA 2000).

Fieldwork took place in the MABR and in the adjacent non-protected landscape of the Marquez de Comillas region (MCR; approx. 93,300 ha), where fragmentation of previously continuous forest started over 40 years ago. Cornfields, cattle ranches and more recently oil-palm plantations surround the remaining forest patches.

Selection of study sites

We delimited prospective study fragments in the fragmented landscape using satellite images in QGIS. Potential study sites were inspected *in situ* to assess

their suitability for the purposes of our study. This resulted in seven study sites located in forest fragments adjacent to pasture fields containing cattle. For comparison we selected seven sites within the continuous and protected forest delimited by the Lacantun River (Figure 1a). All 14 sites were restricted to lowlands and flat areas between 140 and 210 metres above sea level. To reduce the degree of non-independence of study sites, individual sites were separated by a minimum distance of ~3,000 m. We aimed to minimize problems of spatial autocorrelation in the data set by evenly spreading the sampled sites across both landscapes (e.g. not all fragments were located in the same area of the MCR). During the study period, we noticed few signs of human activity in the forests of the study sites.

Surveys of palms

All data were collected during the dry season (January-April) in 2016. To document the palm community, we set up a 500 m transect perpendicular to the edge at each of the 14 study sites. Along each transect, we delimited six 25 × 4 m plots spaced one hundred metres apart (0, 100, 200, 300, 400, 500 m) starting within the first 3 m from the forest edge (Figure 1b), yielding a total sampling area of 0.06 ha per transect. Within each plot, the location and size of all adult (individual with past or present reproductive parts) and juvenile (pinnate leaves without signs of reproduction) palm individuals were recorded and identified to species level (where necessary morphospecies codes were used). Some palms can grow clonal stems. In the context of assessing total abundance (see below), we counted every clonal stem as a separate individual. From every juvenile and adult palm we measured height and basal stem diameter. For species in genera

that do not develop an early stem (e.g. *Attalea* and *Geonoma*) it was not possible to measure basal stem diameter from the juvenile individuals.

Based on the basal stem diameter measurements, we calculated palm stem volume (used as a surrogate for above ground biomass). We assumed a cylindrical shape of the stems, with no variation from the base to breast height (but see Alves et al., 2004) and we calculated stem volume ($V = \pi r^2 h$) using the diameter at ground level and height (below fronds) of the stem.

Within each 25 x 4 m plot, the number of seedlings (singled-leaved individuals) was counted in ten systematically located sub-plots of 5 × 2 m (Figure 1b). Identifying seedlings to species presented some challenges; therefore we could only identify them to genus level. We identified palm species with the aid of two experienced parabiologists and Cerón-Martínez measured variables (see below) for all the palm species within each plot for all sites.

We also collected information on a number of environmental variables that have been reported as important determinants of palm abundance and diversity (Eiserhardt *et al.* 2011). Canopy cover was considered to reflect the degree of forest disturbance. It was estimated from photographs taken with a Nikon camera (Model Coolpix S2900), with a focal length of 4.6 mm at 100 cm from the ground at the centre of each plot. We followed the method proposed by Beckschäfer (2015) to estimate the light availability at each plot based on non-hemispherical photographs. Images were processed using ImageJ 1.50i (Schneider *et al.* 2012). We also recorded the elevation and slope of each plot. Elevation measurements (metres above sea level) were taken using a handheld GPS, and slope was calculated with the aid of a clinometer (Table S1).

Statistical analyses

We analysed how forest type, distance from the forest edge, and environmental variables influence the **abundance of palms** (all species combined) using generalized linear mixed-effects models (GLMMs) with a negative binomial distribution. The analysis was implemented in *R* using the *glmmADMB* (Skaug *et al.* 2016) package. After a visual inspection of the Dunn-Smyth residuals, we concluded that a negative binomial regression model for count data fitted our data better than a Poisson model. The total abundance of palms (all species and life stages pooled) in each 25 x 4 m plot was modelled as a function of the following explanatory variables: landscape type (continuous or fragmented), distance from forest edge (continuous variable), canopy cover, slope and elevation. We included an interaction between landscape type and distance. To account for non-independence of plots within the same transect, the variable *transect* was included as a random effect. No multicollinearity was detected for the explanatory variables: the variance inflation factor was below 3 (Zuur *et al.* 2010). Using an identical approach, we also conducted separate analyses for total abundances (all species pooled) of adults, juveniles and seedlings, as well as species-specific analyses of palm abundance focusing on six species that occurred in a minimum of 9 transects (Table 2): *Bactris mexicana* (14), *Desmoncus orthacanthos* (14), *Chamaedorea tepejilote* (12), *Geonoma interrupta* (11), *G. undata* (10) and *C. neurochlamys* (9).

To test the hypothesis that local **palm diversity** depends on the distance from forest edge and differs between forest types, we used a GLMM with a normal error distribution in which plot-specific palm diversity was modelled as a function of landscape type (continuous or fragmented), distance from forest

edge, canopy cover, slope and elevation. Transect was included as a random effect. As our measure of diversity, we used the effective number of individuals, obtained by calculating the inverse Simpson's dominance index of diversity in the *vegan* package (Oksanen *et al.* 2017) and *log* transformed it prior to analysis to improve normality. The model was implemented in R, using the *glmmADMB* package.

To test the hypothesis that **palm biomass** depends on forest type and distance from the edge, we compared the stem volume (all species combined) from the two landscapes using a GLMM with a normal error distribution (implemented using the *glmmADMB* package) in which plot-specific stem volume was modelled as a function of explanatory variables: landscape type (continuous or fragmented), distance from forest edge, canopy cover, slope and elevation including transect as a random effect. We log transformed the response variable to improve normality.

For all of the above-mentioned dependent variables (**abundance, diversity and stem volume**), we ran a full model followed by a backward selection approach. In each analysis, the best model was selected based on Akaike Information Criterion values obtained using the *bbmle* package (Bolker & Team 2017). GLMM performance was assessed by visual inspection of plots of residuals vs. fitted values. All predictor variables were standardized prior to analysis (centred and divided by standard deviation) (Schielzeth 2010).

We evaluated differences in the **community composition** of palm species between the two forest types (fragmented vs. continuous) using a multivariate analysis fitting a negative binomial in the package *mvabund* (Wang *et al.* 2019) that accounts for the mean-variance relationship (Warton *et al.* 2012).

Community data was visualized with a two-dimensional non-metric multidimensional scaling (NMDS) ordination plot using Bray-Curtis dissimilarity metrics to display the distances between plots. These analyses were performed using the *vegan* package (Oksanen *et al.* 2017). All analyses were performed using *R* version 3.6.0. (R Core Team 2017).

Results

Palm community survey

Across all 14 transects, we recorded a total of 9974 palm individuals (adults, juveniles and seedlings combined) representing 18 palm species (Tables 1 and 2). The average number of palm individuals per transect was roughly twice as high in the protected continuous forest landscape as in the fragmented forest landscape (Table 1), while the number of species was similar in the two forest types (15 and 16, respectively). Two species (the subcanopy species *Cryosophila stauracantha* and the understorey species *Reinhardtia simplex*) were only found in the continuous forest landscape, while three species (*Chamaedorea elegans*, *C. ernesti-augusti* – both understorey, and *Euterpe precatoria* –subcanopy), were only found in the fragmented forest (Table 2).

In the continuous forest, the three most abundant palm species, which accounted for 79% of adults (N = 1200), were *Chamaedorea tepejilote* (47%), *Bactris major* (19%) and *R. simplex* (13%), while 70% of all juveniles (N= 569) belonged to *C. tepejilote* (57%), *Geonoma undata* (7%) and *G. interrupta* (6%). In the fragmented forest, the three most abundant adult palms accounting for 76% (N = 522) of all adults were *Bactris mexicana* (32%), *D. orthacanthus* (25%) and

B. major (19%), while for juveniles (N= 451), *Chamaedorea pinnatifrons* (18%), *C. tepejilote* (14%) and *Chamaedorea neurochlamys* (13%) accounted for 45%.

Abundance

Overall, the total palm abundance (including adults, juveniles and seedlings) was significantly lower in the fragmented forest than in the continuous forest ($z = -2.45$, $p = 0.014$; Figure 2; Table 3). Total abundance was also significantly influenced by distance from the forest edge, increasing towards the forest interior ($z = 2.23$, $p = 0.025$; Table 3, Figure 2). The abundance of adults was significantly lower in the fragmented forest than in the continuous forest ($z = -2.74$, $p = 0.006$) and the number of adult individuals increased when moving from the edge towards the forest interior ($z = 2.31$, $p = 0.02$, Table 3, Figure 2). Juvenile abundance did not differ significantly between forest types ($z = -1.13$, $p = 0.259$, Table 3, Figure 2). The abundance of seedlings was significantly higher in the continuous forest than in the fragmented forest landscape ($z = -3.99$, $p < 0.001$, Table 3, Figure 2). In both forest types, the abundances of juveniles and seedlings increased as canopy cover increased (Table 3). Overall, the major predictor of palm abundances was the type of forest, with more palms occurring in the continuous forest than in the fragmented landscape. While the total abundance of palms increased with distance from the forest edge, this appeared to be largely driven by an increase in the number of adults (but not the number of juveniles and seedlings) with increasing distance from the forest edge.

Of the six palm species that were present in a minimum of nine transects (and therefore included in species-specific analyses of abundances), five were significantly affected by forest type (Table 3). Two species showed higher

abundances in the fragmented forest (*D. orthacanthos* and *C. neurochlamys*), while the other three species presented lower abundances (*C. tepejilote*, *G. interrupta*, *G. undata*) in the fragmented forest than in the continuous forest. *Desmoncus orthacanthus* and *G. interrupta* were the only species significantly affected by distance (with higher abundance towards the interior of fragmented sites). *Desmoncus orthacanthus* was also affected by slope and elevation, with more individuals at steeper and higher plots (Table 3).

Stem volume (biomass)

Analysis of stem volume, used as a proxy for biomass, revealed that the fragmented forest had, on average, significantly lower palm biomass than the continuous forest ($z = -3.25$, $p = 0.001$, Tables 1 and 4). There was a significant increase of the average stem volume related to distance from edge to the forest interior in both forest types ($z = 2.02$, $p = 0.043$, Table 4).

Diversity

Diversity (inverse Simpson's dominance index) was significantly related to forest type, with higher diversity in the fragmented landscape ($z = 2.31$, $p = 0.021$). Diversity significantly increased with distance from the forest edge and was significantly higher at steeper slopes (Table 4).

Community composition

Results from the multivariate analysis of species composition suggested that palm communities differed significantly between the two forest types, and was also significantly affected by distance to forest edge and elevation (Table 5). The

NMDS showed that sites from each forest type (continuous or fragmented) clustered together (Figure 3).

Discussion

We predicted that total palm abundance, diversity and biomass would be affected by the proximity to a forest edge. This prediction was indeed supported, as edge habitat had lower abundance, diversity and biomass of palms than interior parts of the forest. This pattern was found in both forest types (fragmented and continuous), although the responses varied slightly depending on life stage and forest type.

Do palm abundance, diversity, biomass and community composition change from edge to interior?

We found an increased number of seedlings and adults from edge towards forest interior. Most of this increase occurred close to the edge: after 100 m from the edge, abundance was relatively stable throughout the remaining parts of the 500-m transects. This suggests that from the perspective of palms, the edge zone is relatively narrow. Low palm density has been attributed to edge effects, with higher mortality due to mechanical damage and increased solar radiation (Arroyo-Rodríguez *et al.* 2007). More stable environmental and physical conditions towards the forest interior could explain this general pattern. Abiotic and biotic heterogeneity can affect different stages of plant development and establishment (Bruna 1999), therefore it is expected that fast-changing conditions at edges could alter the structure and dynamics of plant communities (Martínez-Ramos & Cristiän 1997). For example, it has been documented that

altered conditions (human presence and hunting) can reduce populations of seed dispersers at edges with consequences for plant recruitment (de Melo *et al.* 2006). Even if seeds are successfully dispersed, physical conditions at the edge (e.g. dryness and higher variability in temperature) can hinder or even stop their germination. On top of lower rates of germination, there is increasing evidence of higher rates of natural enemy attack and mortality of seedlings at edge habitats (Benítez-Malvido 1998, Oliveira *et al.* 2004). Hence, the lower density of seedlings close to edges might signal limited recruitment with potential negative long-term effects (Wang 2008). Lower abundances of palms close to edges might also be a consequence of limited fruit production close to edges. We found that *G. interrupta* produces fewer fruits in fragments (chapter 4), creating a potential deficit for its long-term persistence. Lower reproductive output along with lower density of adults could potentially affect animals that depend on pollen, nectar, fruits and seeds from palms.

Edge effects on palm communities were documented in both landscape types, suggesting that they do occur regardless of whether the edges are created by natural processes or anthropogenic activities. In our study design, 'edge type' (natural vs. man-made) is entirely confounded by 'forest type' (continuous vs. fragmented): there were no natural edges surrounding the fragments and no man-made edges in the continuous forest. Other studies have shown that natural edges and edges created by anthropogenic activities can have different influence on vegetation (see e.g. Harper et al., 2015; Harper and Macdonald, 2001 for examples from temperate and boreal forests). Studies evaluating how palms respond to edge effects (Baez & Balslev 2007, Browne & Karubian 2016, Campbell *et al.* 2017) tend to have focused exclusively on man-made edges.

Results from Ecuador showed that density and demography of palm populations respond negatively to edge disturbance, and indicate that individual palm species differ in their responses to man-made edges. Some palm species might in fact respond positively to the presence of edges. For example, Australian climbing palms, rattans, are more abundant in fragmented forests driven by canopy disturbance of forest edges (Campbell *et al.* 2017). Previous studies suggest that some palm taxa included in our study (e.g. palms in the genera *Chamaedorea* and *Desmoncus*) benefit from human disturbance, while other species (e.g. *Geonoma*) prefer undisturbed old-growth forest (Svenning 1998, Siebert 2000). Interestingly, we found that species of *Chamaedorea* and *Geonoma* were present close to edges in both forest types. It is also worth highlighting the climbing palm *D. orthacanthos*, which could be a potential indicator of perturbed conditions. Since this species grows faster in high-light compared to low-light conditions (Siebert 2000), we expected to find higher abundances in the high-light environments close to edges. Contrary to our expectations, the abundance of *D. orthacanthos* increased towards the forest interior of fragments. This suggests that other factors than light might be more crucial determinants of its distribution along the transects, as this species appears to thrive under a wide range of forest, climatic and edaphic conditions (Siebert 2000).

Do palm abundance, diversity, biomass and community composition differ between forest types?

Our results showed that overall palm abundances were higher in the protected and continuous forest than in the fragmented landscape. There are a number of possible explanations for this. Firstly, harvesting of wild palms has been a part of

the degradation process that the unprotected part of the Lacandona rainforest has undergone for the past > 40 years. We found evidence that this practice is still happening in some of the forest patches in the fragmented landscape. Although we did not include harvesting as an explanatory variable, we cannot rule out the possibility that harvesting events, past and present, have had some negative effects in the abundance of palms. Secondly, palm abundances are influenced by abiotic and biotic factors that influence the reproduction and survival of individual palms, and these abiotic and biotic factors might differ between the two landscape types. For example, pollination, seed dispersal and levels of natural enemy attack might differ between fragmented forest landscapes and more pristine forest environments. If fact, there is also evidence of high palm seed predation activity in fragments of the Lacandona region. For instance, squirrels account for a greater proportion of *A. butyracea* seed mortality than invertebrates, i.e. weevils in fragments compared to a continuous forest (Cerón-Martínez 2009). Palm abundance is a response that obey a series of complex interactions and that deserve further investigation.

Palm species diversity differed between the two forest types, and, contrary to what we expected, the fragmented landscape had a higher diversity (Simpson's D) of palms than the continuous forest. Of the 18 palm species documented in our surveys, two species were found exclusively in the continuous forest and three exclusively in the fragmented one (Table 2). The surveyed fragments represent a heterogeneous part of the landscape, with sites in fragments showing more variability in canopy cover, slope and elevation. This could create a larger number of ecological niches, and may explain the higher diversity found in the fragmented landscape. In other words, although

fragmentation poses a threat to biodiversity by reducing the amount of habitat, it can also create mosaic of habitats that may favour species that are rare in the more uniform continuous forest.

In addition to differences in palm abundances and diversity, the composition of species differed between the two landscape types, and some species were found only in one forest type. For example, the rare species *Reinhardtia simplex* and *Cryosophila stauracantha* are restricted to protected and continuous forest. Both species were completely limited to well-preserved areas of the protected forest and were not detected close to the forest edge. Seed dispersal of *R. simplex* seems to be limited to the forest interior (Cerón-Martínez pers. obs.). On the other hand, *Chamaedorea ernesti-augusti*, enlisted by the Mexican Government as threatened, was only found in fragmented forest. The remaining forested areas of the Lacandona region might therefore be important reservoirs of vulnerable species, and may contribute to the overall diversity of the larger region. Our study highlights fragments as an important strategic element that needs to be taken into account when preserving the regional biodiversity.

In summary, palms respond to forest edges, but such effects seem to operate at a relatively short distance (within the first 100 m). Total palm abundance and biomass (stem volume) were lower in the fragmented landscape than in the continuous forest. Diversity was higher in fragments than in the continuous forest. The environmental variables we measured (canopy cover, slope, and elevation) did not completely explain the results we recorded; this indicates that there may be other important variables (i.e. species interactions and reproductive biology) that are addressed in other chapters of this thesis

(Chapters 4 and 5). Palms are as diverse as their responses to habitat modification. Understanding what conditions affect their abundances and diversity can allow us to implement efforts to improve their conservation.

Tables and figures

Table 1. Mean palm abundance, diversity (Simpson's D), species richness and stem volume (±SE) across transects in the two landscape types (7 continuous and 7 fragmented).

Variable	Landscape type	
	Continuous	Fragmented
Overall abundance per transect	964 ± 16	460 ± 74
Adult abundance per transect	187 ± 104	81 ± 46
Juvenile abundance per transect	64 ± 16	58 ± 28
Seedling abundance per transect	711 ± 379	321 ± 153
Simpson's D	2.14 ± 0.11	2.48 ± 0.18
Stem volume cm^{-3}	30,513 ± 7,418	9,012 ± 2,539
Observed species	15	16

Table 2. Combined numbers of adults and juveniles of the 18 palm species recorded across the 14 transects, grouped by landscape type. Seedlings were not included in this summary since for some taxa seedlings could not be identified to species level. The column 'Occupancy' indicates the number of transects (out of 14) in which the species was observed.

	Continuous							Fragmented							Occupancy
Species	MA1	MA2	MA3	MA4	MA5	MA6	MA7	CH2	LM1	LM2	PR1	PR2	PY1	RF1	
Attalea butyracea	0	9	4	0	9	0	5	0	2	0	0	0	13	0	6
Attalea cohume	0	0	0	0	11	0	0	0	0	0	0	0	0	5	2
Bactris major	187	0	0	0	42	0	0	0	25	0	0	0	0	76	4
Bactris mexicana	8	28	1	21	28	18	32	20	12	108	9	2	50	7	14
Chamaedorea elegans	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1
Chamaedorea ernesti-augusti	0	0	0	0	0	0	0	13	1	0	2	1	0	0	4
Chamaedorea neurochlamys	2	0	0	0	0	4	19	10	0	20	17	13	1	12	9
Chamaedorea oblongata	0	0	0	0	0	0	11	0	0	25	0	0	0	1	3
Chamaedorea pinnatifrons	0	7	0	0	0	0	0	2	3	0	74	14	20	0	6
Chamaedorea tepejilote	93	103	70	74	260	154	136	3	7	0	3	0	9	81	12
Cryosophila stauracantha	0	0	1	0	0	0	3	0	0	0	0	0	0	0	2
Desmoncus orthacanthos	37	5	4	18	2	4	15	48	46	16	19	15	9	33	14
Euterpe precatoria	0	0	0	0	0	0	0	19	0	0	0	9	0	0	2
Geonoma interrupta	7	5	10	6	15	8	4	1	0	0	1	4	11	0	11
Geonoma pinnatifrons	12	0	1	0	0	4	3	0	0	0	2	1	2	0	7
Geonoma undata	2	2	31	9	5	26	5	0	0	11	2	0	6	0	10
Reinhardtia simplex	13	0	0	0	0	163	10	0	0	0	0	0	0	0	3
Sabal mexicana	0	0	0	0	3	0	0	0	13	28	0	0	0	12	4

Table 3. Model outputs (coefficient estimates and their standard errors, z-values and associated P-values) from a set of negative binomial GLMMs assessing the effects of landscape type (continuous or fragmented), distance from edge, canopy cover, slope and elevation on palm abundance and the abundance of the six palm species that were present in a minimum of nine transects. For individual species only adults and juveniles were included in the models, as seedlings could not be identified to species level. Models selected based on Akaike Information Criterion using the procedures described in the statistical analyses section.

Response	Variable	Estimate	SE	z value	*P*
Total palm abundance	Continuous (Intercept)	3.238	0.214	15.11	<0.001***
	Fragmented	-0.540	0.221	-2.45	0.014*
	Distance	0.137	0.061	2.23	0.025*
	Canopy cover	0.300	0.115	2.61	0.009**
	Slope	0.034	0.106	0.33	0.743
	Elevation	-0.029	0.105	-0.28	0.779
Adult abundance	Continuous (Intercept)	2.736	0.282	9.67	<0.001***
	Fragmented	-0.756	0.276	-2.74	0.006**
	Distance	0.211	0.091	2.31	0.020*
	Canopy cover	0.224	0.177	1.27	0.205
Juvenile abundance	Continuous (Intercept)	2.351	0.125	18.77	<0.001***
	Fragmented	-0.202	0.179	-1.13	0.259
	Canopy cover	0.380	0.086	4.4	<0.001***
	Elevation	-0.141	0.085	-1.65	0.099
Seedling abundance	Continuous (Intercept)	4.936	0.211	23.3	<0.001***
	Fragmented	-0.798	0.200	-3.99	<0.001***
	Distance	-0.108	0.061	-1.77	0.077
	Canopy cover	0.514	0.114	4.5	<0.001***
	Elevation	-0.132	0.093	-1.41	0.157
Bactris mexicana	Continuous (Intercept)	1.121	0.378	2.97	0.003**
	Fragmented	0.251	0.573	0.44	0.661
	Slope	0.305	0.268	1.14	0.255
Desmoncus orthacanthos	Continuous (Intercept)	-0.408	0.403	-1.01	0.31
	Fragmented	0.977	0.342	2.86	0.004**
	Distance	0.285	0.113	2.53	0.011*
	Slope	-0.394	0.184	-2.14	0.032*
	Elevation	0.670	0.178	3.77	<0.001***
Chamaedorea tepejilote	Continuous (Intercept)	2.666	0.438	6.09	<0.001***
	Fragmented	-3.202	0.573	-5.58	<0.001***
	Distance	0.154	0.109	1.41	0.16
	Slope	0.322	0.238	1.36	0.17
Geonoma interrupta	Continuous (Intercept)	-0.870	0.474	-1.83	0.066
	Fragmented	-1.613	0.578	-2.79	0.005**
	Distance	0.411	0.121	3.39	<0.001***
Geonoma undata	Continuous (Intercept)	-0.344	0.640	-0.54	0.59
	Fragmented	-1.803	0.810	-2.22	0.026*

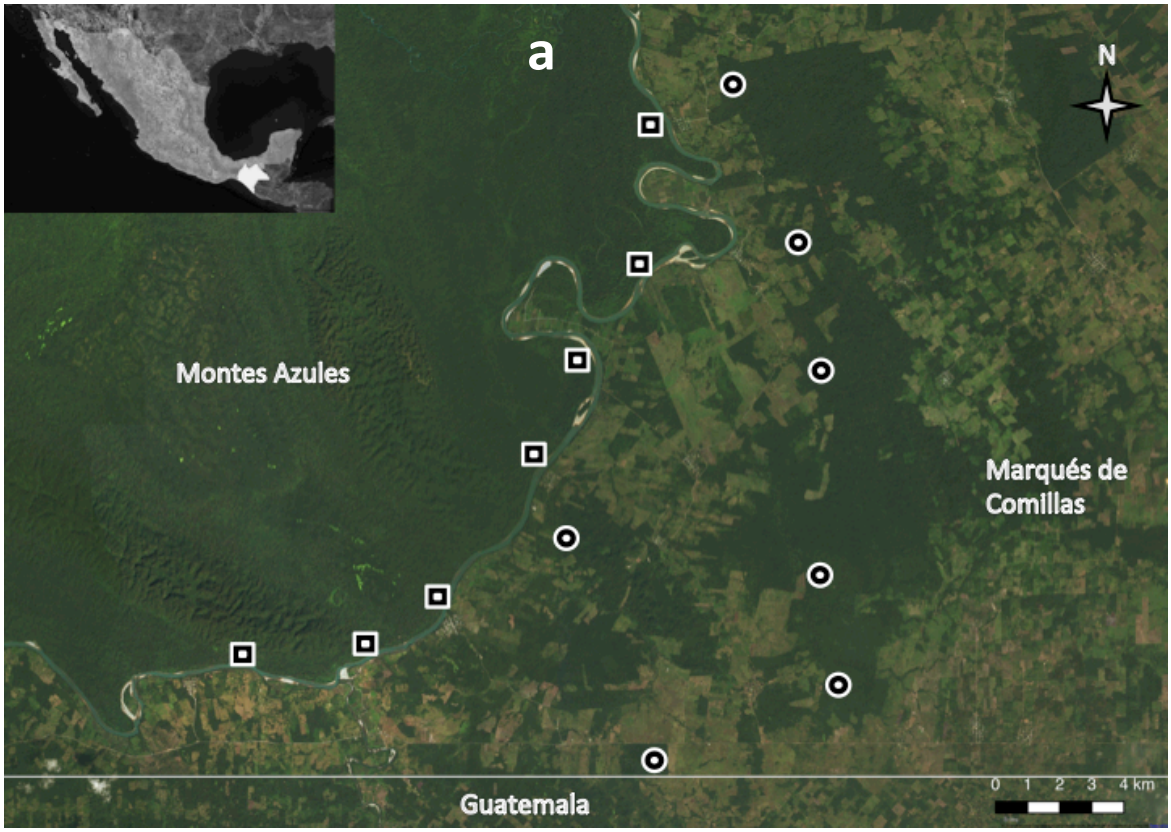
	Distance	0.162	0.153	1.06	0.291
	Canopy cover	0.465	0.334	1.39	0.164
Chamaedorea neurochlamys	Continuous (Intercept)	-2.074	0.823	-2.52	0.012*
	Fragmented	1.552	0.741	2.09	0.036*
	Distance	0.228	0.149	1.53	0.127
	Canopy cover	0.583	0.447	1.3	0.192

Table 4. Coefficient estimates and SE from a GLMM assessing the effects of landscape type (continuous or fragmented), distance from forest edge, canopy cover, slope and elevation on the log-transformed Simpson's diversity index and stem volume as a proxy for above ground biomass – excluding palms with trunk diameters over 10 cm. Only adults and juveniles were used to obtain the index. The best model was selected based on Akaike Information Criterion values.

Response	Variable	Estimate	SE	z value	*P*
Simpson's D	Continuous (Intercept)	1.359	0.200	6.8	<0.001***
	Fragmented	0.452	0.196	2.31	0.021*
	Distance	0.133	0.058	2.3	0.02*
	Slope	0.253	0.100	2.55	0.01*
Biomass	Continuous (Intercept)	8.676	0.442	19.62	<0.001***
	Fragmented	-1.350	0.415	-3.25	0.001**
	Distance	0.268	0.132	2.02	0.043*
	Canopy	0.416	0.230	1.8	0.071

Table 5. Results from the multivariate analysis assessing the effects of landscape type (continuous or fragmented), distance from forest edge, canopy cover, slope and elevation on palm community composition in continuous and fragmented forests. Degrees of freedom (Df).

Variable	Residual Df	Df difference	Deviance	*P-value*
Landscape type	82	1	115.28	0.001***
Distance	81	1	59.39	0.001***
Elevation	80	1	34.81	0.041*
Canopy	79	1	28.45	0.233
Slope	78	1	28.82	0.243



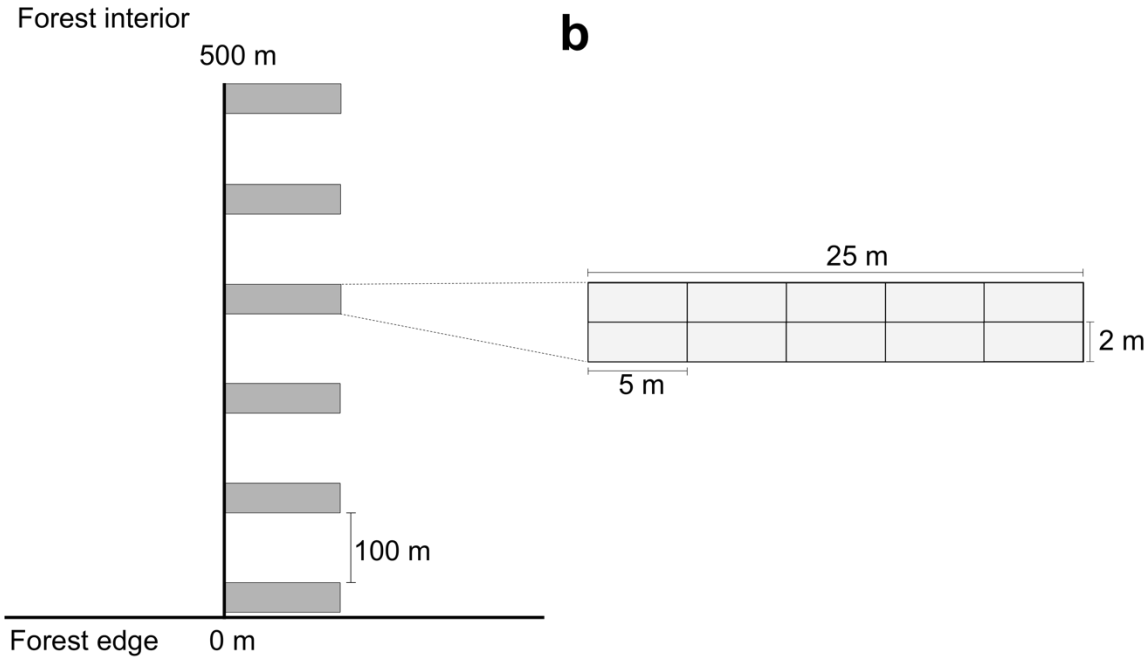


Figure 1. a) Map of the study area in the State of Chiapas, Southeast Mexico. Study sites inside the Protected Area of Montes Azules Biosphere Reserve (squares) and outside in the fragmented landscape of Marqués de Comillas. b) Arrangement of the plots on each sampling site. The map was created in QGIS using an image from Bing maps.

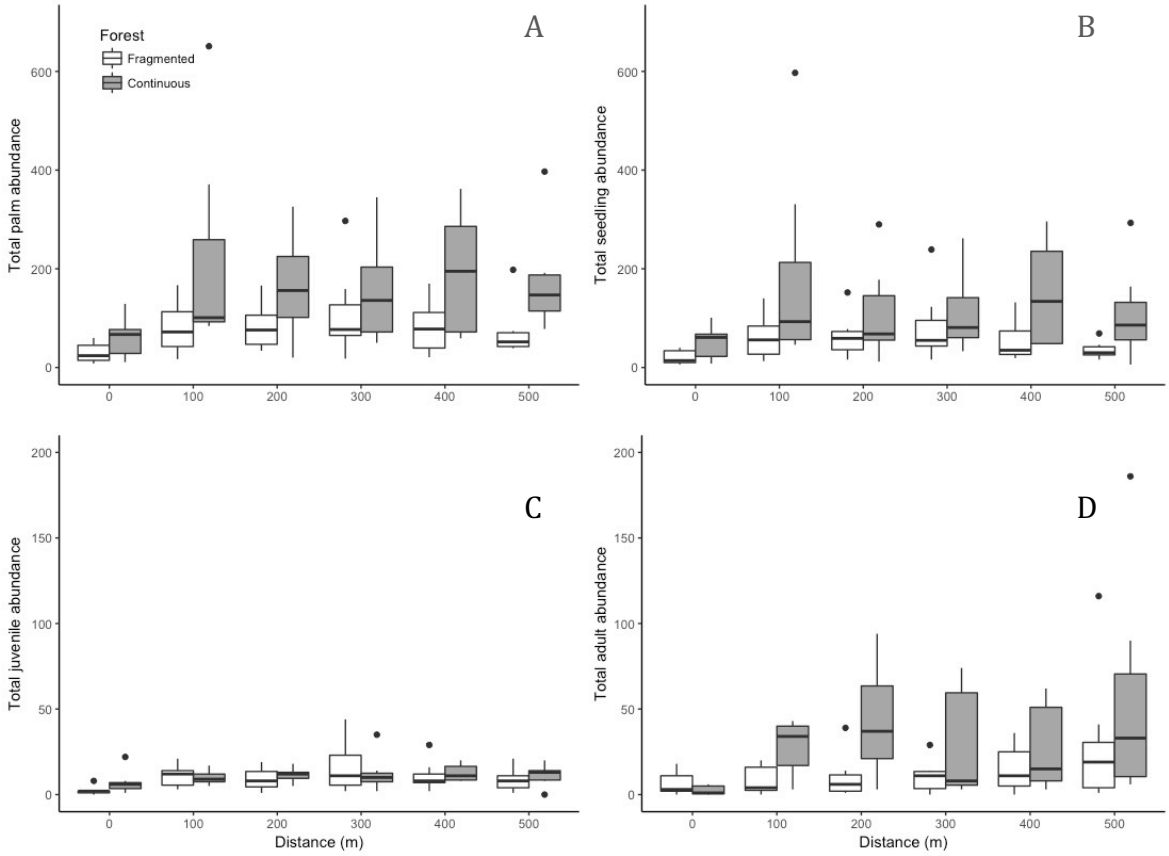


Figure 2. (A) Total palm abundance (all life stages combined), and abundance of (B) seedlings, (C) juveniles and (D) adult palms in transects in two types of forests (fragmented and continuous) in the southeast of Chiapas, Mexico. Boxes show medians and upper and lower inter-quartile ranges.

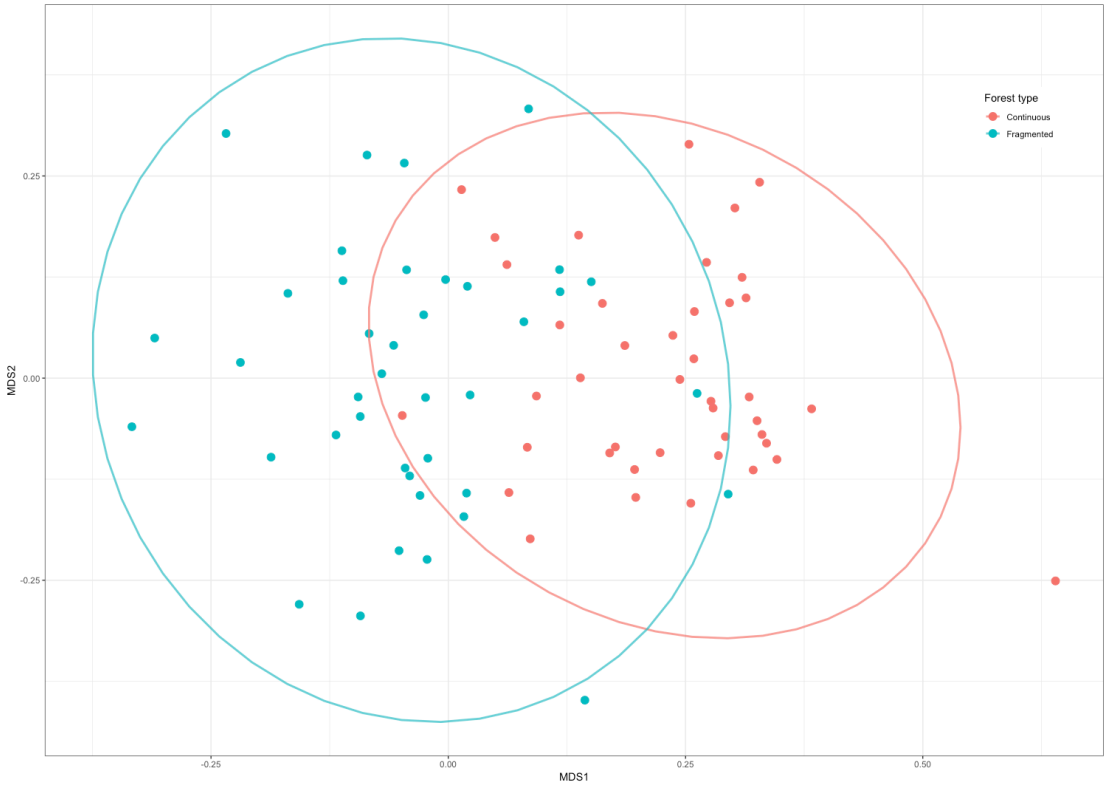


Figure 3. Non-metric multidimensional scaling (NMDS) ordination plot or ecological distance (Bray-Curtis) between assemblages of palms based on total abundances per plot in two types of forests. In blue plots from seven 500-m transects in a fragmented forest and in red from seven 500-m transects in a continuous forest. Closer dots in the ordination space tend to be more similar. The ellipses indicate 95% confidence intervals for the centroid. Stress = 0.18

Supplementary information

Table S1. Mean and range of canopy cover, slope and elevation in the two studied forest landscape types. (m.a.s.l. = metres above sea level).

Variable	Continuous	Fragmented
Canopy cover (%)	91.84 (65.63-98.79)	86.68 (44.78-98.74)
Slope (˚)	3.33 (0-20)	7.81 (0-21)
Elevation (m.a.s.l.)	147.33 (126-168)	175.23 (134-205)

Chapter 4. Fragmentation effects on the number of flowers and fruits of *Geonoma interrupta* and the role of flower visitors

Introduction

Tropical deforestation, driven mostly by conversion of forests to agricultural land, typically creates mosaic landscapes of forest patches, embedded within a matrix of converted land (Aguirre & Dirzo 2008). The resulting fragmentation and habitat loss leads to declines in biodiversity and altered ecological interactions (Neuschulz *et al.* 2016). Within forest patches, the abundance and distribution of species might be directly affected by their responses to altered environmental conditions (such as changes in temperature and humidity) or indirectly affected through changes in biotic interactions such as herbivory and biotic pollination (Murcia 1995).

In a recent meta-analysis, pollination was one of the ecological processes most negatively affected, globally, by human perturbations of forests (Neuschulz *et al.* 2016). Pollination is a key step in plant reproduction (Kearns *et al.* 1998). It has been estimated than over 90% of flowering plant species in tropical forests are pollinated by animals (Bawa 1990, Ollerton *et al.* 2011). Thus, modifications to plant-pollinator interactions, for example by human activities, could have unfavourable consequences for plant reproduction.

Habitat loss and fragmentation have the potential to affect pollination dynamics (Cunningham 2000b, a, Breed *et al.* 2012). Changes in both assemblages of pollinators and forest structure within fragments may disturb

plant-pollinator relationships. Negative effects on pollination services can in turn impact the reproductive success of plants, leading into increased levels of inbreeding (i.e., by changes in pollen flow), although this would highly depend on the behavioural response of pollinators to the new habitat conditions (White *et al.* 2002, Rymer *et al.* 2015, Lander *et al.* 2019). Results from fragmented landscapes in tropical areas have shown that self pollination can yield lower seed set, germination and seedling growth, compared with outcrossing (Rymer *et al.* 2015). In fact, globally, plants in fragmented habitats express signs of genetic erosion, and reduced germination, survival and growth (Aguilar *et al.* 2019). Pollinator declines over recent decades (Steffan-Dewenter & Westphal 2008, Tylianakis 2013) have been linked to reduced plant reproduction, measured as seed set (Breed *et al.* 2012). While in some tropical areas the abundance of pollinators is negatively affected by fragmentation, fruit set is not necessarily affected (Aguirre & Dirzo 2008), showing that the responses of plant reproduction to forest fragmentation and changes to pollinator communities may not be straightforward.

The palm family (Arecaceae) has been the subject of a large number of studies on pollination mechanisms (Barfod *et al.* 2011), but surprisingly few studies have documented the effects of fragmentation on palm pollination (Barfod *et al.* 2011). Here, we investigate the reproductive success of the palm *Geonoma interrupta* in a fragmented forest landscape in Chiapas, Mexico. More specifically, we addressed the following questions: a) what are the main inflorescence visitors and do they differ between a continuous and fragmented forest landscape?; b) does flower and fruit production differ between palms in forest fragments versus a continuous forest and between palms at different

distances from a forest edge?; c) is *G. interrupta* capable of self-fertilization in the absence of flower visitors? Our results allow us to assess the likely demographic consequences of forest fragmentation for this palm species, and to understand the role played by its pollinators.

Methods

Study area

Fieldwork was conducted in the Greater Lacandona Ecosystem, southeast Mexico, from January to May 2017. Field observations and manipulations were carried out at six sites located in two contrasting landscapes (three in a continuous and protected forest and three in a landscape comprising forest fragments embedded in an agricultural matrix; Figure 1). Sites were labelled according to their proximity to the nearest forest edge, i.e. Continuous.1 and Fragmented.1 were the sites closest to a forest edge and Continuous.3 and Fragmented.3 were farthest from a forest edge (Table 1). The protected area of Montes Azules Biosphere Reserve (MABR) is the largest continuous forest in the region, comprising a total of 331,200 ha (PMRBMA 2000). The fragmented landscape of Marquez de Comillas region (MCR; adjacent to the MABR), where fragmentation of previously continuous forest started over 40 years ago, comprises ~93,300 ha. Settlements, crops, cattle pasture and more recently oil-palm plantations surround the remaining rainforest fragments. A natural edge, created by the Lacantún River, borders the MABR sites, while pasture fields (cattle fields) border the closest edges of the study sites in the forest fragments.

Study species

Geonoma interrupta is an understorey palm, distributed from Mexico to Bolivia (Henderson 2011). It is highly polymorphic, and since it was first described, it has been published under at least 20 names (Stauffer *et al.* 2002). It is a small palm with a height of up to 8 m; the average height (±SE) of the individuals in this study was 2.7±0.7 m. Reproductive individuals have one or two peduncle inflorescences from 40 to 70 cm long (Stauffer *et al.* 2002, Quero & Pérez-Farrera 2010) normally with multiple rachillae inserted in a rachis (three branches). Triads of flowers, each consisting of two male flowers and a female flower, are immersed in spirally arranged pits. Female flowers typically become visible only after the first male flowers have fallen. Although *G. interrupta* has been reported to show functional dioecy (i.e. no overlap in flowering between male and female flowers; Stauffer et al., 2002), we found an overlap of the final stages of the anthesis of the second male flower and the beginning of the female anthesis. In the study area *G. interrupta*'s inflorescence buds start to form in December, with male flowering peaking in February and female flowering in late February and early March. Immature fruits start appearing in early March and fruits reach maturity by late April and May.

Study design

In early January 2017, we tagged 166 adult palms bearing an early reproductive bud (continuous forest: N=33, N= 24, N=36; and fragmented forest: N=15, N= 40, N=18 palms per site). Within sites a mean distance of 26 m separated tagged palms. We registered the distance from each palm individual to the nearest forest edge using a handheld GPS. We followed the inflorescence development of

each palm for five months, from bud formation to maturity of fruits (see below). Palm inflorescences were on average (±SE) 185±0.6 cm above the ground.

Flowering phenology

To describe the flowering phenology of *G. interrupta*, weekly observations were carried out for nine weeks (January 17th to March 20th 2017), until all tagged inflorescences had finished anthesis. At each visit, we examined the development of the inflorescence and recorded when the palms had reached male or female anthesis. We used the week when inflorescences were seen to have reached anthesis to construct a phenology curve. Since male and female flowers do not open in synchrony (see above), this was done separately for the two flower types.

The plant individuals included in our study flowered from mid-January to late March 2017, with a peak in February. However, we noted that the overall flowering period of *G. interrupta* was slightly longer (from December to April).

Role of flower visitors in pollen transfer

To investigate if *G. interrupta* relies exclusively on insect vectors for successful pollination and to investigate seed development, we bagged a rachis bearing multiple rachillae on each individual inflorescence with a fine mesh (200 x 400 μm) from 102 palms (54 in the continuous and 48 in the fragmented forest). These bags will from now on be referred to as the '1st bag'. On average (±SE) we bagged 17.7±0.6 and 18.2±0.6 rachillae per site in the continuous and fragmented forest respectively. These bags excluded flower visitors but not wind-borne pollen. As a control we used the rest of the open inflorescence (i.e.

no bag). Bags were attached immediately after the inflorescence had fully opened (late January) but before any flower bud had opened, and removed after all inflorescences had matured fruits (late May, approximately five months later). To assess whether pollination is dependent on flower visitors, we counted the number of fruits developed inside the bags, and assumed those were produced by self-fertilization.

To describe the assemblages of insects visiting *G. interrupta* inflorecenses and to assess whether they differ between the continuous and fragmented forest landscapes, we carried out observations of insects visiting the infloresences. The assemblages of floral visitors were assessed separately for female and male flowers. Prior to the actual catching phase (see below), we carried out pre-observations from 08.00 h to 17.00 h to get a better idea about the peak times of flower visitation. Times from 10.00 to 13.00 h and 15.00 to 17.00 showed the highest abundance of floral visitors. We collected floral visitors from 30 inflorescences (11 at female anthesis, 19 at male anthesis) and 21 (9 at female anthesis, 12 at male anthesis) yielding a total of 4 h and 15 minutes of sampling, 2 h and 30 minutes in the continuous and 1 h and 45 minutes in the fragmented landscape. To maximise our chances of capturing a wider range of visiting taxa, this was performed by two persons from 10.00 h to 12.00 h for periods of 5 minutes for each individual inflorescence, and repeated at a different site from 15.00 to 17.00 by the same persons. We interchanged sites to avoid visiting two sites from the same landscape on the same day (e.g. site 1 from a continuous forest in the morning and site 1 from a fragmented forest in the afternoon and *vice versa*). Flower visitors were caught, using an aspirator for small insects and a net for Lepidoptera, over a four-week period from the last week of January to

the third week of February. Except for Lepidoptera, all captured insects were kept in individual tubes (to avoid cross transfer of pollen), killed using a freezer, mounted using entomological pins and preserved at ambient temperature. Parallel to insect catching, we recorded the main activity and behaviour of the species captured in order of gaining a better understanding towards whether a flower visitor is likely to be a pollinator. We matched our observations of behaviour to the categories described by Listabarth (2001). We separated activity based on movement in or out of the inflorescence, i.e., if a visitor arrive and leave the inflorescence (come and go), had a few movements without leaving (few movements) and if it was almost immobile (almost sedentary). Observed behaviour was based on the purpose of the visits, i.e. collecting or feeding on pollen, nectar feeding, mating and not clearly determined. For safety reasons only diurnal trapping was performed. Bees were identified to species level at El Colegio de la Frontera Sur (Ecosur), Chiapas. Other floral visitors were identified to family and morphospecies at the Colección Nacional de Insectos, at the Universidad Nacional Autónoma de México in Mexico City.

We examined every visitor collected using a stereoscopic microscope to search for transported pollen. To verify if the pollen carried by the flower visitors corresponded to *G. interrupta* we employed a chemical procedure (using the potassium hydroxide (KOH) method) to remove the pollen from at least one flower visitor from every species/morphospecies (following Caccavari and Cilla, 2010). Pollen grains obtained from insects were mounted on microscope slides, with glycerine jelly and dyed with fuchsin (Caccavari and Cilla, 2010), for identification and compared to pollen collected directly from *G. interrupta* male flowers. We did not find other palm species flowering nearby. As we were not

able to calculate pollen loads, we established three categories based on the visual amount of *G. interrupta*'s pollen removed from the visitor's bodies: high, medium and low (high >100 pollen grains; medium = between 20 and 100 pollen grains; low <20 pollen grains) in the field of view of the microscope; at 40X.

Reproductive output

In late January and early February 2017, we counted the total number of rachillae per inflorescence before anthesis. This was done to allow us to estimate the total number of flowers and fruits produced per inflorescence. For each inflorescence (or infrutescence), we estimated the following:

First, we estimated the ***number of flowers*** by counting the total number of flower scars on ten rachillae at the end of the fruiting season (May 2017). Using the mean number of scars per individual rachillae and the total number of rachillae per inflorescence (see above), we estimated the total number of flowers for every individual inflorescence.

Second, we estimated the ***total number of fruits*** (mature and immature) that would likely have developed on the inflorescence in the presence of insects. After the window for fertilisation had passed (when stigmas were dry; towards the end of February) we placed an additional bag (hereafter referred to as the '2nd bag'), made with the same material as the previous bag, on the inflorescence of 21 palms at each forest type (42 in total). These bags, which enclosed a subset of five rachillae to which insect pollinators had had access, were left on the infrutescence until the end of fruiting season. By counting the number of fruits developed inside the 2nd bags, we could estimate overall fruit production,

accounting for fruits that were prematurely aborted or removed before reaching maturity.

Third, we used the estimated number of flowers and fruits to calculate ***seed set***. Seed set is usually reported as the proportion of fruits to flowers on each inflorescence expressed as a percentage. In this case, as each female flower has one ovary, producing a single-seeded fruit, fruit set and seed set are identical.

To gain an understanding of the breeding system of *G. interrupta*, we assessed if the number of fruits developed in the presence of pollinators was different from the number of ***self-fertilised fruits***, we compared the number of fruits produced in the 1st bag (pollinators excluded) and the 2nd bag (open access to pollinators). Given that the number of rachillae was different in the two bagged treatments, we standardized both by calculating the number of fruits produced per centimetre of rachillae. Using the mean length of rachillae (2nd bag : open pollination: N = 100; 12.9±0.3; 1st bag: pollinators excluded: N= 100; 12.8±0.3 cm) and the mean number of fruits produced per rachillae (2nd bag : open pollination: 23.5±6; 1st bag: pollinators excluded: 2±1.1) we calculated the number of fruits produced per centimetre of rachillae. Finally, to assess if the proportion of fruits that were aborted before reaching maturity were affected by forest type and distance to a forest edge, we counted the number of fruits that were not fully developed inside the 2nd bag. We obtained the percentage of aborted fruits from the total estimated fruit production.

Statistical analyses

To assess the effects of forest type and distance from the forest edge on the reproductive output of *G. interrupta*, we concentrated on the following response variables: 1) proportion of palms with flower buds that successfully developed an inflorescence; 2) number of inflorescences (one or two) produced by an individual palm; 3) total number of female flowers (as both male and female flowers were highly correlated; $r_{Spearman} = 0.97$, $p<0.001$); 4) total number of fruits (as fruit production and seed set were significantly correlated; $r_{Spearman} = 0.6$, $p<0.001$); 5) number of self-fertilized fruits; and 6) proportion of fruits that were aborted before reaching maturity. For total number of female flowers, total number of fruits and the percentage of aborted fruits variables, we use linear mixed-effects models (LMM) in which the fixed explanatory variables were forest type (continuous or fragmented) and distance (metres) to the nearest forest edge, while site was included as a random effect. The variable distance was standardised using the *standardize* package in R (Eager 2017). We did not detect collinearity among explanatory variables (variance inflation factor < 2).

To test whether the proportion of palms successfully developing an inflorescence was affected by forest type, we employed a Pearson's Chi-squared test to compare them to the number of individuals that did not develop an inflorescence. To test whether the number of inflorescences (one or two) produced by an individual palm was affected by forest type, we used a Pearson's Chi-squared test. For both analyses we used the *chisq.test* function in *R* without Yates' continuity correction.

To assess if the number of self-fertilized fruits per centimetre of rachillae inside the bags (i.e. with pollinators excluded) differed significantly from the number of fruits produced with open pollination (2nd bag) we carried out a Paired t-test using the *t.test* function in R.

For total number of female flowers, total number of fruits and the percentage of aborted fruits (arcsine transformed), we used LMMs assuming a Gaussian distribution with an identity link function. We first fitted the maximal model, including all predictors and interactions. The model was then simplified by removing predictors that did not significantly improve model fit (Crawley 2012). LMMs were performed using the package *lme4* (Bates *et al.* 2014). We used the *Anova* function from the *car* package (Fox *et al.* 2018) to assess the significance of the predictor variables. All analyses were performed in *R* version 3.6.0.

Results

Role of flower visitors in pollen transfer

We identified 49 species/morphospecies of flower visitors from 21 families belonging to six orders (Table 2). Hymenoptera and Diptera were the most represented families with 18 species (~38%) each. In the continuous forest, inflorescences with male flowers were collectively visited by 47 species versus 18 species in the fragmented forest. Inflorescences with only female flowers were visited by 19 species in the continuous forest and by 16 species in the fragments. Since sampling effort was higher in the continuous forest than in the fragmented landscape (150 minutes versus 105 minutes; see methods), care should be taken when comparing the species richness of flower visitors between

the two habitat types. Nevertheless, the relative increase in the number of insect species observed on inflorescences with male flowers in the continuous versus fragmented forest landscape was still larger than the corresponding increase in sampling effort, suggesting that the insect communities associated with male inflorescences in the continuous landscape were indeed more diverse.

Ninety-five per cent of the species/morphospecies were visitors during the male anthesis in the continuous forest, while only 28% in the fragments (Table 2). We recorded a range of activities and behaviours (Table 3). Most bees and flies were active during the entire anthesis, although the two groups showed different behaviour. Bees were more active in collecting pollen and/or feeding on nectar, while species from Drosophilidae presented less movements in the inflorescence and were repeatedly seen mating. Wasps were active in foraging with constant movements within the inflorescence. Most beetles presented low activity and few movements within the inflorescence, and their behaviour could not be easily categorised. Butterflies were active foragers with both short and long visits to individual inflorescences.

Visual inspection of insects revealed that pollen from *G. interrupta* was present in all ten species of bees in the continuous forest, but only on three from fragments (Table 3). Pollen in bees was found all around the body (head, upper part of the thorax and abdomen) with high numbers packed in their corbiculae. Overall, pollen was also observed in ~55% of Dipteran species, ~30% of wasp species, ~30% of ant species, and ~30% of beetle species (see table 3 for specifics). Results from the acetolysis confirmed our above-mentioned visual inspections. We found high numbers of *G. interrupta* pollen on all bees; wasps and flies were categorised as medium pollen carriers; and, ants and beetles

presented low numbers of pollen. Cockroaches, butterflies and Heteropterans did not have *G. interrupta* pollen on their bodies.

Inflorescence development

Of the initial 166 tagged palms, only 102 (61%) developed a fruit-bearing infrutescence; 54 (32%) and 48 (29%) from continuous and fragmented forest respectively (table 1). Failure to fully develop an infrutescence did not differ between forest types ($\chi^2 = 0.72$, d.f. = 1, p = 0.34). The fraction of palm individuals producing one *versus* two inflorescences differed significantly between forest types, with a higher proportion of palms bearing two inflorescences in the continuous forest than in the fragmented forest landscape (~22% versus ~6%; $\chi^2 = 5.17$, d.f. = 1, p-value = 0.02; figure 4).

Male flowers opened before female flowers (Figure 3). Female flowers typically opened after the male flowers had finished anthesis and started to drop. Male flowers reached anthesis a week earlier than female flowers, but we noticed an overlap of male and female flowers from the same inflorescence. Flowers at the base of the rachillae opened before flowers closer to the tips of the rachillae. Both types of flowers emitted a fermented scent that could be perceived up to 2-3 metres from the plant.

Reproductive output

There was no effect of forest × distance ($LR\chi^2 = 0.005$, d.f. = 1, p = 0.94), distance ($LR\chi^2 = 0.5$, d.f. = 1, p = 0.48) and forest type ($LR\chi^2 = 0.69$, d.f. = 1, p = 0.4) on the total number of female flowers (figure 5). Fruit production was not significantly affected by the interaction between forest × distance ($LR\chi^2 = 0.005$, d.f. = 1, p =

0.94) nor distance ($LR\chi^2$ = 0.24, d.f. = 1, p = 0.62). However, fruit production differed significantly between palms in the two forest types, with fruit production being significantly higher in the continuous forest than in the fragmented forest landscape ($LR\chi^2$ = 8.56, d.f. = 1, p = 0.003; figure 5).

We found that 31% (17 out of 54) of the palms in the continuous forest and 28% (14 out of 48) of the palms in the fragmented forest landscape produced self-fertilized fruits (i.e., fruits found inside the 1st bags). The mean number (±SE) of fruits per centimetre of rachillae (2.1±1.1) inside the 1st bags (self-fertilisation) was not significantly different from the mean number (±SE) of fruits per centimetre in the 2nd bags (open pollination) (1.4±0.9; paired t-test, t = 0.95, d.f. = 30, p-value = 0.35).

The proportion of aborted (i.e. not-fully developed) fruits inside the bags was not affected by the forest × distance interaction ($LR\chi^2$ = 2.67, d.f. = 1, p = 0.1), but palms in forest fragments aborted a higher proportion of their fruits ($LR\chi^2$ = 7.66, d.f. = 1, p = 0.005; figure 6), and fruit abortion rates were also highest close to the edge ($LR\chi^2$ = 6.09, d.f. = 1, p = 0.013).

Discussion

Our study investigated the reproductive ecology of the palm *G. interrupta* in two types of landscapes, a fragmented rainforest and a protected and continuous rainforest. We found varying responses to fragmentation, depending on the aspect of palm flowering and fruiting investigated. Our study also suggests that fragmented and continuous forest habitats might differ in terms of the community of insect flower visitors, although (given differences in sampling effort) this observation should be interpreted with care.

a) What are the main inflorescence visitors and do they differ between a continuous and fragmented forest?

We recorded a wider community of species visiting the male flowers in the continuous forest, compared to fragments. Hymenoptera and Diptera were the most diverse orders overall visiting the flowers (both male and female). From Hymenoptera, ~64 % belong to stingless bees of the Apidae family. All bees presented higher numbers of pollen than the other flower visitors, around the body and especially in their corbiculae. Pollen transported in "safe" parts of the body has been hypothesised to be important for pollination (Koch *et al.* 2017). Our results are consistent with other observational studies on palms, where male flowers received higher frequency visitation than female flowers (Listabarth 2001). However, fragmentation can affect the foraging behaviour of species from the Apidea family, resulting in lower visitation rates indicating a limitation of pollinators (Goverde *et al.* 2002).

Because the abundance of flower visitors may differ between environments, their actual contribution towards the reproduction of *G. interrupta* may also differ between environments. Unfortunately, we were not able to gather information about the abundances of flower visitors. Such data would have allowed us to infer more about the relative role that those species play in the reproduction of this palm in the two studied landscapes.

b) Does flower and fruit production differ between palms in forest fragments versus a continuous forest and by the distance from the edge?

Neither inflorescence production nor subsequent flower production (male and female) differed significantly between the forest types. In a study comparing the reproduction of four shrubs in fragmented vs. continuous woodland, two of the species did not differ in flower production between habitats (Cunningham 2000b). This partially supports our findings of no difference in flower production. In the inflorescences that we followed, similar flower production in both forest types suggests that palms are able to invest a similar amount of resources towards reproductive tissue in both landscapes (Cunningham 1997). However, we found that in continuous habitats a higher proportion of palms produced two inflorescences per individual, but it was impossible to follow the fate of the second inflorescence. Future research may consider this information to design new studies.

Fruit production was significantly lower in the fragmented sites than in the intact forest sites, suggesting possible pollen limitation. This is consistent with previous studies of pollination in other flowering plants, where reduced fruit production occurred in fragmented sites where flowers received less pollen (Cunningham 2000a). Although lower fruit production and seed set might not in itself threaten the persistence of *G. interrupta* populations in fragments, it may – in combination with other factors – still contribute to elevate the risk that populations of this palm species face (see Cunningham, 2000a).

The lower fruit production in the fragmented landscape than in the continuous forest might be related to differing environmental conditions between the two landscape types. In particular, edge habitats might experience

drought and increased temperature, which could be detrimental for the development of fruits. Additionally, biotic factors may limit fruit production in fragments due to limited pollinator services (Ashman *et al.* 2004). Compared to the continuous forest, we recorded a diminished community of flower visitors in the fragments. Even with the difference in sampling effort (see methods), there is a possibility that palms in fragments suffer from pollinator service limitation. For example, other studies have shown that flowers are visited less frequently in experimentally fragmented grasslands compared to unfragmented controlled plots (Goverde *et al.* 2002).

Reduced seed production could affect other interactions that are key in maintaining communities and ecosystems. For example, if pollen limitation as a consequence of fewer biotic vectors results in lower fruit and seed production, this could reduce resources for seed predators and pathogens (Ashman *et al.* 2004). On the other hand, non-viable or aborted seeds may be a consequence of selfing. It has been reported that the number of aborted fruits is higher in fragments than in continuous forests (Franceschinelli *et al.* 2015), affecting processes that maintain the structure of tropical forests.

c) Is this species capable of self-fertilization in the absence of flower visitors?

Although it has been reported that *G. interrupta* is functionally dioecious (i.e. no overlap between male and female flowers; Stauffer et al., 2002), we found an overlap of the final stages of the second male anthesis and the beginning of the female anthesis as well as fruit development on sections of the inflorescences from which insects had been fully excluded. Exclusion of pollinators resulted in

significantly reduced fruit production compared to the open part of the inflorescence, this raises questions as to the degree of functional dioecy that this palm exhibits. In other dioecious understorey palms pollinated by wind, exclusion of pollinators showed no effect on seed production (Otero-Arnaiz & Oyama 2001). Since we found evidence of fruit production in parts of the inflorescence where pollinators were excluded, it is valid to assume self-pollination. Nonetheless, we cannot ignore the possibility of wind-mediated cross-pollination. If both scenarios are not mutually excluding, this indicates that *G. interrupta* can, to some extent, ameliorate the lack of insect pollinators (Ward *et al.* 2005). Nevertheless, if the absence of insects makes self-pollination more likely, then the offspring may suffer negative fitness consequences as a result of inbreeding.

Our study shows that the reproduction of an understorey palm species can be affected by habitat fragmentation. Fruit production was significantly lower in fragments. Furthermore, and parallel to the lower number of fruits, the proportion of aborted fruits was higher in fragments, particularly near the forest edge. Whether these effects carry over to affect the longer-term dynamics of the palm will need to be addressed in future studies. Even though we found that the abundances of adults and juveniles of *G. interrupta* are lower in fragments (Chapter 2), a potential effect from the fragmentation process.

Tables and figures

Table 1. The number of studied palm individuals and their average distance to the nearest edge at each of the six study sites. Of the initial 166 palms selected, only 61 % developed inflorescences. SE = standard error. Area is the approximate 'size' in hectares of each site.

Forest	Site	No. palms	Mean distance (m)	SE	Area
Continuous	Continuous.1	18	49.33	6.6	88
	Continuous.2	18	183.11	4.4	80
	Continuous.3	18	378.33	9.5	110
		54	203.59	18.9	278
Fragmented	Fragmented.1	13	24.08	3.7	90
	Fragmented.2	14	71.36	11.7	95
	Fragmented.3	21	336.52	22.2	116
		48	174.56	23.3	301
Total		102			1158

Table 2. Number of species or morphospecies per order (grey rows) and family observed visiting male versus female flowers of *Geonoma interrupta* in each of the studied forest types.

	Order	Family	Continuous		Fragmented	
			Male	Female	Male	Female
1	Blattodea		1	1	0	0
		Blattidae	1	1	0	0
2	Coleoptera		6	3	0	0
		Chrysomelidae	1	0	0	0
		Curculionidae	3	2	0	0
		Melandryidae	1	0	0	0
		Nitidulidae	1	1	0	0
3	Diptera		17	14	13	12
		Culicidae	1	1	1	1
		Drosophylidae	2	1	1	1
		Muscidae	1	1	1	1
		Neriidae	1	1	0	0
		Sarcophagidae	3	2	3	2
		Syrphidae	2	2	2	2
		Tachinidae	2	1	2	2
		Tephritidae	5	5	3	3
4	Heteroptera		3	1	0	0
		Cicadellidae	1	0	0	0
		Pyrrhocoridae	1	0	0	0
		Rhopalidae	1	1	0	0
5	Hymenoptera		17	6	5	5
		Apidae	11	4	3	3
		Braconidae	1	1	0	0
		Formicidae	2	0	2	2
		Vespidae	3	1	0	0
6	Lepidoptera		3	3	0	0
		Nymphalidae	3	3	0	0
	Total		47	28	18	17

Table 3. Activity and behaviour of flower visitors. The table shows general activity and behaviour (both forest types pooled). The column 'Pollen/forest type' indicates whether *G. interrupta*'s pollen was found on specimens of the species (+: present; -: absent) in the continuous and fragmented forest (* indicates that species was not collected from a specific forest type).

			Activity		Behaviour		Pollen/forest type	
Order	Family	Taxon	Male	Female	Male	Female	Cont.	Frag.
Blatttodea	Blattidae	Blattidae sp1	s	s	m	m	-	*
Coleoptera	Chrysomelidae	Chrysomelidae sp1	fm		ne		-	*
	Curculionidae	Curculionidae sp1	fm	fm	nc	nc	+	*
		Curculionidae sp2	fm		nc		+	*
		Curculionidae sp3	fm	fm	nc	nc	-	*
	Melandryidae	Melandryidae sp1	cg		nc		-	*
	Nitidulidae	Nitidulidae sp1	fm	fm	nc	nc	-	*
Diptera	Culicidae	Culicidae sp1	cg	cg	ne	ne	-	-
	Drosophilidae	Drosophilidae sp1	fm	fm	ne, m	ne, m	+	+
		Drosophilidae sp2	fm		ne, m		+	*
	Muscidae	Muscidae sp1	cg	cg	ne	ne	+	+
	Neriidae	Neriidae sp1	fm	fm	ne	ne	-	*
	Sarcophagidae	Sarcophagidae sp1	cg	cg	ne	ne	+	+
		Sarcophagidae sp2	cg		ne		-	-
		Sarcophagidae sp3	cg	cg	ne	ne	-	-
	Syrphidae	Syrphidae-*Copestylum*	cg	cg	ne	ne	+	+
		Syrphidae-*Polybiomyia*	cg	cg	ne	ne	+	+
	Tachinidae	Tachinidae sp1	cg	cg	ne	ne	+	+
		Tachinidae sp2	cg	cg	ne	ne	+	+
	Tephritidae	Tephritidae sp1	cg	cg	ne	ne	+	+
		Tephritidae sp2	cg	cg	ne	ne	+	*
		Tephritidae sp3		cg		ne	-	*
		Tephritidae sp4	cg	cg	ne	ne	-	-
		Tephritidae sp5	cg	cg	ne	ne	-	-
		Tephritidae-*Tephritis*	cg		ne		-	*
Heteroptera	Cicadellidae	Cicadellidae sp1	s		nc		-	*
	Pyrrhocoridae	Pyrrhocoridae sp1	s		m		-	*
	Rhopalidae	Rhopalidae sp1	fm	fm	m	m	-	*
Hymenoptera	Apide	*Apis mellifera*	cg	cg	p	ne	+	+
		Neocorynura cribrita	cg		p		+	*
		Neocorynura sp.	cg		p		+	*
		Partamona bilineata	cg	cg	p, ne	ne	+	*
		Partamona orizabaensis	cg		p		+	*
		Plebeia frontalis	cg	cg	p, ne	ne	+	+
		Plebeia llorentei	cg		p		+	*
		Plebeia pulcra	cg	cg	p, ne	ne	+	+
		Trigona corvina	cg		p		+	*

		Trigona fuscipennis	cg	cg	p, ne	ne	+	*
		Trigonisca pipioli	cg		p		+	*
	Braconidae	Braconidae sp1	cg		ne		-	*
	Formicidae	Formicidae sp1	fm	fm	nc	ne	+	+
		Formicidae sp2	fm	fm	nc	ne	*	-
		Formicidae sp3	fm		nc		-	*
	Vespidae	Vespidae sp1	cg	cg	p, ne	ne	+	*
		Vespidae sp2	cg		p, ne		-	*
		Vespidae-*Polybia*	cg		p, ne		-	*
Lepidoptera	Nymphalidae	Hamadryas sp1	cg		ne		-	*
		Ithomia patilla	cg	cg	ne	ne	-	*
		Pteronymia cotytto	cg	cg	ne	ne	-	*

Activity: cg -come and go; fm -few movements; s -almost sedentary
Observed behaviour: p -pollen feeding or collecting; ne -nectar feeding; m -mating; nc -not clear.

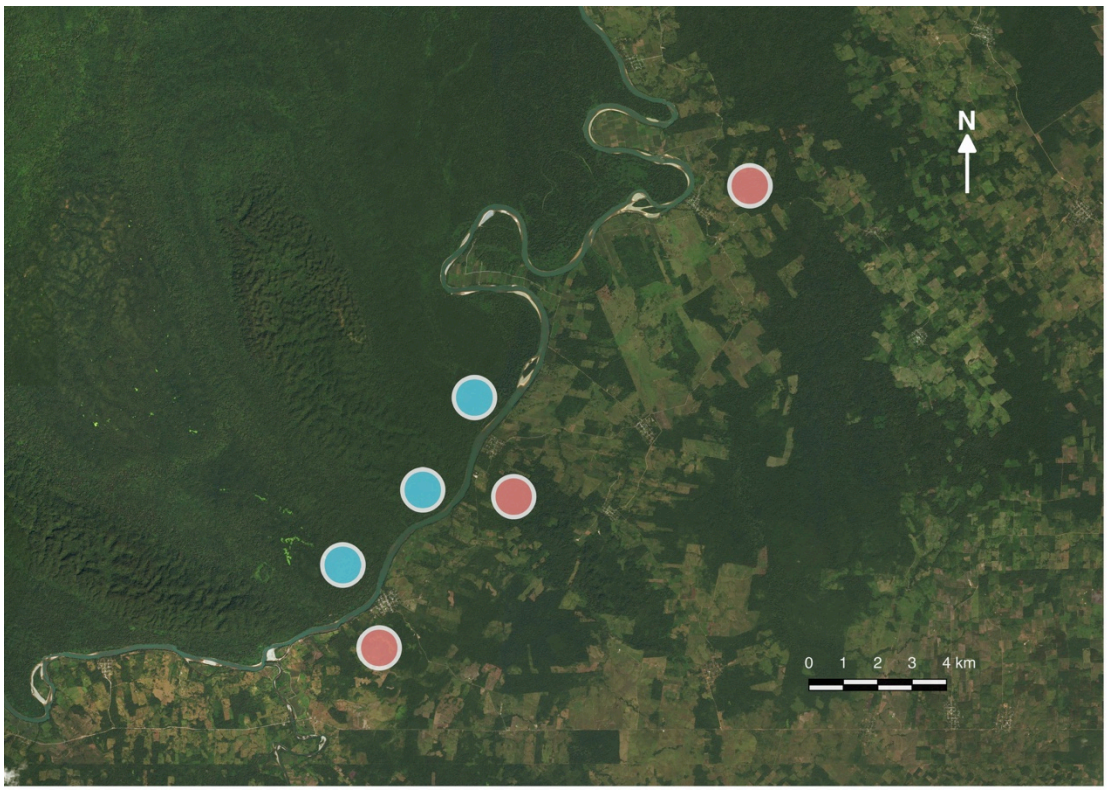


Figure 1. The study sites were located in a continuous forest (blue dots) and in a fragmented landscape (pink dots) in southeast Chiapas. The continuous and protected forest is part of the Montes Azules Biosphere Reserve, separated from the fragmented landscape of Marques de Comillas by the Lacantun River.

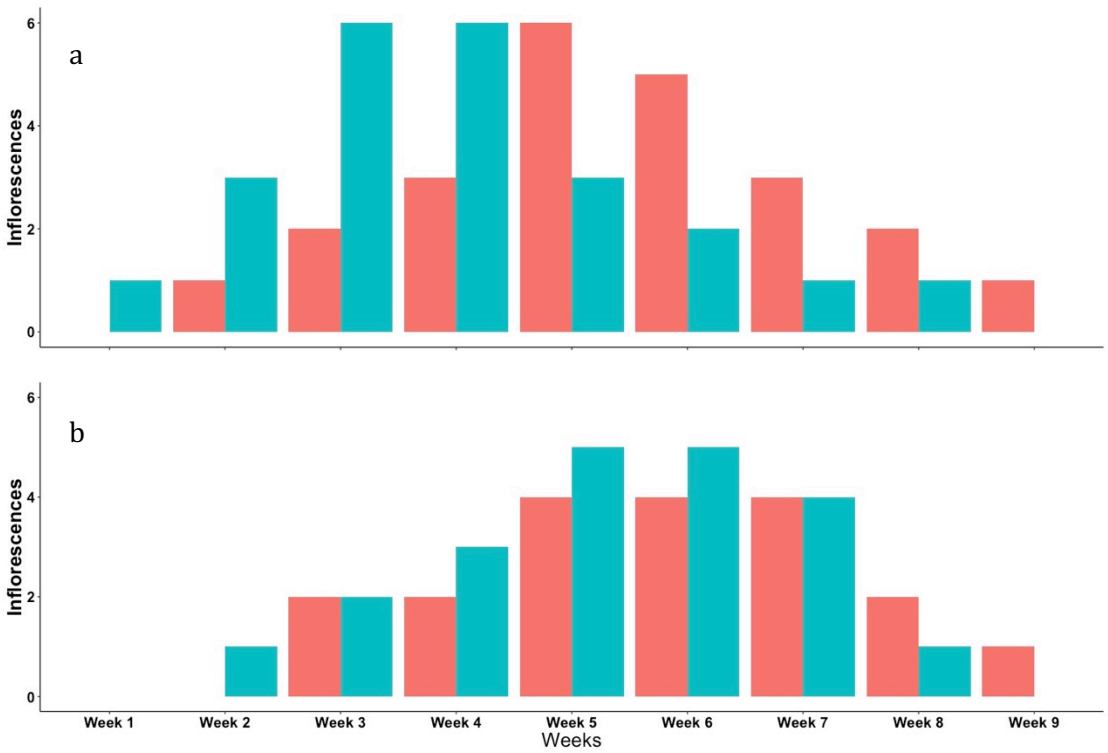


Figure 3. Flowering phenology of *Geonoma interrupta* over a nine-week period (from January 17th to March 20th 2017), represented as the number of inflorescences that reached anthesis in a given week. Bars represent the number of inflorescences with a clear dominant flower phase (male in blue and female in red) in the continuous forest (a) and fragmented forest (b).

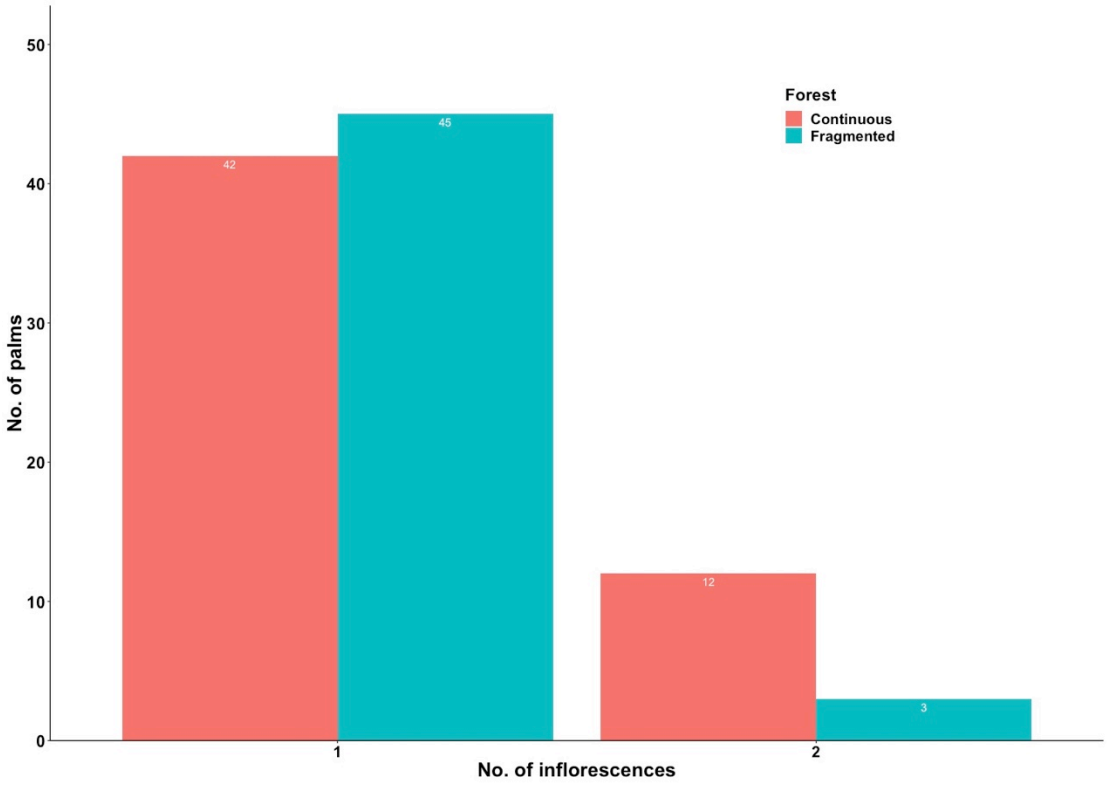


Figure 4. Number of palm individuals with one inflorescence or two inflorescences in each forest type.

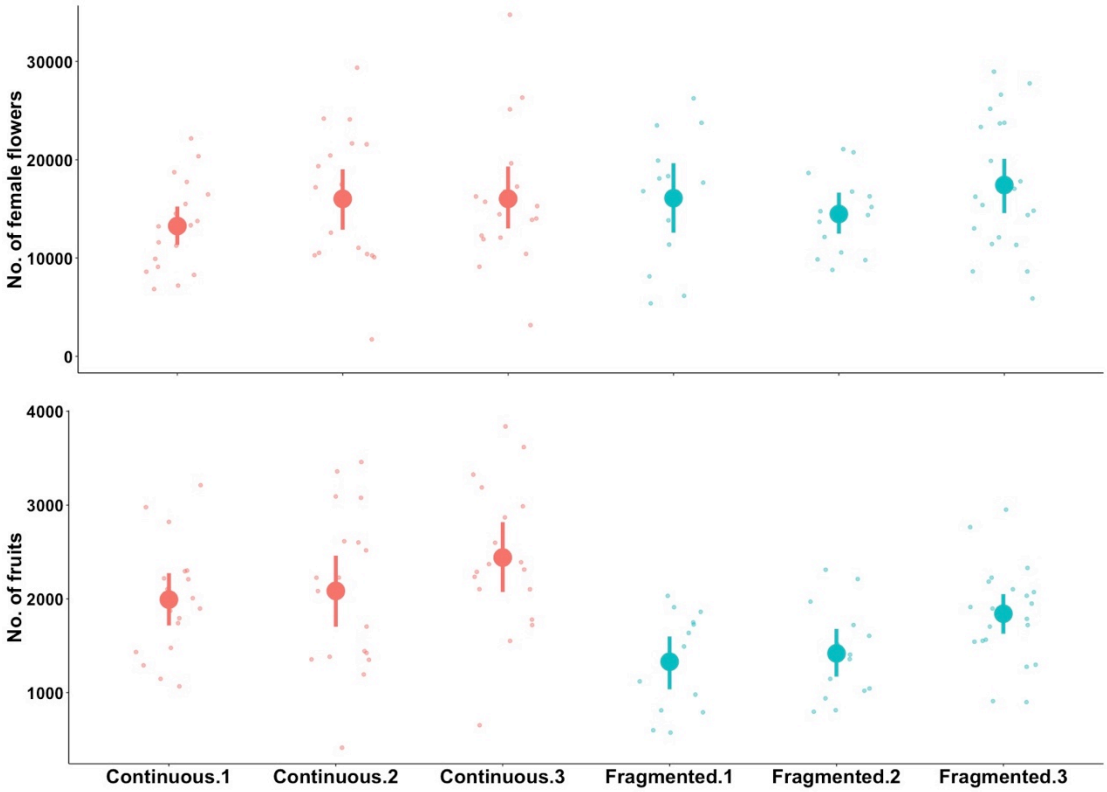


Figure 5. Estimated mean number of female flowers (top) and estimated mean number of fruits (bottom) produced by palms at each site. Lines represent 95 % CI and small dots represent individual palms. Within forest type, sites are sorted according to the mean distance of sampled palms to the nearest forest edge: Continuous.1 and Fragmented.1 are closest to a forest edge (Table 1).

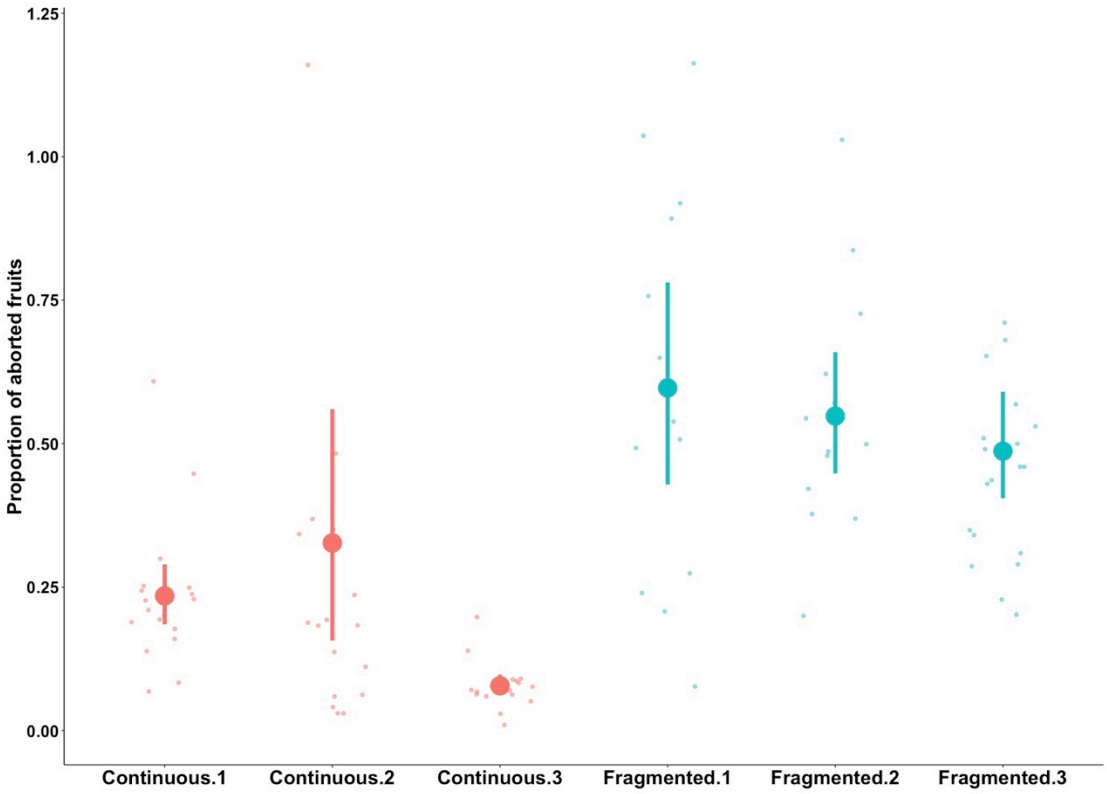


Figure 6. Mean proportion of aborted fruits at each of the six study sites. Mean ± 95% CI is shown. Small dots represent individual palms.

Chapter 5. Effects of natural enemies and distance from forest edge on the recruitment of palms

Introduction

Rainforest plants are in constant interaction with a wide range of natural enemies such as herbivores and pathogens. These natural enemies can be important factors influencing plant establishment, distribution and abundance (de la Cruz & Dirzo 1987, Wright 2002, Freckleton & Lewis 2006, Swamy & Terborgh 2010, Bagchi *et al.* 2014). Operating across multiple species, plant-enemy interactions can also leave an imprint at the community level. If species that are locally abundant are disproportionally attacked, local plant diversity could be enhanced (Connell, 1971; Gripenberg et al., 2014; Janzen, 1970; and literature therein). This notion has been central in explaining the high plant diversity in tropical forests. Changes in the abundance and identity of plant enemies are therefore expected to have consequences for the plant community.

Recruitment limitation of seedlings, following successful germination, is considered a crucial step for the maintenance of tropical plant diversity (Hubbell *et al.* 1999, Harms *et al.* 2000, Gripenberg *et al.* 2014). In the early stages of their development, plants may be particularly susceptible to enemies, leading to high mortality (Harms *et al.* 2000, Freckleton & Lewis 2006, Green *et al.* 2014). Effects at these initial stages can have considerable repercussions in later life stages (Sagers & Coley 1995). The seed to seedling transition and seedling establishment can be influenced by both the biotic and abiotic environments. For instance, when herbivorous mammals are absent, seedlings can reach higher densities than at sites with relatively intact mammal communities (Dirzo &

Miranda 1991), leading to shifts in the plant species composition (Theimer *et al.* 2011). Understanding how plant-enemy interactions affect seedling establishment and diversity, and how these interactions are altered by anthropogenic changes to the biotic and abiotic environments, will thus allow us to understand more fully the consequences of global environmental change for biodiversity.

Human disturbance of continuous forests has the potential to disrupt ecological interactions. For example, changes associated with newly formed forest edges have the potential to modify plant-enemy interactions. Recent estimates suggest that nearly 30% of the world's remaining forests are within 200 m of an edge (Haddad *et al.* 2015). Generally, these forest habitats are characterized by differences in microclimatic conditions including temperature, humidity and light, factors which are expected to have marked direct effects on plants (Murcia 1995), as well as on their interactions with enemies (Murcia 1995, Thompson *et al.* 2010, Haddad *et al.* 2015). For example, lower humidity at edges, relative to interior areas, is expected to reduce fungal activity associated with seedling mortality (Murcia 1995, Álvarez-Loayza *et al.* 2011, Crockatt 2012, Krishnadas *et al.* 2018). Moreover, increased light intensity near edges could allow seedlings to grow rapidly and to invest more in defenses, hence reducing damage and enabling them to recover faster from any damage caused by enemies (Augspurger & Kelly 1984, Sagers & Coley 1995, Coley & Barone 1996). Although there is some evidence that levels of insect herbivory decline with forest fragmentation (Ruiz-Guerra *et al.* 2010), other studies have shown that altered conditions created by edge effects can in fact favour pathogens and

herbivores, intensifying biotic damage to seedlings (Benítez-Malvido & Lemus-Albor 2005).

Here we describe a field experiment in a fragmented landscape in Southern Mexico, where we investigated the effects of three enemy groups (fungal pathogens, invertebrates and vertebrate herbivores) on the recruitment of two species of palms. We examined whether natural enemies act as "filters" at the seed to seedling transition and at seedling establishment, and whether their effects differ between the forest edge and interior. Field experiments have shown the effects that insects (Bagchi *et al.* 2014), pathogens (Bell *et al.* 2006, Bagchi *et al.* 2010, 2014) and vertebrates (particularly mammals; (DeMattia *et al.* 2006, Camargo-Sanabria *et al.* 2015), can have on plant recruitment, and more recently, experiments have also incorporated forest edge effects (Krishnadas *et al.* 2018). However, to our knowledge, most studies excluding natural enemies tend to focus on specific enemy groups, and studies that jointly assess the effects of e.g. insects, pathogens, and vertebrate enemies of plants are rare. The potential synergistic and interacting effects of plant enemies and edge effects need more attention. Our experiment was designed to address the following questions: 1. Do rates of seed germination and seedling survival differ between forest edge and interior? 2. Do fungal pathogens, insects and vertebrates influence rates of seed germination and seedling survival? 3. Does the contribution of natural enemies to seed germination and seedling survival differ between edge and interior? We predicted that, 1) seed germination and early seedling survival is higher close to the edge because of higher light availability associated with forest edges than forest interiors; 2) recruitment of seedlings is higher in the absence of natural enemies, and 3) the effects of natural enemy

exclusion will differ between edge and interior habitats, because different enemy groups are likely to respond differently to the altered environmental conditions near the forest edge.

Methods

Site

Our field experiment was conducted in a forest fragment close to the Ejido Boca de Chajul in the southwest state of Chiapas, Mexico (16°06'20.4"N, 90°56'21.9"W). The fragment was created ~40 years ago with a mixed vegetation of old-growth forest and secondary lowland tropical rainforest. The owners protect the fragment and extraction of timber and non-timber products is prohibited. Hunting is also prohibited although there has been evidence of poaching. The fragment is adjacent to agricultural land were the main crops are maize, beans, squash and chilli (Cerón-Martínez, per. obs.). The area is located south of the protected Biosphere Reserve of Montes Azules, at an elevation of 120 metres from sea level. The climate is warm and humid with an annual average temperature of 24.1°C and a yearly mean rainfall of 3187 mm (O'Brien 1998). The region experiences a dry season, normally from January to May. The region in which our study site is located, Marques de Comillas, is a mosaic of disturbed forests and human settlements. Among the main anthropogenic activities are cattle ranching, agriculture and palm oil production.

Study species

Geonoma is the third largest Neotropical palm genus (Chazdon 1991). *Geonoma interrupta* is an understorey palm, distributed from Mexico to Bolivia. It can

reach a height of up to 8 m. Both seeds and fruits are ellipsoid. Seeds are on average (±SE) 5±0.03 mm long and 3.9±0.04 mm in diameter (N= 50; pers. obs.). The fruits attract a range of frugivorous birds and mammals that often take the fruits directly from the infructescence and potentially disperse the seeds (Cerón-Martínez pers. obs.). Seeds that fall to the ground are often removed by birds and ground-dwelling mammals (Cerón-Martínez pers. obs.). *Geonoma* species have a strong association with moist, shaded habitats, suggesting that *G. interrupta* is a shade-tolerant species.

Reinhardtia is a genus of Neotropical palms that includes six species. *Reinhardtia simplex* is a small understorey palm (max height 1.2 m) that occurs in lowland moist forests from southeast Mexico to northern Colombia (Henderson 2002). Both seeds and fruits are ellipsoid. Seeds are on average (±SE) 8.8±0.05 mm long and 6.3±0.04 mm diameter (N= 50; pers. obs.). Fruits attract birds, and seed dispersal is also carried out by squirrels and raccoons (Mendoza & Dirzo 2007). To our knowledge, there is no published information about the habitat preference of this species. Its strong association with moist, shaded sites suggests that it is likely to be shade-tolerant (Chapter 3 of this thesis).

Enemy exclusion experiment

We established 10 experimental stations on the forest floor: five within 5 m of the forest edge and five in the interior of the forest. Within habitats (edge or interior), stations were separated by ~50 m and there was a minimum distance of 150 m between edge and interior stations (Figure 1a). All stations were set up in flat areas to avoid any treatment cross contamination. Additionally, and

between each spaying, we place a piece of plastic film as a barrier to avoid spaying into other treatments.

At each of the 10 stations, we excluded ground-dwelling vertebrates from a 1 m^2 plot using plastic mesh with 1 mm apertures. The mesh barrier was approx. 30 cm in height and was dug 10 cm into the ground. Each 1 m^2 plot was subdivided into four equally-sized subplots. At each station, an extra open control subplot (50 cm by 50 cm) was set up adjacent to the 1 m^2 plot to allow us to quantify the effects of vertebrates on seed removal and seedling survival. Before the initiation of the experiment, each subplot was carefully inspected and all existing seedlings removed. We also removed litter, as it has been linked to lower growth and higher levels of damage by herbivores and pathogens in seedlings (García-Guzmán & Benítez-Malvido 2003). However, we allowed natural litter accumulation during the rest of the experiment. In each subplot we planted 10 seedlings of *Geonoma interrupta*, and sowed 10 seeds of *G. interrupta* and 10 seeds of *Reindhartia simplex*. Seedlings and seeds were arranged in six rows and separated by ~7 cm from each other (Figure 1b). Seedlings were obtained from underneath reproductive palms and transplanted to the experimental plots the same day (15th January 2017). For *G. interrupta*, seeds were collected from the previous fruiting season (May 2016), from only two adult palms to minimise genetic variation. Because *R. simplex* produces ~25 single-seeded fruits per plant, seeds were collected from ~30 different individuals (May-June 2016).

At each station, each of the four vertebrate-excluded subplots was assigned to one of four treatments: exclusion of fungal pathogens, exclusion of insects, exclusion of both fungal pathogens and insects, and control. Treatments

consisted of spraying 50 ml of 1) fungicide, 2) insecticide, 3) fungicide + insecticide, or 4) water. The insecticide used was Actram 75 WDG (Agricultura Nacional, S.A. de C.V.; active ingredient: thiamethoxam), and the two fungicides were Maxtrobyn (Helm de Mexico, S.A.; active ingredient: azoxystrobin) and Cyrizate (Helm de Mexico, S.A.; active ingredient: mancozeb and cymoxanils). Following manufacturer's instructions each chemical was dissolved in 50 ml of clean water (Actram 0.015 gr, Cyrizate 0.25 gr and Maxtrobyn 0.01 ml). The two types of control plots (vertebrate excluded and open control plots) were sprayed with 50 ml of water. Treatments were applied biweekly with a hand mister from January 2017 to January 2018. Seedling survival and seed germination were recorded bimonthly for the first 12 months. The number of leaves and height (cm) of seedlings were recorded at the start of the experiment (for *G. interrupta*) and after 12 months.

Statistical analysis

Since only 11 out of 500 planted *G. interrupta* seeds germinated, we focused our analyses on the performance of *G. interrupta* individuals planted as seedlings. Specifically, we assessed seedling survival, height and the number of leaves after 12 months of experimental treatments. For *R. simplex* we analysed the proportion of planted seeds that germinated and were still alive 12 months into the experiment. We did not perform analyses on the number of leaves and height of *R. simplex* seedlings, because after one year all remaining seedlings had developed only one leaf and the apical meristem was still at ground level (i.e. height = 0 mm).

Seedling survival (*Geonoma interrupta*)

To analyse survival of *G. interrupta* seedlings we used the proportion of the original 10 seedlings planted in each subplot remaining after one year (January 2018) from the start of the experimental treatments. We used a generalised linear mixed-effects model (GLMM) where the response variable was the fraction of seedlings surviving in each subplot, expressed using the *cbind* function in R. The predictor variables were habitat (edge or interior), treatment (i.e. type of enemy exclusion), and their interaction. We used the *glmer* function from the *lme4* package (v. 1.1-12) with a binomial error distribution and a logit link function. Previous to the GLMM, we carried out a Fligner-Killeen test of homogeneity of variances (Cohen *et al.* 2018, Ashton *et al.* 2019), using the *fligner.test* function, and found no significant heterogeneity ($\chi^2 = 5.18$, d.f. = 9, p = 0.81). We first fitted the maximal model, including all predictors. The model was then simplified by removing predictors that did not significantly improve model fit (Crawley 2012), using the *Anova* function from the *car* package (Fox *et al.* 2018) to assess the significance of the predictor variables. We compared differences among treatments with a Tukey post hoc test using the *glht* function in the *multcomp* package (Hothorn *et al.* 2008).

Seedling growth and number of leaves (*Geonoma interrupta*)

To assess the effects of habitat and enemy exclusion treatments on seedling performance of *G. interrupta*, we built two GLMMs in which a) the number of leaves and b) the height of each surviving seedling were the response variables. In each of these analyses, habitat, treatment, and the interaction between habitat and treatment were fixed factors, while subplot and station were included as

random effects to account for non-independence of seedlings within a subplot and between subplots within the same station. In the model on the number of leaves we used the *glmmadmb* function with Poisson-distributed residuals with a log link function, and in the model on seedling height we used the *lmer* function assuming a Gaussian distribution with an identity link function. In both cases we first fitted a full model (including all predictor variables and their interactions), and then simplified the model using the approach explained above. Residuals were visually inspected to assess model performance.

Seedling survival (*Reinhardtia simplex*)

To investigate *R. simplex* seed germination and seedling survival we fitted a GLMM using an identical approach to the one described above for the survival of *G. interrupta* seedlings. The response variable was the proportion of planted seeds germinating and remaining (as seedlings) in each subplot after one year. The Fligner-Killeen test found no significant deviation from homogeneity of variances ($\chi^2 = 4$, d.f. = 9, $p = 0.91$). We compared differences among treatments with a Tukey post hoc test using the *glht* function in the *multcomp* package.

All analyses were performed using R 3.3.3 (R Core Team 2017) and the packages *glmmADMB* 0.8.3.3 (Skaug *et al.* 2016) and *lme4* 1.1-12 (Bates *et al.* 2015) for GLMMs.

Results

Of the 500 *G. interrupta* seedlings planted, 318 (63.6 %) were still alive after 12 months. One hundred and eleven (22.2 %) seedlings died within the first two

months of the experiment (Jan-Mar 2017), particularly in the open control plots in the forest interior (Table S1). We identified disturbances in the open plots caused by vertebrates. Only 11 out of 500 *G. interrupta* seeds germinated (this germination took place in June-July 2017). Germination of *R. simplex* seeds started in May 2017, four months after the beginning of the experiment. In total 373 (74.6 %) out of the 500 planted seeds germinated, and 309 seedlings (61.8 %) were still alive after 12 months.

Geonoma interrupta seedling survival and performance

Seedling survival. The habitat × treatment interaction was not significant ($LR\chi^2$ = 8.37, d.f. = 4, p = 0.08) hence we removed it from the model. Habitat was also removed, as it did not significantly improve the model ($LR\chi^2$ = 0.17, d.f. = 1, p = 0.68) implying that seedling survival did not differ between forest edge and interior. The minimal adequate model only included treatment, which significantly affected seedling survival ($LR\chi^2$ = 68.99, d.f. = 4, p = <0.001). Seedling survival was higher in the subplots treated with fungicide and fungicide + insecticide than in the closed control plots, while seedling survival was significantly lower in the open controls than in any of the other treatments (Tables 1, 2, Fig. 2). In general, open controls showed the lowest percentage of surviving seedlings, followed by the closed control (Table 1).

Number of leaves. The habitat × treatment interaction did not improve model fit significantly and was removed from the model ($LR\chi^2$ = 0.66, d.f. = 4, p = 0.95). Likewise, enemy-exclusion treatment was removed from the model in the process of model simplification ($LR\chi^2$ = 0.18, d.f. = 4, p = 0.99). The only remaining fixed effect in the minimum adequate model was habitat, which had a

significant effect on the number of leaves per seedling ($LR\chi^2 = 17.96$, d.f. = 1, p = <0.001). More specifically, *G. interrupta* seedlings located close to the forest edge had a greater number of leaves than seedlings in the forest interior (Figure 1; Table 1; Table 3).

Seedling height. In the process of model simplification, the interaction habitat × treatment ($LR\chi^2 = 0.72$, d.f. = 4, p = 0.95) and treatment ($LR\chi^2 = 1.16$, d.f. = 4, p = 0.88) were removed from the full model. The minimal adequate model included only habitat, which had a significant effect on seedling height ($LR\chi^2 = 32.38$, d.f. = 1, p = <0.001). Seedlings close to the forest edge were taller than seedlings in the forest interior (Figure 4; Table 1; Table 3).

Survival of *Reinhardtia simplex*

We removed the interaction habitat × treatment ($LR\chi^2 = 2.35$, d.f. = 4, p = 0.67) and habitat ($LR\chi^2 = 0.93$, d.f. = 1, p = 0.33) because neither improved the model. Overall, there was a significant effect of treatment ($LR\chi^2 = 14.53$, d.f. = 4, p = 0.005) on seedling survival of *R. simplex*. Seedling survival was significantly lower in the open control treatment than in the insecticide and fungicide + insecticide treatments (Table 5).

Discussion

Our field experiment investigated the effects of three enemy groups on the recruitment success of two species of palms in a fragmented rainforest in southern Mexico. Our results suggest that altered habitat conditions created by fragmentation can have an effect on the early stages of palm development, with the effect depending on the exact response (e.g. seedling survival, growth and

number of leaves). Our study also shows that the investigated natural enemy groups (pathogens and insect and mammalian herbivores and seed predators) can play a crucial role at the early stages of palm development and establishment. Seedlings protected from natural enemies were more likely to survive than seedlings exposed to enemies. Contrary to our prediction, the effects of enemy-exclusion did not differ between the forest edge and interior.

Does seed germination and seedling performance differ between the forest edge vs. interior?

Our results showed mixed effects of habitat on the performance of *G. interrupta* seedlings and the germination and survival of *R.* simplex. For *R. simplex*, the proportion of planted seeds that germinated and were still alive 12 months after the onset of the experiment did not differ between the two habitat types. For *G. interrupta*, seedling survival did not differ between edge and interior, whereas seedlings grew taller and produced more leaves near the edge.

It has been argued that hotter and drier conditions close to edges are less suitable for the germination of certain species (Bruna 1999, Benitez-Malvido & Martínez-Ramos 2003). We therefore expected that altered microclimatic conditions near fragment edges would affect the germination and establishment of the studied palm species. Even though our two study species are presumably adapted to understorey conditions, we did not detect any effect of habitat on germination and survival. Soil moisture is likely to be one of the factors that change rapidly in relation to the proximity to forest edge (Camargo & Kapos 1995), with potential impacts on germination and survival of seedlings. While it has been reported that moisture increases significantly towards the interiors of

temperate forest fragments (Riutta *et al.* 2012), in tropical areas the recorded patterns are not consistent. For example, in fragments of the Amazon forest, soil moisture can be higher within the first 20 m from the forest edge than at sites up to 500 m inside the forest (Camargo & Kapos 1995).

There are also other microclimatic factors than soil moisture that may differ between the forest edge and interior. For example, air temperature and canopy openness might depend on the distance from the edge. Since plant growth is dependent on light availability (Svenning 2001, 2002), such differences may help to explain the difference in growth recorded for *G. interrupta* seedlings close to the edge versus in the forest interior: seedling growth was slower and the number of leaves on each seedling was lower inside the forest fragment than near the edge. Our results are in line with other studies reporting an increase in seedling growth as a response of the increase in light intensity near or at forest edges (Murcia 1995). Seedlings receiving more photosynthetically active radiation can grow and recover faster from damage to foliage, up to 40 m from the edge (Kapos 1989, Sagers & Coley 1995, Svenning 2002). Light intensity has indeed been shown to be important for growth of other palms, such as the climbing palm *Desmoncus orthacanthos* (Siebert 2000) and *Geonoma macrostachys* (Svenning 2002). At our experimental sites, canopy openness (as a proxy for light availability) near the edges was on average ~40%, while in the fragment interior it was only ~3% (Cerón-Martínez; unpublished data).

Do natural enemies influence palm seed germination and seedling survival?

Excluding particular groups of natural enemies significantly increased seedling establishment and performance for both studied palm species. By comparing seedling survival between treatments within the plots from which vertebrates were excluded we can assess the effects of pathogens and insects. Within the *G. interrupta* plots, from which vertebrates were excluded, the proportion of seedlings surviving to the end of the experiment was higher when fungal pathogens were excluded and when fungal pathogens and insects were jointly excluded. Seedling survival in the open control plots was significantly lower than in any of the other treatments. For *R. simplex*, there were no significant differences in seedling survival between control subplots and subplots treated with pesticides. In both species, the proportion of seedlings surviving to the end of the study was significantly higher when vertebrates were excluded.

The significant increase in seedling survival for *G. interrupta* following fungicide application (either on its own or combined with insecticide application) suggests fungal pathogens are important agents of mortality at the early stages of development of this species. This is in accordance with results from other studies where the effect of applying fungicides to early stages of plants increases their survival (Bell *et al.* 2006, Bagchi *et al.* 2014). In *R. simplex*, neither insects nor pathogen appear to play an important role in seedling mortality during the first year of the life cycle. We sprayed pesticides to ~6 months old seedlings of *G. interrupta*, while for *R. simplex* it was applied from the seed stage. The difference in the responses of the two species to pesticide application might be related to the developmental stages at which fungicides were applied. Finally, differences in responses could be due to (still unknown) species-specific traits making them differ in their susceptibility to enemy attack.

Results from our experiment suggest that vertebrates play an important role in establishment and survival of seedlings of the two studied palm species. In *G. interrupta* seedling survival was lower in open control plots and in any of the other treatments. In *R. simplex*, seedling survival was significantly lower in open control plots than in insecticide and insecticide plus fungicide treated plots. In accordance with other studies (Paine & Beck 2007), we did find evidence that small, medium and large mammals were removing seeds and seedlings from the open controls (Cerón-Martínez; pers. obs.). Seeds and seedlings are a valuable source of energy for many ground-dwelling mammalian herbivores. We observed rodents (*Heteromis* sp., *Peromyscus* sp., *Sciurus* sp.), agoutis (*Cuniculus paca*) and peccaries (*Tayassu tajacu*) in the open access plots. Experiments on seed consumption and seed removal, carried out in the same region as our experiment, have found that small palm seeds (such as those from *R. simplex*) are more likely to be removed by small and medium mammals than bigger palm seeds (such as *Attalea cohume*) under similar ground conditions (Mendoza & Dirzo 2007). Despite the defaunation process that the region has experienced for ~4.5 decades, populations of these mammals not only persist within the fragmented landscape but can also have a strong effect on seed and seedling survival.

Although it has been suggested that plants can grow faster when other stresses such as natural enemies are absent, there was no effect of any of the pesticide treatments on the mean number of leaves or mean height of seedlings of *G. interrupta*. Similar results have been reported for other tropical plant species, where application of pesticides had no effect on seedling height (Solé *et al.* 2019).

Does the contribution of natural enemies to seed germination and seedling survival differ between edge and interior?

Our experiment did not detect a significant interaction effect between habitat and treatment. This suggests that the effects of natural enemies on seedling survival do not differ between edge and interior, a consistent outcome for both species. This was in contrast with our predictions: Since pathogens, insects and vertebrates may be expected to respond to the altered environmental conditions close to the edge, we had expected that this would also be seen in the mortality inflicted on seeds and seedlings. Although patterns of enemy attack observed in this study were not related to habitat (i.e. edge versus interior), there is still a possibility that enemies might respond to other aspects of fragmentation. Given that fragment size can be a strong predictor for plant-enemy interactions (Viswanathan *et al.* 2019), designing new experiments incorporating fragment metrics may reveal some new aspects that we were not able to capture. Multiple distances could also be incorporated into studies to gain knowledge about how far from the edge plant-enemy interactions can be affected by edge effects (Krishnadas & Comita 2018, Krishnadas *et al.* 2018).

Our study is one of the first to experimentally assess the effects of natural enemies on seedling survival and performance in a fragmented forest landscape. Given the potential importance of enemy-inflicted seed and seedling mortality, we call for more studies on other species and in other settings to achieve a more general understanding of how plant recruitment is affected by natural enemies in fragmented forest landscapes.

Tables and figures

Table 1. Summary table showing the number of surviving *Geonoma interrupta* seedlings, number of leaves and height after 12 months of enemy exclusion treatments (fungicide, insecticide, fungicide + insecticide, control (water; no vertebrate access) and open control (water)) at plots located close to the edge and in the forest interior (~150 m from the edge) in a forest fragment. The pooled number of seedlings and leaves across treatments per habitat (N= 5 subplot per treatment per habitat) is shown. Mean height in cm ± SE.

Habitat	Treatment	Seedlings 2017	Seedlings 2018	Leaves 2017	Leaves 2018	Height 2017	Height 2018
Edge	Fungicide	50	41	50	114	0	1.43±0.22
	Insecticide	50	34	50	100	0	1.36±0.19
	F+I	50	38	50	111	0	1.32±0.19
	Control	50	30	50	92	0	1.3±0.16
	Open control	50	21	50	63	0	1.37±0.21
	Total	250	164	250	480	0	1.35±0.02
Interior	Fungicide	50	41	50	63	0	0.5±0.002
	Insecticide	50	38	50	63	0	0.5±0.006
	F+I	50	38	50	54	0	0.5±0.007
	Control	50	28	50	42	0	0.49±0.02
	Open control	50	9	50	12	0	0.53±0.03
	Total	250	154	250	234	0	0.5±0.006

Table 2. Parameter estimates from a minimum adequate model of a GLMM testing the survival of *Geonoma interrupta* seedlings under different enemy exclusion treatments. The response variable is the proportion of seedlings alive 12 months after the application of treatments began. F+I = fungicide and insecticide combined. SE=standard error. The column 'Post hoc' provides results from Tukey post hoc test assessing differences between treatments. Treatments sharing letters are not significantly different.

Predictors	Estimate	SE	t-value	p-value	Post hoc
Control (Intercept)	0.358	0.311	1.153	0.249	a
Fungicide	1.314	0.346	3.794	<0.001	b
Insecticide	0.691	0.317	2.178	0.029	ab
F+I	0.920	0.326	2.821	0.005	b
Open control	-1.304	0.316	-4.122	<0.001	c

Table 3. Parameters from a minimum adequate model of a GLMM estimating the effects on seedling performance (number of leaves and height) of *G. interrupta* under different treatments in two fragmented habitats, edge and interior. Responses were measured after 12 months of the beginning of the experiment. F+I = fungicide and insecticide combined. SE=standard error.

Response	Predictors	Estimate	SE	z-value	p-value
Number of leaves	Edge (Intercept)	1.027	0.103	10.01	<0.001
	Interior	-0.648	0.153	-4.24	<0.001
Height	Edge (Intercept)	1.345	0.104	12.95	<0.001
	Interior	-0.840	0.148	-5.69	<0.001

Table 4. Total number of seedlings surviving (from germinated seeds) of *Reinhardtia simplex* in two fragmented forest habitats, edge and interior, after 12 months of treatments (fungicide, insecticide, fungicide + insecticide (F+I), control (water) and open control (water)). % = percentage of surviving seedlings in Jan 2018.

Habitat	Treatment	Jan.17	Jan.18	%
Edge	Fungicide	50	27	54
	Insecticide	50	34	68
	F+I	50	34	68
	Control	50	28	56
	Open control	50	24	48
Interior	Total	250	147	58.8
	Fungicide	50	35	70
	Insecticide	50	34	68
	F+I	50	37	74
	Control	50	33	66
	Open control	50	23	46
	Total	250	162	64.8

Table 5. Parameter estimates from a minimum adequate model of a GLMM estimating the survival (seed germination and seedling survival) of *Reinhardtia simplex* under different treatments in two fragment habitats, edge and interior. The response variable is the proportion of germinated seedlings remaining after 12 months after the application of treatments began. F+I = fungicide and insecticide combined. SE=standard error. Tukey post hoc test among treatments; treatments sharing letters are not significantly different.

Response	Predictors	Estimate	SE	z-value	p-value	Post hoc
Survival of seedlings	Control (Intercept)	0.461	0.236	1.951	0.051	abc
	Fungicide	0.043	0.295	0.148	0.883	ab
	Insecticide	0.315	0.301	1.048	0.295	ac
	F+I	0.460	0.305	1.510	0.131	ac
	Open control	-0.585	0.291	-2.009	0.044	b

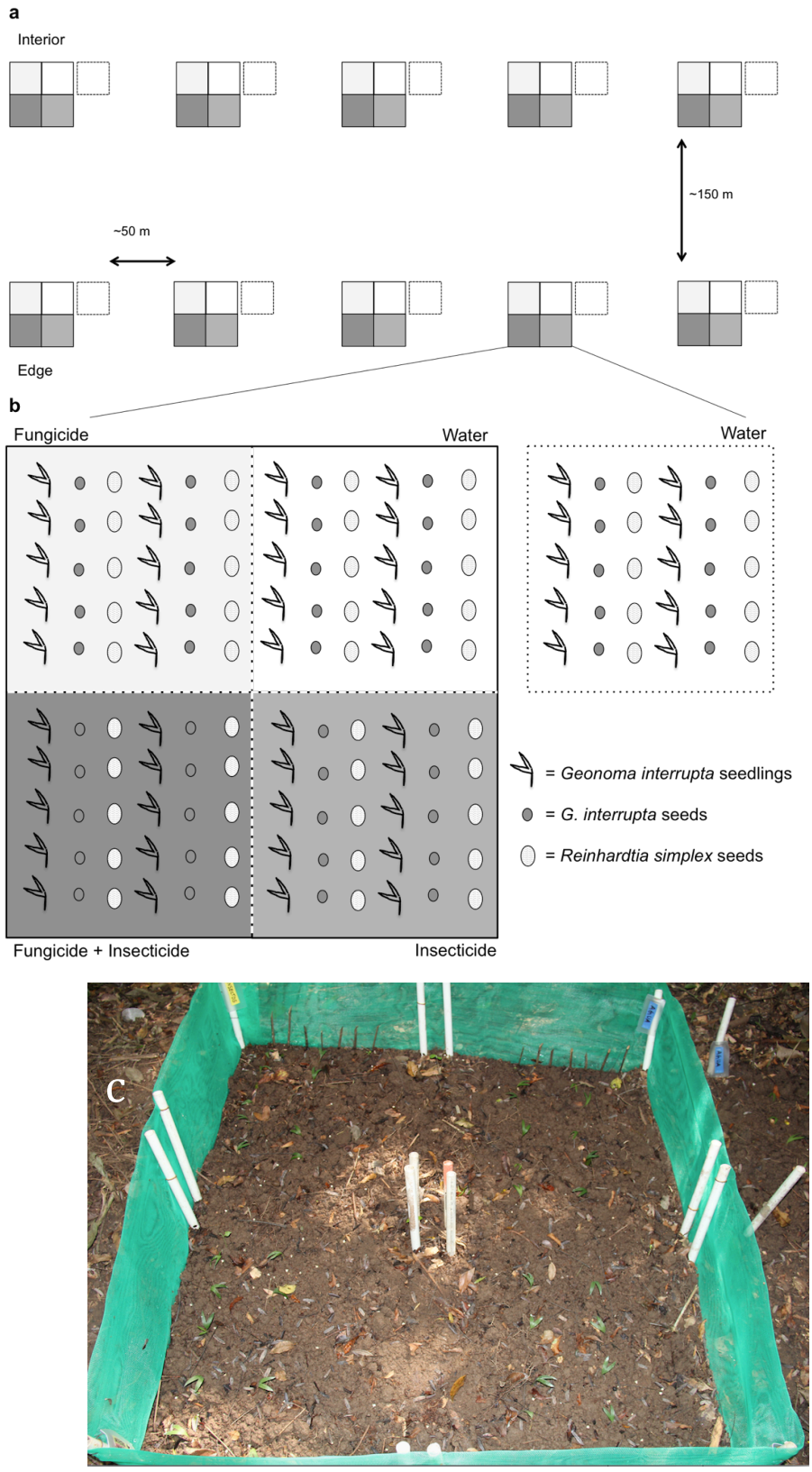


Figure 1. a) Distribution of enemy exclusion plots at the study site. b) Detail of plots and subplots showing the arrangement of seeds and seedlings and the treatments applied to each. The periphery of the 1×1 m plot (solid lines) was excluded with a 1-mm plastic mesh, approx. 30 cm in height and 10 cm into the ground. The open control plot (50×50 cm) position is represented by the dotted square, ~10 cm away from the excluded plot.

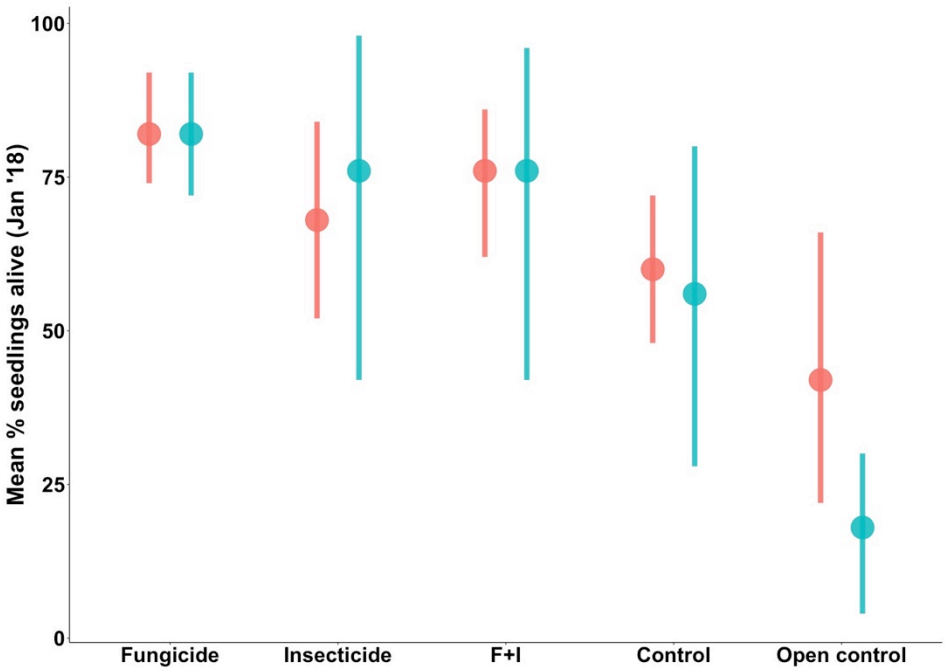


Figure 2. Mean percentage of *Geonoma interrupta* seedlings alive after 12 months of application of five different enemy exclusion treatments in two fragmented forest habitats, edge (red) and interior (blue). Mean values within each enemy exclusion treatment × habitat (n = 5 per treatment × habitat combination) and error bars show the 95 % confidence intervals.

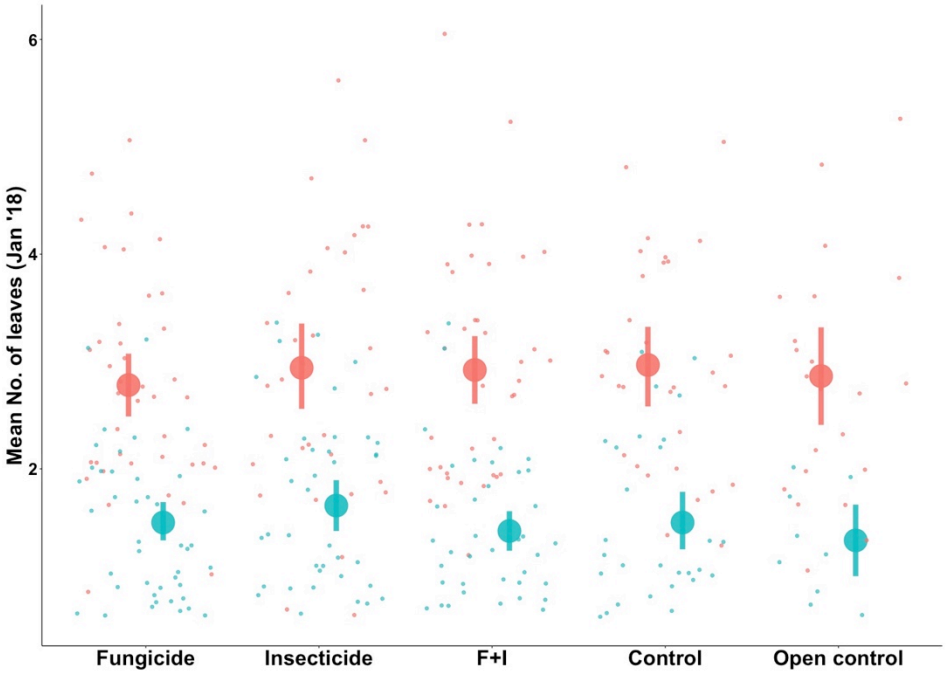


Figure 3. Mean number of leaves per seedling of *G. interrupta* in the two studied habitat types, edge (red) and interior (blue), after 12 months of treatments (2018). F+I = fungicide and insecticide combined. Larger dots represent the mean and lines the 95 % confidence intervals of the mean.

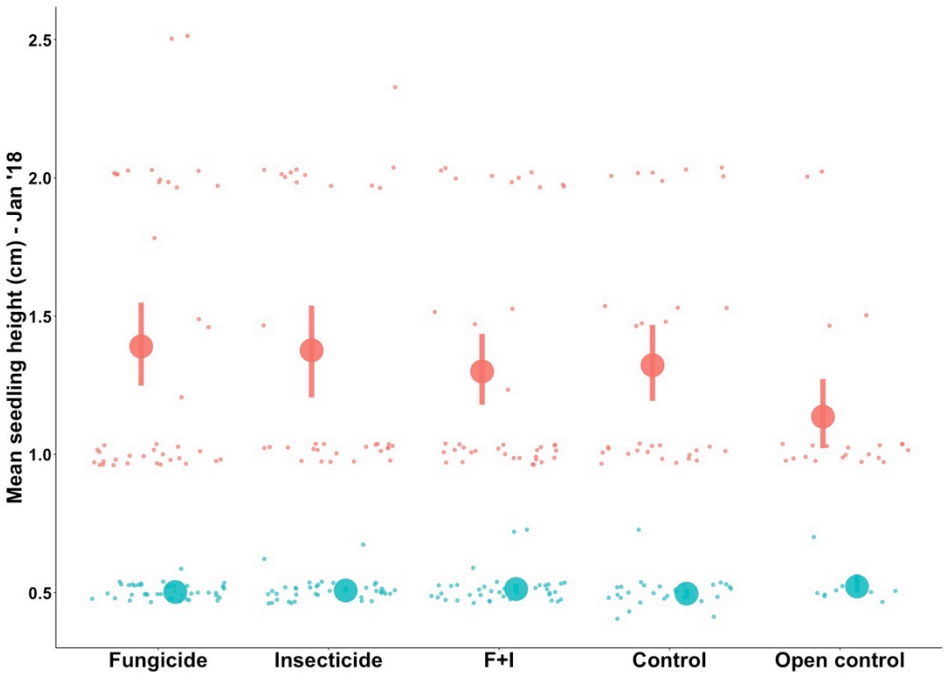


Figure 4. Mean height (cm) of *G. interrupta* seedlings in two fragment habitats, edge (red) and interior (blue), after 12 months of treatments. F+I = fungicide and insecticide combined. Larger dots represent the mean and lines the 95 % confidence intervals of the mean.

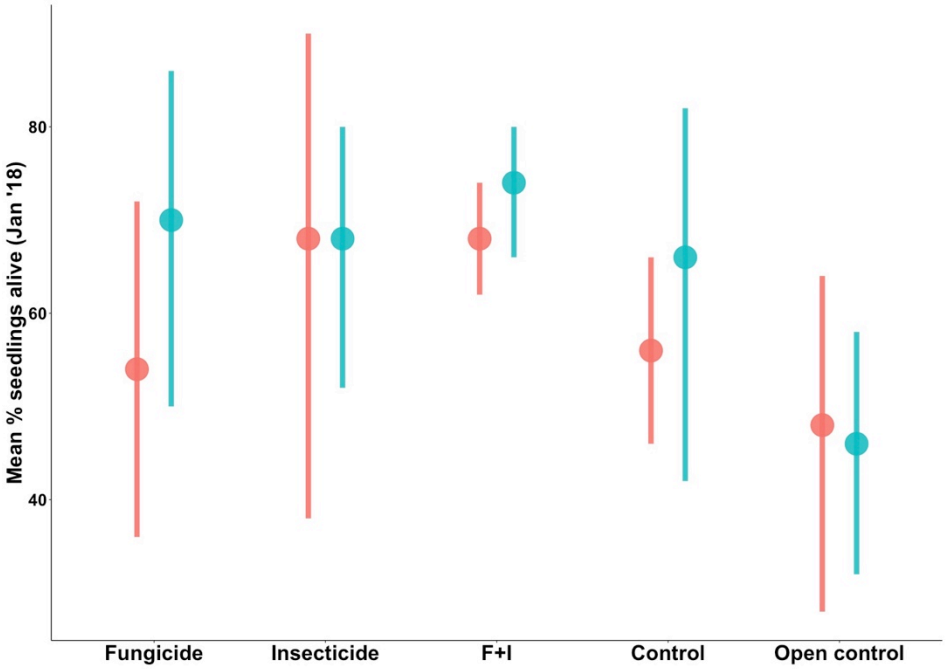


Figure 5. Mean percentage of *Reinhardtia simplex* seedlings alive in two fragmented habitats, edge (red) and interior (blue), after 12 months of enemy exclusion treatments. F+I = fungicide and insecticide combined. Dots represent the mean and lines the 95 % confidence intervals of the mean.

Supplementary information

Table S1. Summary table showing the number of *Geonoma interrupta* seedlings surviving within 12 months of treatments (fungicide, insecticide, fungicide + insecticide, control (water; no vertebrate access) and open control (water)) at plots located close to the edge and in the forest interior (~150 m from the edge) in a forest fragment.

Site	Treatment	Jan.17	Mar.17	May.17	Jul.17	Sep.17	Nov.17	Jan.18	Jan.19
Edge	Fungicide	50	41	41	41	41	41	41	33
	Insecticide	50	44	42	40	38	34	34	28
	F+I	50	45	43	40	39	38	38	30
	Control	50	39	36	34	32	32	30	26
	Open control	50	33	30	29	28	27	21	14
	Total	250	202	192	184	178	172	164	131
Interior	Fungicide	50	46	46	46	45	43	41	25
	Insecticide	50	44	44	42	40	40	38	23
	F+I	50	44	42	42	42	41	38	21
	Control	50	42	42	40	37	38	28	16
	Open control	50	11	10	10	8	9	9	1
	Total	250	187	184	180	172	171	154	86

Chapter 6. General discussion

Introduction

In this thesis I explore how human activities have shaped palm communities of the Lacandona rainforest – a previously continuous forest area that has undergone extensive fragmentation over the past ~40 years. I started by examining patterns in palm abundance and community composition across the landscape (in relation to forest cover and distance to edge) and proceeded with investigating how some interactions between palms and other organisms (pollinators, seed and seedling predators) vary across fragmented and non-fragmented forests. In Chapter 2 I found that local palm abundances were generally higher in a protected and continuous forest reserve than at forest sites in an adjacent fragmented forest landscape. Within the fragmented forest landscape, there were some indications of effects of fragment size and/or degree of human influence: palm abundances were lowest in totally unprotected forest sites than in fragment sites that have more protection from human activities. The abundances of seedlings were consistently lower in the fragmented forest landscape (regardless of site type) than in the continuous forest. There were no clear differences in community composition between any of the studied site types. In Chapter 3 I studied the effects of the forest edge on the distribution, diversity and abundance of palms. Here I compared sites in two forest landscapes differing in their degree of fragmentation (a continuous forest versus a fragmented forest landscape). The change in palm abundances was most pronounced within the first 100 m from the forest edge, and the response was similar in both types of forests. A similar trend was also found for diversity of

palms. In Chapters 4 and 5, I explored the consequences of forest fragmentation on selected ecological interactions between palms and other organisms. In Chapter 4, I focused on the reproduction of *Geonoma interrupta*. I investigated the reproductive success of this species in two different settings, a fragmented forest and a continuous and protected forest. *Geonoma interrupta*'s fruit production was significantly lower in the fragmented forest landscape than in the continuous forest. This might be attributed to differences in the pollinator community, since native bees were the most frequent visitors and active pollen carriers, particularly in the continuous and protected forest sites. In Chapter 5 I carried out a factorial enemy-exclusion experiment to investigate the role of different types of natural enemies in the early stages of the life cycle of palms in different contexts (forest edge versus interior). I found that seedlings protected from natural enemies were more likely to survive than unprotected seedlings, but the effect of enemies did not differ between forest edge and interior. Below, I discuss the key findings of the work and their broader implications.

Key findings

Palm abundances, but not assemblages, differ between a continuous forest and a fragmented forest landscape

The study area provided an opportunity for comparing palm assemblages between two landscapes: a continuous protected forest and a fragmented forest landscape. A relatively consistent pattern arising from the work in this thesis is that the abundance of palms was lower at the study sites in the fragmented landscape (Chapters 2 and 3). This suggests that fragmentation does indeed

influence palm abundances. A speculative explanation for this result is that even if the sampled areas (Chapter 2) were in the heart or centre of forest fragments (beyond 200 m from the forest edge), strong edge effects influencing palm populations may persist (Laurance 1991).

Another explanation for lower palm abundances in the fragmented landscape may be related to differences in the reproductive success of palms (Chapter 4). Reduced fruit production, likely due to a reduction in pollination services, could lead to lower abundances of palms. Other studies (e.g. Beck, 2006; Bruna, 1999; Cerón-Martínez, 2009; Cramer et al., 2007; Wright and Duber, 2001) have reported disrupted seed dispersal and lower seed germination in forest fragments than in continuous sites. Although not assessed in the context of this thesis, such effects, caused by loss of beneficial interactions through 'defaunation' could possibly also contribute to the differences in palm abundances between the continuous and fragmented forest landscapes documented in Chapters 2 and 3.

While palm abundances differed between the two landscape types, I did not detect any significant differences in the diversity and species composition of palm assemblages between the two landscape types. These 'negative' results need to be interpreted in the temporal context of the study. The fragmentation of the Lacandona region started ~45 years ago, and given the relatively long life cycle of palms it is possible that the palm communities currently observed reflect the pre-fragmentation landscape and are not yet in equilibrium with current, modified, landscape structure (Hylander & Ehrlén 2013). In other words, the palm communities might suffer from 'extinction debt' (Kuussaari *et al.* 2009, Hylander & Ehrlén 2013), and compositional changes in palm assemblages

between the two landscape types might be more likely to be detected in the future (Tilman *et al.* 1994).

Palms respond to edges, but the edge zone is relatively restricted in space

I found that abundance and diversity of palms increases towards the forest interior, a pattern that was detected both in the continuous and the fragmented forest landscape. Since the edge type (man-made vs. natural), differed between forest types, palm responses to forest edges appear not to be strongly driven by the exact nature of the edge. Other studies have found that, depending on the measured variable (e.g. temperature or humidity), edge effects can reach up to 500 m from the forest edge towards the interior, but the most evident changes are found within 200 m from edges (Laurance 1991). I found that responses of palms to edge effects are limited to the first 100 m (Chapter3). Notably, adult palms responded more strongly to edge habitats than seedlings and juveniles. These patterns reflect those from a study by Baez and Balslev (2007), who studied changes in palm abundances and diversity along 100-m transects from the edge towards the forest interior. I found that juveniles did not respond strongly to edges, with the abundances and diversity of juveniles being relatively constant across the full length of the 500-m transects. This contrasts with the findings of Browne & Karubian (2016), who reported stronger responses of juvenile than of adult palms to fragment edges. Nevertheless, a methodological flaw of the study by Brown and Karubian is that the fragments used were so small that points along transects could have been under the influence of edges from several directions. Putting this problem aside, the difference in results between my study and the one by Browne and Karubian suggests that responses

of palms to fragmentation may vary depending on, for example, geographical location (Eiserhardt *et al.* 2011) and species present (Campbell *et al.* 2017). Additional explanations as to why adults may be more sensitive to edge effects than other stages, such as juveniles and seedlings, might be related to environmental conditions. High winds, water stress and increased solar radiation at edges stresses and kills adult palms, trees and old-growth plant species (Dirzo *et al.* 1992, Camargo & Kapos 1995, Ezcurra 2016).

Fragmentation significantly reduced the number of fruits and increased abortion of fruits of *Geonoma interrupta*

Fragmentation has the potential to alter plant populations and communities through changes in the interactions between plants and other organisms, such as those between palms and their pollinators. Indeed, in chapter 4, I found that even if flower production in *Geonoma interrupta* was very similar in fragmented and continuous forest, the number of fruits produced was significantly lower on individuals in the fragmented landscape than in the continuous forest, and a higher proportion of fruits were prematurely abscised. I speculate that this is due to a decrease in pollination services following fragmentation, even if pollen limitation is common in plant populations (Burd 1994) fragmentation could intensify its effects (Ghazoul 2005). Palms can offer different types of rewards to flower visitors, including nutritional rewards (such pollen grains and nectar) but also sites for oviposition and/or shelter (Uhl & Moore 1977). If palm abundances decrease (Chapter 2 and Chapter 3), then these resources and rewards will also decrease, and this could have consequences for the flower visitor communities. Indeed, I found a lower diversity of flower visitors, especially of native bees, in

the fragmented forest landscape than in the continuous forest, indicative of a defaunation process in the flower visitor community.

Even if fragmentation significantly affects the reproduction of palms, this alone might not be enough to put a species at risk. There are other processes that combined can be highly detrimental to the long-term persistence or survival of a species. For example, fragmentation-driven defaunation can reduce seed size (Galetti *et al.* 2013) and promote rapid changes in allelic frequencies in the palm *Euterpe edulis* (Carvalho *et al.* 2016). If similar processes were to occur in *G. interrupta* in the Lacandona rainforest, then the added effects of lower fruit production and higher abortion of fruits (Chapter 5) could definitively pose a serious threat to the long-term persistence of this palm species in the fragmented forest landscape.

Natural enemies are important agents of mortality in the early life cycle of palms

To further explore the ramifications of factors influencing the survival of palms, I followed the fate of seeds and seedlings of two palm species in the presence or absence of selected guilds of natural enemies (Chapter 5). I found that exposure to natural enemies diminishes a large proportion of seeds and seedlings within the first year of their life. The experiments revealed that ground-dwelling vertebrates were responsible for almost all of the removal of seeds and seedlings (Cerón-Martínez, per. obs.). I also learned that when vertebrates are excluded, fungi and insects can be important agents of seedling mortality, as seen in the high survival of seedlings under the exclusion of fungi and insects.

Natural enemies of palms are not immune to fragmentation, and I predicted that the effect of enemies on the survival of palm seeds and seedlings would differ between the forest edge and interior. However, although camera-trapping revealed higher abundances of vertebrates in the interior of fragments than close to the edge (Cerón-Martínez, unpublished data; Photo 1), there was no indication of differences between forest edge and interior in terms of enemy-inflicted mortality. Although I did not compare enemy pressure between continuous and fragmented forests, it is plausible to expect that differences in enemy pressure might exist between the two landscapes. As the continuous and protected forest harbours a more intact community of vertebrates than the fragmented landscape (Cerón-Martínez 2009), a higher vertebrate-inflicted mortality is expected (although some vertebrates might also be important seed dispersers, hence increasing seed survival). In the case of invertebrates, the fact that I found a poorer community of insects visiting flowers of palms in the fragmented sites (Chapter 4) indicates that the invertebrate community may be affected by fragmentation, and that insect-inflicted seed and seedling mortality could differ between the two landscape types. This is a hypothesis that needs to be tested in future studies, given that insects and pathogenic fungi also respond to edge effects (Crockatt 2012, Ezequiel *et al.* 2016). Overall, the relatively high proportion of seeds and seedlings removed or killed by natural enemies indicates that these enemies should not be ignored in studies of palms or other plant taxa (Krishnadas *et al.* 2018).

Conservation implications

The research theme of this thesis is both important and timely. Forest fragmentation, defaunation and deforestation are major threats to biodiversity (Dirzo & Miranda 1990, Broadbent *et al.* 2008, Dirzo *et al.* 2014), and projections are that an ever-increasing proportion of tropical forests will occur as fragments in human-modified landscapes (Lewis *et al.* 2015). Understanding how different taxa respond to fragmentation is therefore a key priority. Although the conservation implications of the work might not be immediate, documenting changes in palm community composition triggered by human activities and investigating their likely causes are necessary first steps for assessing conservation needs and for developing appropriate strategies for conserving biodiversity in the longer term. By working with the local communities in the Lacandona rainforest area, my thesis work also gave me the opportunity to contribute to increasing the awareness of conservation-related issues in the area.

I found that palm assemblages in the fragmented landscape are as diverse as those found in continuous and protected forest, suggesting that the fragmented landscape can harbour species-rich palm assemblages – at least in the short and/or medium term. As discussed above, the longer-term consequences of fragmentation might not be immediately obvious and delayed changes in the palm communities might still occur in the fragmented landscape. Moreover, the presence of endangered palm species in forest fragments under strong human influence supports the idea that fragments have an intrinsic conservation value. This is encouraging, considering that fragments are sometimes the only way to maintain and preserve biodiversity (Arroyo-

Rodríguez *et al.* 2009). Finally, the information presented in this thesis also highlights the importance of local communities managing their remnants of forest.

Intact forests or a myth of modern times?

The inclusion of a continuous and protected forest has given me a baseline to contrast and to understand the relative impact of the anthropogenic effects on palm communities. Nonetheless, the idea of a pristine or intact forest can be more complex. In a recent conference (Intact Forests in the 21st Century Conference, Magdalen College, Oxford, 18 - 20 June 2018), the working definition of "intact forest" was "forest free of significant anthropogenic degradation", where anthropogenic degradation includes all human activities known to cause physical changes in a forest (including faunal changes) that lead to declines of ecological function.

Historically, tropical forests have been considered as pristine reservoirs of an immeasurable biodiversity. However, often this notion seems to ignore that present old-growth tropical forests have been altered by past civilizations (Denevan 1992). Recent discoveries from the Mayan region in Guatemala revealed the impact that past human civilizations had on the rainforest. Remaining habitat structures hidden under the dense forested areas showed that an estimated population between 7 and 11 million humans inhabited an area of 95000 km^2 (Canuto *et al.* 2018). There are also estimates that Mayans cultivated as much as 95% of the available landscape (Canuto *et al.* 2018). There is also similar evidence from the Amazonas (McKey *et al.* 2010). Past human landscape modifications helped to shape the tropical forest we observe today. Our modern

perception about how “intact” and “pristine” those forests really are might be just a myth (Denevan 1992).

Directions for future research

Studying processes that operate at large spatial scales, such as the effects of landscape-level fragmentation, poses challenges to ecologists and conservation biologists in terms of study design. I am aware of the shortcomings of some of my study designs; this is, comparing sites in only two landscapes (one continuous landscape and one fragmented landscape). In particular, it is rarely feasible to include true replication (Ryan 2011) of continuous forest reference sites. In my studies, I attempted to minimise issues of pseudoreplication by spreading my study sites widely and by blocking or interspersing (as far as possible) the location of sites in different forest-type categories. Finding several big, accessible areas of relatively undisturbed forests is increasingly challenging since those areas are rapidly disappearing, and obtaining permits from local land owners for work is not always straightforward and might take longer than expected. Nevertheless, increased replication (and perhaps redefining what constitutes a “continuous forest”, given the contextual reality of the region under study) is something to strive for in future work.

Further research is needed to identify the underlying mechanisms that generate the non-consistent responses to fragmentation by the different age classes of palms (adults and juveniles vs. seedlings) documented in this thesis. In the enemy-exclusion experiment, habitat (interior vs. edge) did not show an effect on the survival of seedlings in the presence or absence of enemies. In order to corroborate this finding, future research should include additional fragments,

different distances from the edge, and consider the addition of a continuous forest. Another aspect to consider in this type of experiment is adding a density treatment. Since natural enemies often respond to the densities of their hosts (e.g. Bagchi et al., 2014; Solé et al., 2019) different results may arise depending on the density of seedlings.

Further work is needed to disentangle the complex ecological interactions between palms and other species, both mutualistic and antagonistic. A detailed study on the relationship of the abundance of flower visitors, effective pollinators and pollen dispersal range among habitats may aid us in achieving this ambitious goal. For example, reduced fruit production as a result of fragmentation highlights concerns about the potential functionally important changes happening to the community of pollinating insects. On the other hand, assessing fitness consequences by germinating seeds produced from outcrossing and inbreeding experiments is also imperative. Additional data on pollinators and how their abundance and diversity varies throughout the fragmented landscape are urgently needed, as part of on-going, wider efforts to understand the consequences of habitat fragmentation and degradation for ecological communities in the tropics and more widely.

Conclusion

My thesis has taken some steps forward in understanding how tropical forest fragmentation can affect populations, communities and interactions for an important plant family in tropical forests, the palms. For example, I have revealed heterogeneity in the way that different species respond to fragmentation, and highlighted critical habitat zones for future protection.

Encouragingly, I found some indications that the efforts of local communities to protect forests might be effective to maintain palm communities. Unpicking how ecological interactions are affected by fragmentation, and the functional consequences of these changes for populations and communities, has proved more challenging. My work indicates that the effects of fragmentation on palm species abundance, diversity and distribution cannot be based exclusively on assessing abiotic factors and presence/absence data without including biotic interactions, such as pollination and natural enemies.



Photo 1. Cottontail rabbit, *Sylvilagus brasiliensis*, feeding on seedlings of *Bactris mexicana* and *Geonoma interrupta* at the border of a fragment. Upper photo shows the rabbit chewing on a seedling (bigger circle). Small circles in both photos highlight the position of the seedlings, removed in the lower photo.

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