Dynamics of the Tropical Tree

Poulsenia armata in the Fragmented Forest of Los Tuxtlas

BY

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B.S. Universidad de los Andes, Colombia, 2006

THESIS

Submitted as partial fulfillment of the requirements

for the degree of Doctor of Philosophy in Biological Sciences

in the Graduate College of the

University of Illinois at Chicago, 2014

Chicago, Illinois

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ACKNOWLEDGMENTS

I would like to thank my advisor Hank Howe for giving me the opportunity to pursue a graduate degree and for his guidance throughout the process. I am very grateful to the members of my dissertation committee, Mary Ashley, Miquel Gonzalez-Meler, Catherine Pfister and Corine Vriesendorp for their assistance and suggestions throughout all the stages of the work.

My colleagues in the Howe lab, Pia Sethi, Luca Borghesio, Carrie Seltzer, Crystal Guzman, Kesha Braunskill, Erika Arnold, Marines de la Peña-Domene, Yi-An Xiao and Helena Puche. David Zaya and Mike Jorgensen also provided much help and useful comments of the chapters. I thank Hormoz BassiriRad for his suggestions on Chapter 2 and Chris Whelan for his assistance and comments on Chapter 3. I am indebted to Roberto Salguero-Gomez for his invaluable help in developing the population models and his collaboration in Chapter 5.

For the work in Los Tuxtlas, Mexico, I am indebted to Rosy Coates for not only her support and help while conducting my field work, but also for her comments and suggestions on the chapters. I thank Santos, Domingo Velazquez, Erly Velazquez and Jorge Velazquez from the Balzapote and Laguna Escondida communities, Sonia Shweiki and Omar Becerra for their help during the fieldwork. I would also like to thank the staff of the “Los Tuxtlas” Biological Station for their assistance. I thank Cristina Martinez for her help throughout the work. Funding came from the Rufford Foundation, Idea Wild, Sigma Xi Scientific Society and NSF (DEB 0516259 to Henry Howe). I thank the
University of Illinois for supporting me with a Hadley Award (2011) and a Provost Award (2012) that were crucial for the development of my field work.

Finally, I thank my family and friends for their help and encouragement throughout my work. Especially, I would like to thank my parents, sister and my husband for their invaluable support.
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1. INTRODUCTION

Lowland tropical forests are of special concern for they are the most diverse and the most ecologically complex of all terrestrial ecosystems (Myers 1984), and their destruction would significantly reduce global biological diversity (Turner & Corlett 1996). Forests around the globe are experiencing unprecedented rates of deforestation as a result of burgeoning human populations, with tropical countries having the highest human population growth rates (Laurance 1999). By 1990, almost 24% of the worldwide lowland tropical rainforest was lost, with considerable variation among regions at the level of disturbance (Turner & Corlett 1996). Areas experiencing a dramatic loss of forest cover include the African forests of Madagascar (Smith 1997), Nigeria and the Ivory Coast (Boahene 1998), which possess the highest rates of deforestation. The Asian forests of New Guinea still retain large tracts of original forest but are experiencing rapid conversion due to an intensification of human land use (Myers 1994). In the Neotropics, rapid forest deforestation occurs mainly in Central America, the Caribbean and the southeastern Amazon forest (Laurance 1999).

Habitat loss inevitably leads to forest fragmentation (Laurance & Bierregaard 1997), resulting in the reduction of a continuous forest into several small isolated remnant patches (Fahrig 2003). Island biogeography theory (MacArthur & Wilson 1967) predicts that smaller and more isolated habitats will experience reduced species richness and abundance. Additionally, habitat fragmentation leads to the creation of edges between the forest and a surrounding matrix composed mainly of human-made vegetation (e.g. pastures and agricultural fields) (Fahrig 2003). Reduced humidity, elevated temperatures, low relative humidity, low soil moisture, increased wind turbulence and increased luminosity have been described as potential microclimatic
conditions affecting fragmented plant populations (Kapos 1989, Laurance 1991). However, vulnerability of the remaining plant species to forest fragmentation depends on several factors that range from differences in plant life history to modification of plant-animal interactions.

Forest fragmentation may affect plant populations through the modification of plant-animal interaction such as pollination and seed dispersal. Several studies have documented reduced fruit production (Alvarez-Buylla _et al._ 1996) and decreased genetic diversity (Young _et al._ 1996, Aguilar _et al._ 2006, Kramer _et al._ 2008) in forest fragments, due to reduced pollination (Aizen & Feinsinger 1994, Aguirre _et al._ 2011) or changes in abiotic conditions. Additionally, many tropical frugivores are at risk of becoming locally extinct due to habitat loss and fragmentation (Peres 2001, Wright & Duber 2001). Decreased abundance of frugivore species may reduce seed dispersal in forest fragments, leading to a magnification of the negative results of limited dispersal (e.g. density dependence mortality) and reducing seedling recruitment (Santos & Tellería 1994, Cordeiro & Howe 2001, 2003). But not all plant and animal species are negatively affected by forest fragmentation.

Forest fragmentation could have positive effects for certain species. Many studies have documented changes in patterns of regeneration of forest fragments with increased colonization of weedy species (Janzen 1983), such as lianas and vines (Laurance 1991, Laurance & Bierregaard 1997, Laurance _et al._ 1997) and early-successional tree species, as altered microclimatic conditions favor germination and recruitment of these plant species (Laurance _et al._ 1998b). Moreover, as human impact progresses, small mammals may remain unaffected or even increase in abundance due to an ecological release in the absence of top competitors (Terborgh _et al._ 2001, Wright 2003, Dirzo _et al._ 2007). This in turn, could lead to an increase in seed removal rates for small-seeded plants, due to a competitive release of the unpreferred game
species, while seed removal rates for larger-seeded species may decline (Beckman & Muller-Landau 2007, Dirzo et al. 2007, Melo et al. 2010). As a result, forests will tend to have an over-representation of large-seeded plants while populations of small-seeded plants will decline as human activities intensify.

In this context, I documented the dynamics of a late-succesional tropical tree, *Poulsenia armata* (Moraceae), in the severely fragmented forest of Los Tuxtlas, Veracruz, Mexico. This is an area of great relevance as it represents the northern most limit of tropical rainforest in the New World and is a highly diverse hotspot combining elements of tropical and temperate origins (Dirzo & Miranda 1990b). While many studies have documented the effects of forest fragmentation on the fauna of Los Tuxtlas (Estrada & Coates-Estrada 1988, Dirzo & Miranda 1990b, Estrada et al. 1993a, Estrada et al. 1994, Estrada & Coates-Estrada 1996, Estrada et al. 1997, Estrada & Coates-Estrada 2002, Cristobal-Azkarate & Arroyo-Rodriguez 2007, Dirzo et al. 2007, Arroyo-Rodriguez et al. 2008, Aguirre et al. 2011), far fewer studies have addressed the implications on the flora (Arroyo-Rodriguez & Mandujano 2006b, Arroyo-Rodriguez et al. 2007, Arroyo-Rodriguez et al. 2009). I examined the impact of forest fragmentation on the dynamics of *P. armata* by comparing reproductive success and subsequent offspring performance (Chapter 2) in a continuous forest and forest fragments at Los Tuxtlas. I considered whether trees in fragmented forest traded quality for quantity (lower mass and higher C-to-N-ratios than continuous forest counterparts), resulting in lower germination success and offspring fitness. I also observed seedling and juvenile recruitment patterns (Chapter 3) and examined seed predation and fruit removal (Chapter 4) of *P. armata* in a continuous forest and forest fragments. Reduced juvenile recruitment may affect the regeneration of *P. armata*, jeopardizing persistence of fragmented populations of this widespread rainforest tree. Moreover, differences in seed
predation and fruit removal likely reflect differences in mammal communities in forest fragments. Finally, to test if forest fragmentation resulted in declines in populations, I compared population growth rates of *P. armata* in the continuous and fragmented forests with the use on Integral Population Models (Chapter 5). Results of this study will significantly contribute to the knowledge of the effects of forest fragmentation on plants populations at Los Tuxtlas forest.
2. EFFECTS OF FOREST FRAGMENTATION ON THE RECRUITMENT SUCCESS OF THE TROPICAL TREE POLLENIA ARMATA AT LOS TUXTLAS, VERACRUZ, MEXICO

2.1 Introduction

Seedlings must recruit and make the transition to older life stages for plant populations to persist. The ability of plants to successfully recruit is limited by a wide range of biotic and abiotic factors (Kitajima & Fenner 2000), including fruit production and seed dispersal (Nathan & Muller-Landau 2000, Russo et al. 2006, Schupp et al. 2002, Turnbull et al. 2000). Cohorts of seedlings under reproductive trees are likely to experience strong distance- or density-dependent mortality as a result of increased intraspecific competition and/or pathogen and insect attacks (Alvarez-Loayza & Terborgh 2011, Connell 1971, Harms et al. 2000, Janzen 1970, Terborgh 2012). Seed dispersal away from fruiting trees is expected to improve the chances for seedling establishment and transition to later life stages (Howe & Smallwood 1982). As seed and seedling densities decrease with distance from fruiting trees, probability of survival is expected to increase, leading to greater recruitment at distances from the adult trees that vary with species and presence or absence of pathogens, as well as insects that kill seeds or seedlings. However, the distribution of new recruits may also be influenced by microclimatic conditions. Local depletion of critical nutrients, light and water availability, and increased temperature can severely impact seedling recruitment (Clark & Clark 1989). With fragmentation of tropical forests occurring throughout the world, it is useful to distinguish expected density-dependent effects of biotic interactions from mortality by abiotic causes.
Current knowledge suggests poor regeneration of animal-dispersed trees in fragmented forests due to limited seed dispersal (Cordeiro & Howe 2001). Loss of primary seed dispersers is potentially catastrophic for tree populations, as lack of dispersal leads to higher seed mortality, which then reduces seedling establishment and survival of seedlings that do establish (Muller-Landau 2007, Wright 2003). Additionally, fragmented forests often experience altered microclimatic conditions such as elevated temperatures, reduced humidity, greater ambient light and increase evapotranspiration, often resulting in the loss of soil moisture (Kapos 1989, Malcolm 1998). Drought-sensitive plant species may experience reduced seedling survival and growth in forest fragments as a result of physiological stress imposed by altered microclimatic conditions (Bruna 2002). Many plant species may be missing from forest fragments as a result of unfavourable abiotic challenges to the recruitment process.

We report regeneration patterns of *Poulsenia armata* (Moraceae), a widespread animal-dispersed old-growth canopy tree, in a continuous forest and forest fragments in the lowland rain forest of Los Tuxtlas in southern Veracruz, Mexico. The Los Tuxtlas region is heavily fragmented by forest conversion to pastures, plantations and crops (Mendoza et al. 2005). Declines or local extinctions in Los Tuxtlas forest fragments are well known for the howler monkey (*Alouatta palliata mexicana* Merriam, 1902), quite likely the primary seed disperser of *P. armata* in continuous forests of the Los Tuxtlas region (Estrada & Coates-Estrada 1984). Consistent with evidence elsewhere in the tropics (Benitez-Malvido 1998, Bruna 2002, 2003; Cordeiro & Howe 2001), we predicted that regeneration of *P. armata* is negatively affected in forest fragments. We used densities of *P. armata* close to adult trees to test for poor regeneration in forest fragments due to strong density-dependent mortality. Additionally we predicted low seedling and juvenile survival and growth as a result of strong density-dependent effects. We
included seedlings as well as juveniles as density dependence may also affect later life-stages. We hypothesized: (1) denser aggregations of seedlings near fruiting *P. armata* trees in forest fragments when compared to the continuous forest, (2) low densities in forest fragments due to greater seedling mortality, and (3) strong negative density-dependent effects on seedling survival and growth. Alternatively, we tested for evidence that seedling survivorship and growth might be the result of higher daily temperatures due to forest fragmentation.

2.2 Methods

2.2.1 Study area

The Los Tuxtlas region represents the northernmost limit of Neotropical rain forest (18°30′N, 95°04′W) (Guevara *et al.* 2004). Study sites were in lowland forest in a rugged landscape of volcanic origin, within the 118 km² of forest remaining (García-Aguirre *et al.* 2010). The Los Tuxtlas forest experiences a dry season from March to June and a wet season from July to February (Bongers *et al.* 1988). The continuous forest of this study encompasses the 640-ha property of the Los Tuxtlas Biological Field Station created in 1967 by the Universidad Nacional Autonoma de Mexico; this reserve is embedded in 35,000 ha of rain forest that forms part of the Los Tuxtlas Biosphere Reserve (Mendoza *et al.* 2005). Four forest fragments near the Los Tuxtlas Biological Station were selected for this study based on the presence of reproductive trees of *P. armata* (Fig. 2.1). Forest fragment sites included here are Rancho Eugenia (19.4 ha), Playa Escondida (40 ha), Balzapote (34.6 ha) and Ruiz Cortinez (~20 ha). All forest fragments have been isolated for 30-40 y (Mendoza *et al.* 2005). As part of a demographic study of *P.*
armata, four 1-ha permanent vegetation plots were established within the continuous forest and four 1-ha plots in the selected fragments (Figure 2.1).

![Figure 2.1: The northern area of Los Tuxtlas Biosphere Reserve. Rectangles represent the area of study inside the Biological Field Station “Los Tuxtlas”. Forest fragments included in this study are denoted by F1, F2, F3 and F4. Image was provided by Alejandro Estrada and modified by J. Zambrano.](image)

2.2.2 Study species

*Poulsenia armata* (Moraceae) is a monoecious, shade-tolerant late-successional canopy tree (Croat 1978). This is an old-growth and moderately common species of moist and wet lowland tropical forests from Mexico to Bolivia (Aide & Rivera 1998, Brewer *et al.* 2003, de la Quintana 2005, Dick *et al.* 2013, Smith & Killeen 1998). Despite low wood density (Chave *et al.*
2006, 0.35 g cm$^{-3}$), growth is slow to a maximum stature of 20-40 m (Martínez-Garza et al. 2005). Seedlings and later life-stages of $P. \text{armata}$ are drought-sensitive (Martínez-Garza et al. 2013a, b). Individuals produce separate male and female inflorescences; likely pollinators are thrips (Thysanoptera; Sakai 2001). Bimodal fruit production occurs April-May and October-November. Medium-sized fleshy fruits (average width ~ 40 mm) hold 2-17 seeds with a thin, smooth coating. Seeds are 7-9 mm long and 5-8 mm wide, and weigh 0.146 ± 0.017 g. Seeds germinate in less than 30 d (Rodriguez et al. 2000).

The brownish $P. \text{armata}$ fruit of moderate size appeals to a variety of mammals throughout its vast range. In large forest tracts of the Los Tuxtlas region, a particularly important seed dispersal agent for $P. \text{armata}$ is the mantled howler monkey ($Alouatta \text{palliata mexicana}$) (Estrada & Coates-Estrada 1984). Fruits are also consumed by fruit bats ($Artibeus \text{jamaicensis, A. lituratus}$) at this site. Seeds deposited in caves have dim prospects for survival (Vazquez-Yanes et al. 1975), but some are likely to be effectively dispersed. An additional study at Los Tuxtlas reports $P. \text{armata}$ seeds recovered from captured brown jay ($Psilorhinus \text{morio}$) and ground dove ($Leptotilia \text{plumbeiceps}$), suggesting that fruit-eating birds are at least potential dispersal agents (Trejo-Pérez et al. 1976). Seed predators include small rodents ($Heteromys \text{desmarestianus;}$ Dirzo et al. 2007, Martínez-Gallardo & Sanchez-Cordero 1993) and likely larger rodents (e.g. $Dasypodita \text{mexicana, Cuniculus pac}$).

### 2.2.3 Data collection

To assess recruitment of $P. \text{armata}$ in the continuous and fragmented forests, we established a 40º wedge-transect extending 30 m from the base of 22 fruiting trees. In 2010, we
randomly sampled 11 adult individuals in the continuous forest and another 11 adults in forest fragments inside the vegetation plots. Wedge transects estimate recruitment as a consequence of dispersal away from fruiting trees. Initial direction of each transect was chosen randomly; to avoid confounded transects from different fruiting trees, transects were discarded and replaced if they approached another reproductive tree within 40 m. Study trees were located inside the forest fragments at least 100 m from the forest edge. We counted all the individuals of *P. armata* and classified these into seedlings with cotyledons and juveniles <150 cm in height. Seedlings were from the 2009 fruiting period. We measured, tagged, and calculated the distance to conspecific adults for all individual seedlings and juveniles encountered along transects. For data analysis, we corrected by area the number of individuals, as area increased with distance from adults, and converted these to estimates of density (ind. m\(^{-2}\)) of *P. armata*. To evaluate survival in the 2011 and 2012 censuses, we recorded the number of surviving seedlings and juveniles previously tagged in 2010. We identified causes of mortality as either tree fall, herbivory (insects or vertebrates), pathogen infestation, trampling or desiccation. Herbivory occurred mostly in seedlings that had not fully developed spines on the leaves.

To compare vertical plant growth between the continuous and forest fragments, height increment was calculated for each individual plant from 2010 to 2012. Height increment (cm) was estimated as:

\[
(\ln H_{t2} - \ln H_{t1})/ (t_2 - t_1)
\]

Where \(H_{t2}\) = height recorded at \(t_2\), \(H_{t1}\) = height recorded at \(t_1\), and \(t_2 - t_1\) = time elapsed between measurement (1 y). Additionally, we recorded adult tree diameter at breast height (dbh) and
canopy size. Estimates of canopy size were measured for each reproductive adult using a crown radius. Crown area was calculated as an ellipse and determined by:

\[ 0.25 \pi D_1 D_2 \]

Where \( D_1 \) and \( D_2 \) are two perpendicular cross-section diameters of the crown (Bongers et al. 1988). Fruit production was recorded from 2010 to 2012. We quantified fruit production by directly counting fruits on five randomly selected branches, estimating the average number per branch and multiplying by the total number of comparable branches on the tree.

HOBO data loggers (HOBO UA-002-08) were used to record daily temperature (°C) from May to July of 2010 to 2012. The temperature sensor has a range from -20°C to 70°C with an accuracy of ± 0.53°C from 0° to 50°C. Loggers were attached at the height of standard dbh on the trunks of selected \( P. \) armata trees. Hourly measurements over the span of each day were averaged to compute daily means as well as daily maximum and minimum temperatures. Using temperature data during the dry period, when plants will be water stressed, may indicate a stronger correlation with plant survival and growth.

2.2.4 Statistical analyses

We conducted all the analyses using the R environment (version 2.15.1, 2012). A common feature of ecological data is the tendency to contain many zero values (Martin et al. 2005), which was the case of this study. An alternative to analyze this type of data is to separately model the occurrence of a zero values and the positive values (Fletcher et al. 2005). Therefore, to analyze factors affecting density and distribution of \( P. \) armata with respect to
distance from adult trees we used two complementary models one including presence/absence data and the other one describing density data. We created two datasets: one indicating whether P. armata was present or not within vegetation transects (presence data), the other showing density data when P. armata was present (density data). Density data were logarithmically transformed and distance data were binned (e.g. 0-1 m, 1-2 m, etc.). We constructed two models; a generalized linear mixed model (GLMM), with a binomial distribution, to describe factors affecting the presence and absence of P. armata in the transects, and a linear model to describe density data. Results of both models were used to make inferences regarding which factors best explain the distribution and density of P. armata in forest fragments. In both models, we defined fixed factors as habitat type (continuous forest or forest fragments), life stage (seedlings or juveniles), distance to parental adults as a continuous variable, and reproductive trees (n = 22) as a random effect nested within plot (n = 8). We used the Akaike’s Information Criterion (AIC) for model selection. We then calculated the best-fit curves to represent the relationships between distance to adult trees and seedling and juvenile densities in both habitats to determine if dispersal limitation resulted in dense aggregation of seedlings under reproductive adults.

Differences in fruit production, tree and crop size were determined using Student’s t-tests. Furthermore, we applied an ANOVA to test for differences on mean daily temperature and the absolute range (differences between daily maximum and minimum temperatures) between habitat type and census year.

To determine potential relationships between density and distance from adult trees and recruitment success, we used a linear mixed model for plant growth and a generalized linear mixed model (GLMM) for plant survival. We included habitat type (continuous forest or forest fragments), life stage (seedlings or juveniles), mean daily temperature and census year (2011,
2012) as fixed effects. Reproductive tree (n = 22) was nested within plot (n = 8) and included as random effect. The GLMM assumed a binomial data structure (individuals either survive or die) and included a logit link function. Since density and distance from adult trees were highly correlated, we ran the models separately to avoid density and distance continuous variables. We used F-tests for linear mixed models and Wald Z-test for GLMMs to determine the significance of fixed effects. Each random effect was tested by comparing nested models with- and without the random effect using a $\chi^2$ test. Best models fitting plant survival and growth data were selected using the AIC values to compare models including all fixed and random effects against more simplified models.

2.3 Results

2.3.1 Fruit production and adult tree size

Trees in the continuous forest and forest fragments differed in crop and tree sizes. Fruit crop sizes of reproductive trees (mean ± SD) differed significantly between habitats ($t = 2.70$, $P < 0.001$), with greater fruit production in the continuous forest (123 ± 14.9 fruits) than in forest fragments (78.1 ± 12.7 fruits). Habitat type also differed in tree size ($t = 2.04$, $P = 0.04$) and crown size ($t = 12.1$, $P < 0.01$), with trees from the continuous forest larger in size (39.6 ± 7.76 cm dbh) than trees in forest fragments (29.5 ± 8.02 cm dbh). Similarly trees from the continuous forest had a larger crown area (225 ± 70.0 m²), than trees from forest fragments (128 ± 46.0 m²).
2.3.2 Temperature in the continuous forest and forest fragments

Average daily temperature differed 2°C between habitats and significantly varied between plots ($F_{7,377} = 25.0$, $P < 0.001$). Mean daily temperature for the continuous forest (26.5°C ± 1.98°C) was generally lower than mean daily for forest fragments (28.5°C ± 1.80°C). However, a post hoc analysis revealed that differences between habitats were mainly explained by high temperatures found in the Balzapote (27.2°C ± 1.62°C), Playa Escondida (28.8°C ± 1.97°C) and Rancho Eugenia (28.5°C ± 1.43°C) plots. Absolute ranges in daily temperature significantly differed between habitat type ($F_{1,377} = 189$, $P < 0.001$) and plots ($F_{7,377} = 31.9$, $P < 0.001$). Absolute ranges in daily temperature were significantly lower in the continuous forest (5.56°C ± 2.26°C), than in forest fragments (9.82°C ± 3.99°C), implying a more even daily temperature condition in this environment. A post hoc analysis revealed that differences between habitats were mainly due to higher fluctuations of temperature in plots from the forest fragments, with the Balzapote plot displaying the highest fluctuation (11.6°C ± 2.53°C). Year had a significant effect on mean daily temperature ($F_{1,377} = 125$, $P < 0.001$) and temperature absolute range ($F_{1,377} = 49.9$; $P < 0.001$). In 2012, most of the vegetation plots experienced an increase in average temperatures (2012 = 28.3°C ± 2.02°C) and larger ranges (8.54°C ± 1.51°C) compared to the previous census year (average temperature = 26.6°C ± 1.89°C, absolute range = 6.79°C ± 1.32°C).

2.3.3 Poulsenia armata density

Presence of Poulsenia armata was significantly affected by habitat type ($Z = -2.23$, $P = 0.025$), with more individuals present in forest fragments. No significant variation was explained
by reproductive tree ($\chi^2 = 18.1$, $P = 0.99$) or plot ($\chi^2 = 0.21$, $P = 0.64$). We found no effect of distance ($Z = 1.65$, $P = 0.09$) and life stage ($Z = -1.30$, $P = 0.19$). There was a significant interaction between habitat type and life stage ($Z = 3.44$, $P < 0.001$), with more seedlings present in forest fragments than in the continuous forest. Of 238 individuals tagged in 2010, 34% represented seedlings in the forest fragments while 15% of *P. armata* individuals were seedlings in the continuous forests.

As expected, *P. armata* density was significantly affected by distance to adult tree ($t = -10.7$, $P < 0.001$). Overall recruitment occurred close to adult trees (Fig. 2.2). We found a strong negative correlation between to distance from adult tree and density of the species studied ($R^2 = -0.83$, $t = -19.3$, $P < 0.001$). No significant variation was explained by reproductive tree ($\chi^2 = 5.48$, $P = 1.00$) or plot ($\chi^2 = 0.56$, $P = 0.56$). Plant density (mean ± SD) did not differ between habitats (continuous forest = 0.20 ± 0.03 ind. m$^{-2}$, fragments = 0.24 ± 0.06 ind. m$^{-2}$, $t = -0.85$, $P = 0.39$). However, there was a strong interaction between habitat type and life stage ($t = 5.38$, $P < 0.001$). Densities of forest fragments were mostly represented by seedlings (74%), while densities in the continuous forest were mainly represented by juveniles (73%). Moreover, we found a significant interaction between habitat type, life stage and distance to adult tree ($t = 3.07$, $P < 0.01$). Seedling densities were significantly higher close to adult trees in forest fragments compared with continuous forest sites (Fig. 2.2a, b). Seedling distributions in forest fragments fitted a non-linear regression (Fig. 2.2b, $R^2 = 0.51$, $F_{1,16} = 14.8$, $P < 0.01$), while seedlings in the continuous forest fitted a linear regression (Fig. 2.2a, $F_{1,27} = 21.1$, $P < 0.001$). Similarly, juvenile distribution was best described by simple linear regressions in the continuous (Fig. 2.2c, $R^2 = 0.74$, $F_{1,27} = 72.4$, $P < 0.001$) and forest fragments (Fig. 2.2d, $R^2 = 0.82$, $F_{1,18} = 76.68$, $P < 0.001$).
2.3.4 Plant survival and growth

Probability of survival over 2 y was higher in continuous forest sites (0.93 ± 0.16) than in forest fragments (0.62 ± 0.28), and likelihood of survival was greater for juveniles (0.95 ± 0.12) than seedlings (0.61 ± 0.29). Fifty-four per cent of seedlings died in forest fragments, while 29%
of seedlings died in the continuous forest. Neither reproductive tree ($\chi^2 = 31.3$, $P = 0.94$) nor plot ($\chi^2 = 23.4$, $P = 0.99$) explained any of the variation observed in the data. Plant survival was significantly affected by habitat type ($Z = -4.33$, $P < 0.001$), life stage ($Z = -6.23$, $P < 0.001$) and daily temperature ($Z = -2.89$, $P < 0.01$). Relationship between survivorship and daily temperatures was best described by a simple linear regression (Fig. 2.3a, $R^2 = 0.73$, $F_{1, 22} = 54.5$, $P < 0.001$). Contrary to expectation, survival was independent of plant density ($Z = 0.50$, $P = 0.61$) and distance from adult tree ($Z = 0.30$, $P = 0.77$). Census year had a significant effect on plant survival ($Z = -2.89$, $P < 0.01$), with lower plant survival in the year of 2012 ($0.74 \pm 0.24$) when compared to the previous census year ($0.83 \pm 0.18$).

Seedling carpets close to conspecifics in forest fragments suggested little if any influence of insects or pathogens on seed mortality. We did not find evidence of trampling in either habitat. With 65% of dead individuals ($n = 50$), death by desiccation was the primary source of mortality for new recruits and juveniles in the forest fragments, while with 60% of dead individuals ($n = 12$), vertebrate herbivory was the source in continuous forest.

Similarly to plant survival, no significant variation in plant growth was explained by reproductive tree ($\chi^2 = 0.06$, $P = 1.00$) or plot ($\chi^2 = 0.02$, $P = 1.00$). Plant growth was lower in forest fragments ($1.41 \pm 0.49$ cm) than in continuous forest sites ($2.11 \pm 0.27$ cm) and was greater for seedlings ($2.16 \pm 3.34$ cm) than juveniles ($1.45 \pm 0.42$ cm). Plant growth was significantly affected by habitat type ($t = -2.15$, $P < 0.001$), life stage ($t = -3.18$, $P < 0.01$) and temperature absolute range ($t = -2.02$, $P = 0.04$). Relationship between plant growth and temperature absolute ranges was best described by a simple linear regression (Fig. 2.3b, $R^2 = 0.74$, $F_{1, 22} = 56.2$, $P < 0.001$). Census year had no significant effect on growth ($t = 1.72$, $P = 0.09$). As with survivorship, we found no patterns of density-dependent ($t = -1.36$, $P = 0.18$) and
distance-dependent growth (t = 1.5, P = 0.14). Therefore, seedling and juvenile growth depended on habitat type, life stage and temperature absolute range.

**Figure 2.3:** Effects of temperature on survival and growth of *Poulsenia armata*. Dots indicate mean survival and plant growth after 2 y of census based on habitat type (a) and life stage (b). Survival likelihood was greater at lower mean daily temperature, and growth in height increments was higher at low absolute ranges of temperature (differences between daily maximum and minimum temperatures). Relationships between temperature and plant survival and growth were described by linear regressions

### 2.4 Discussion

Most mortality in the life cycle of trees occurs in the seed or seedling stages (Howe & Miriti 2004). Tree species vary widely in the extent to which this early mortality is density-dependent, with most species showing substantial negative density-dependent mortality in the
seed stage (Harms et al. 2000) or in dense cohorts of seedlings near fruiting conspecifics (Alvarez-Loayza & Terborgh 2011). Here we predict that loss of key dispersal agents results in higher densities of seedlings and juveniles under fruiting trees in forest fragments than in continuous forest with a full complement of dispersal agents. Many dispersal agents in continuous forests are missing in fragments at Los Tuxtlas, and higher densities of P. armata seedlings do occur near fruiting conspecifics in forest fragments. As yet, however, there is no indication that diminished dispersal assemblages in fragments result in more density-dependent mortality than in continuous forest. Dense aggregations of seedlings near fruiting trees in forest fragments instead succumb to desiccation rather than mortality from biotic causes. The prediction that strong density-dependent mortality would be exacerbated in forest fragments due to disperser loss was not born out in the case of P. armata. Absence of measurable negative density-dependent mortality, at least through the seedling and juvenile stages, suggests that P. armata may be tolerant to loss of some of its dispersal agents. However, negative effects of higher temperatures on seedling survival indicate that this tree may not be tolerant to abiotic changes due to forest fragmentation such as increased ambient temperature.

Despite potentially heavy use by bats and other fruit-eating mammals, P. armata is likely to be dispersal-limited where the howler monkey (Alouatta palliata mexicana) is no longer an effective dispersal agent at Los Tuxtlas. Primates play a well-recognized role in seed dispersal and plant recruitment for tree species in unbroken tropical forests (Anzures-Dadda et al. 2011, Chapman & Chapman 1995, Effiom et al. 2013, Nuñez-Iturri et al. 2008). Absence of a primary dispersal agent affects tree recruitment to different degrees. In Himalayan foothills, large-seeded Chisocheton paniculatus (Meliaceae) fails to recruit seedlings in areas where hornbills have been hunted out, while smaller-seeded Polyalthia simiarum (Annonaceae) shows substantial
recruitment where hornbills, the usual dispersal agents, have been exterminated, but where the imperial pigeon persists (Sethi & Howe 2009). Poor recruitment of large-seeded tree species also occurs in Africa and the western Amazon in areas where primates and large fruit-eating birds have been exterminated by hunting, as compared with similar sites where hunting with firearms does not occur (Effiom et al. 2013, Nuñez-Iturri et al. 2008, Terborgh et al. 2008). In this study, the observation that seedlings occur and survive in dense aggregations indicates a species that is initially resistant to immediate agents of seed and seedling mortality (Howe 1989). Substantially higher seedling densities under reproductive trees of *P. armata* in forest fragments in the absence of howler monkeys indicate loss of the primary dispersal agent, and failure of other fruit-eating animals to compensate for their loss.

As expected, our results show differences in survival patterns, with seedling survival significantly lower in forest fragments than in the continuous forest. Fewer seedlings surviving to older stages further confirm decreased recruitment success due to demographic differences in continuous forest as compared with fragmented forest habitats. The expectation that higher densities near fruiting trees and lower recruitment beyond the seedling stage results from density-dependent mortality (Connell 1971, Harms et al. 2000, Janzen 1970) was not supported in our study. For the census years of our study, individual survival is independent of plant density and distance to conspecifics.

Differences observed in *P. armata* seedling and young juvenile densities could be explained by other factors. Decreased fruit production observed in forest fragments could have negatively impacted plant recruitment by decreasing the number of potential recruits. Although, *P. armata* fruit production was greater in the continuous forest, seedling densities were higher in forest fragments, which is inconsistent with an important effect of low fruit production for
limited *P. armata* recruitment. Additionally, leaves of *P. armata* sustained damage by pathogens (chlorotic spots) and herbivorous insects as previously described by García-Guzman & Dirzo (2004), this was not associated with plant mortality at the study sites.

Changes in the terrestrial mammal community are likely to account for differences in recruitment success observed in the continuous forest and forest fragments. The collared peccary (*Pecari tajacu* Linnaeus, 1758) may have an important negative impact on seedling establishment due to herbivory and trampling. Camera traps showed that this peccary is still present in the continuous forest of Los Tuxtlas area, but it is nearly extinct in forest fragments (Chapter 3). The absence of potential herbivores makes herbivory an unlikely explanation for increased mortality in forest fragments. Greater seed predation in fragmented forests occurs for some tree species (Jorge & Howe 2009, Wright & Duber 2001), but we had no evidence of it in this study. Results from a removal experiment conducted in the same study sites showed that differences in the faunal communities were associated with reduced fruit removal and seed predation of *P. armata* in forest fragments (Chapter 3). The fauna of the fragmented forest was mainly represented by omnivorous species such as the coyote (*Canis latrans* Say, 1983), raccoon (*Procyon lotor* Linnaeus, 1758), opossum (*Philander opossum* Linnaeus, 1758), armadillo (*Dasypus novemcinctus* Linnaeus, 1758) and skunk (*Conepatus semistriatus* Boddaert, 1785). Frugivorous and seed-eating species such as the peccary, agouti (*Dasyprocta mexicana*, Saussure, 1860), pacas (*Cuniculus paca* Linnaeus, 1766) and coatis (*Nasua narica* Linnaeus, 1766) were only recorded in continuous forest. Presence of large frugivores and herbivores may explain the observation of reduced density of seedlings in the continuous forest, while their absence might have resulted in greater seedling densities in forest fragments.
Altered microclimatic conditions are another possible mechanism affecting recruitment success. In this study, differences in abiotic conditions in forest fragments were associated with lower survival and growth in *P. armata*. Forest fragments are generally characterized by increased temperatures (Benitez-Malvido 1998, Bruna 2002), paralleling our results. Elevated temperatures generally result in increased photorespiration reducing photosynthetic rates and carbon gains (Saxe *et al.* 2001). Therefore, by limiting photosynthetic activity, higher temperatures have the potential to reduce plant growth (Higuchi *et al.* 1999), which may explain our observations in forest fragments. Limited growth may affect the capacity of water reserves and water transport (McDowell *et al.* 2002), reducing drought tolerance and seedling survival in forest with higher temperatures. *Poulsenia armata* is known to be drought-sensitive in Panama (Condit *et al.* 1995, 1996); excessive evapotranspiration at high temperatures may be the explanation for low survival in forest fragments. Moreover, high temperatures combined with poor soil conditions may significantly reduce survivorship and growth as plants experience abiotic stress (Laurance *et al.* 1998). Soils from forest fragments at Los Tuxtlas have significantly less nitrogen and water available to plants which, combined with the lack of plasticity of *P. armata* in allocation of biomass to roots (Chapter 4), may explain the differences in survival and growth patterns observed between both habitats. Increased survival suggests that the growth strategy observed in the continuous forest seems to be more advantageous for individuals of *P. armata*.

Finally, it should be noted that patterns of cohort mortality occur at different times in the life cycle in different tree species (Comita *et al.* 2010). It is notable that seedlings were recorded in higher densities under fruiting *P. armata* in forest fragments than in continuous forest, but did not experience measureable distance- or density-related mortality in the first years after
establishment. Long-term studies of tree demography in Panama indicate that few species show the same associations with different habitats (plateau, slope, streamside, swamp) as seedlings than as adults (Comita & Hubbell 2009). The same study indicates that most species for which data are sufficient show stronger negative effects of conspecific neighbours than heterospecific neighbours. Mortality from desiccation, reported here for the first time linked to higher ambient temperatures in fragments than continuous forest, appears to be density-independent in early seedling and juvenile stages, but may or may not be density-dependent later in life.

2.5 **Conclusion**

As fragmentation of natural habitats in tropical regions continues to be a major threat to biodiversity, it is necessary to evaluate the consequences on the remaining flora and fauna of these areas. Results of this study are consistent with other studies conducted in Los Tuxtlas area where plant recruitment is affected by fragmentation (Arroyo-Rodriguez & Mandujano 2006, Arroyo-Rodriguez *et al.* 2007). The apparent sensitivity of this species to drought dims its prospects in highly fragmented landscapes, particularly in landscapes where temperatures are likely to increase over the foreseeable future.
3. SEED PREDATION IN A HUMAN-MODIFIED-LANDSCAPE: OPPORTUNISTIC CHOICE

3.1 Introduction

The fate of many tropical trees is inextricably dependent on the role played by the animals with which they interact. Many mammals have an important impact on plant communities as they determine the fate of seeds for several plant species. Terrestrial mammals may prey upon fruits and seeds encountered under adult trees, while others may transport seeds away from reproductive adults, caching and scattering them throughout the forest, thus increasing seed survival (Asquith et al. 1997, DeMattia et al. 2004, Jansen et al. 2004). Seed removal varies with animal guild, as well as with body size and food availability. Large frugivores that remove and deposit several thousands of seeds in a day are better seed dispersers quantitatively than many smaller frugivores (Howe 1989, Howe & Smallwood 1982). Additionally, the number of seeds and fruits harvested may be density-dependent, as dense food patches may suffer from disproportionately higher removal rates since they are more profitable for foragers (Sanchez-Cordero & Martinez-Gallardo 1998). As seed survival depends on the foraging behavior of potential seed dispersers and predators, the effects of density dependence on seed removal is key information for understanding reproductive biology of trees. Any changes in the role played by mammals can significantly alter removal patterns.

Burgeoning human populations in rural tropical regions have accelerated the fragmentation of these natural habitats, severely affecting mammal communities. This is the case for the Los Tuxtlas forest, where many animal species occur in low numbers. Below we provide examples of studies conducted in the Los Tuxtlas forest in order to illustrate this idea. The avian
community at this site is still relatively diverse; however bird species richness and relative abundance are negatively affected by habitat loss and isolation distance of forest fragments (Estrada et al. 1993b). Similarly, the presence and abundance of mammals was determined by the size and isolation degree of forest fragments (Estrada et al. 1993a), with frugivores and non-flying mammals being the most affected by forest fragmentation, while omnivores such as Didelphis marsupialis, D. virginiana and Philander opossum being predominant (Estrada et al. 1994). Low occurrence of birds and mammals in pastures suggests that this habitat is unsuitable due to the lack of food resources, extreme climatic conditions and increased risk of predation (Estrada et al. 1994, Estrada et al. 1997). The absence or low occurrence of large- to medium-sized mammals has classified the Los Tuxtlas forest as a severely defaunated site when compared to less disturbed forests such as the Lacandon Forest (Dirzo & Miranda 1990b) or the Biosphere Reserve of Montes Azules (Mendoza & Dirzo, 2007), both located in the Mexican state of Chiapas (Mendoza et al. 2005). Small rodent seed predators, particularly Heteromys desmarestianus and Peromyscus mexicanus remain very common in the forest understory at Los Tuxtlas (Dirzo et al. 2007, Sanchez-Cordero & Martinez-Gallardo 1998), exhibiting the capacity to maintain their populations in disturbed forests and may even experience an ecological release due to the absence of their competitors (Mendoza et al. 2005). This contemporary defaunation cited for the Los Tuxtlas forests may turn small forest-dwelling rodents into main food consumers (Dirzo et al. 2007). If this is the case, then future composition of forest fragments in Los Tuxtlas will depend on food choice and avoidance by small rodents. If small vertebrate seed predators experience an ecological release, large-seeded species would be overrepresented on forest the floor since they are less preferred by small mammals (Beckman & Muller-Landau 2007, Dirzo et al. 2007, Mendoza & Dirzo 2007). Alternatively, the remaining fauna might well
compensate for the missing animal species, resulting in equivalent or nearly equivalent removal rates (e.g. Sethi & Howe 2009), especially for plant species that offer food to a wide range of animals.

Several species within the Moraceae are important dietary resources for tropical frugivores (Estrada & Coates-Estrada 1984, Fashing 2001, Janzen 1979, Kays 1999, Terborgh 1986). This is the case of *Poulsenia armata*, a common tree of lowland Neotropical rainforests from Mexico to Bolivia. *Poulsenia armata* is generally mammal-dispersed. At Los Tuxtlas, *P. armata* represents an important food source for howler monkeys (*Alouatta palliata*) (Arroyo-Rodriguez & Mandujano 2006). Fruits and seeds of this tree are primarily dispersed by howler monkeys and secondarily by dung beetles (Estrada & Coates-Estrada 1984, Estrada & Coates-Estrada 1986); this interaction appears to be the prevailing two-step process of effective dispersal of this tree in continuous forest. Fruits are also consumed by fruit bats (*Artibeus jamaicensis, A. lituratus*) at this site, however the seeds deposited in caves have dim prospects for survival (Vazquez-Yanes et al. 1975). An additional study at Los Tuxtlas reports *P. armata* seeds recovered from captured brown jays (*Psilorhinus morio*) and a forest-dwelling dove (*Leptotilia plumbeiceps*), suggesting that fruit-eating birds are at least potential dispersal agents (Trejo-Pérez 1976). Elsewhere this tree is known to be dispersed by a variety of other primates (Chaves et al. 2012, Gonzalez-Zamora et al. 2009, Wehncke et al. 2003), kinkajous (*Potos flavus*) (Kays 1999), and other bat species (Giannini & Kalko 2004). *Poulsenia* fruits are likely to be dispersed by other mammals and sparingly dispersed by large birds, but published observations are unavailable. Seed predators include small rodents (*Heteromys demarestianus*; Martinez-Gallardo & Sanchez-Cordero 1993, Dirzo et al. 2007) and larger terrestrial mammals such as peccaries (*Pecari tajacu*) and deer (*Odocoileus virginianus*) (Martínez-Gallardo &
Sanchez-Cordero 1993). Since the fruits and seeds of *P. armata* are consumed by a wide variety of mammal species, this species serves as a candidate for the evaluation of the general impact of defaunation on seed predation and fruit removal patterns. Documenting fruit, as well as seed removal adds a dimension of mammalian use of plant resources that remains little understood.

It is reasonable to expect that forest fragments lacking large-bodied frugivores should affect the proportion of removed fruits and predated seeds. Following this rationale, we hypothesize that the lack of medium- to large-bodied terrestrial mammals in forest fragments at Los Tuxtlas leads to significant changes in the fate of fallen fruits and seeds. To address this hypothesis, we first tested whether or not the absence of large-bodied frugivores is related to decreased fruit removal. Secondly, we questioned if a possible ecological release of small mammals would result in increased seed predation. Thirdly, we tested for a density-dependent effect, with low fruit removal and seed predation when fruits or seeds are encountered in dense patches due to animal satiation.

### 3.2 Methods

#### 3.2.1 Study site

The study was conducted in the continuous forest and nearby forest fragments at the Biological Station Los Tuxtlas in Veracruz, southeastern Mexico (18° 30’N, 95° 04’W). The continuous forest of this study encompasses 640 ha which is property of the Biological Station created in 1967 by the Universidad Nacional Autonoma de Mexico. In 2010, eight permanent 1 ha vegetation plots were established in the area of the Los Tuxtlas forest. Four sites were selected within the continuous forest where we established four 1ha vegetation plots. Four more
1 ha plots were established in four forest fragments in the surrounding landscape. The four forest fragments were selected for this study based on the presence of reproductive adults of *P. armata*.

### 3.2.2 Seed and fruit addition experiment

We collected freshly fallen fruits from the forest floor during the fruiting period of May 2010. At each study site we divided each 1 ha plot into four 50-x-50 m subplots, where we placed experimental stations representing high or low seed and fruit density treatments. We randomly set up high and low density stations by assigning letters (A to D) to each 50 m subplot. Subplot A was designated as high seed density (120 seeds/25m²) and subplot B represented low seed density (12 seeds/25m²). Subplot C was designated as high fruit density (20 fruits/25m²) while subplot B represented low fruit density (2 fruits/25m²). We took great care to ensure fruits were not damaged prior to placement in the field and that the seeds were thoroughly cleaned of pulp. We marked the initial location with a wooden stake. To distinguish dispersal from predation we used a free marking method, where durable nylon lines (50 cm) were glued to the seed tegument. This technique allows relocation of removed seeds to distinguish seed predation from scatterhoarding (Forget & Wenny 2005). We used this technique instead of drilling the seed in order to avoid damage to the embryo, which is preferred by animal species such as squirrels (pers. obs). Each nylon line measured 50 cm and we added a thin metal label at the end of the line to number each seed individually. We recorded the number of seeds and fruits left intact, eaten in situ or removed from the experimental stations. We considered dispersal occurred if seeds were found intact and away from the original location. We monitored each experimental station weekly for a period of 60 days.
3.2.3 Fauna data

We live-trapped each plot one week after the experiment to estimate the minimum number of small rodents and recorded which species were present. Rodent censuses were conducted in June of 2010 and June of 2011. We set up 40 Sherman traps for 3 nights at each plot at 5m intervals along a 95m transect. To confirm whether or not the small mammals caught in the traps acted as possible seed predators, we baited one half of the traps with seeds of *P. armata* and the other half with sunflower seeds and oatmeal. Each individual caught was identified to species and then immediately released at the point of capture. In June 2011, we set up four camera traps to record other animals that might consume the fruits and seeds of *P. armata*. A pile of 20 to 30 fruits was placed at a random location in each 1 ha vegetation plot. The camera traps (Bushnell Trophy Cam/ model 119405) were attached to the trunks of trees at a distance of 1 m from the fruit piles. The delay between pictures was set to 30 seconds and the sensitivity of the infrared sensor was set to high. Each trigger event captured a number of three sequential photographs with a quality of 5 megapixels. Cameras were operated for 24 h each day and were recovered after 7 days at each plot. The data was filtered to exclude images of the same species at the same plot within a period of 60 minutes in order to ensure that observations were independent. We recorded the identity of the animals and the time of removal. We calculated the capture proportion of a given species as the number of photos/ 7days captured by a camera as a measure of animal activity per habitat.
3.2.4 Statistical Analyses

In order to test for differences in animal activity in the continuous and fragmented forest sites, we used capture frequencies recorded by camera traps. We used a 2-way analysis of variance where habitat (continuous, fragments) and animal guild (predator and disperser) were included as factors. Additionally, we applied a Fisher Exact Test to compare the number of trapped individuals by the Sherman traps in the continuous and fragmented forests in the years of 2010 and 2011.

We applied a generalized linear mixed model (GLMM) assuming a Poisson distribution to test for differences in seed fate. Estimates of scatterhoarding were unavailable, as we were unable to recover lost seeds, however, we considered seeds that were absent from the experimental stations to be removed. We included habitat type (continuous forest /fragments), density (high/low) and fate (intact, eaten in situ, removed) as fixed effects and subplot as a random effect nested within location. Similarly, we applied a GLMM assuming a Poisson distribution to test for differences in fruit fate. We included habitat type (continuous forest /fragments), density (high/low) and fate (intact, eaten in situ, removed) as fixed effects and subplot as a random effect nested within location. In both cases, we selected the best models with an ANOVA test comparing the different models and AIC values of each model. Then, we used a Wald-Z test to determine the significance of fixed effects. All the analyses were carried out with the R package (R Development Core Team 2012). Means are accompanied by standard deviation.
3.3 **Results**

3.3.1 **Fauna at Los Tuxtlas forest**

Detection frequencies by camera traps differed considerably between feeding guild \((F_{2, 20} = 172.76, P < 0.001)\), with more predators recorded \((1.83 \pm 0.43)\), while dispersers \((0.81 \pm 0.09)\) had lower capture frequencies. Habitat had a strong effect on detection frequencies \((F_{2, 20} = 55.80, P < 0.001)\), with animal species in the continuous forest recorded more often \((mean = 2.17 \pm 0.50)\) than in forest fragments \((mean = 0.87 \pm 0.16)\). Additionally, we found a significant interaction between animal guild and habitat type \((F_{2, 20} = 190.97, P < 0.001)\), with considerably less seed dispersers in forest fragments \((mean = 0.48 \pm 0.16)\) than in the continuous forest \((mean = 1.14 \pm 0.14)\). Agoutis \((Dasyprocta mexicana)\) and coatis \((Nasua narica)\) were only recorded in continuous forest, while coyotes \((Canis latrans)\) were only present in forest fragments. We observed coyote feces with intact seeds of \(P. armata\) suggesting a dispersal role by this mammal; however we detected their presence only in forest fragments. Detection frequencies were significantly affected by the species of the animal recorded \((F_{9, 20} = 3.51, P = 0.03)\). For all the species recorded, squirrels \((Sciurus sp.)\) were detected most frequently in both habitat types \((Table 3.1)\). The remaining species showed a lower interaction with fruits of \(P. armata\). As expected, fruits of \(P. armata\) attracted a diversity of animal species, especially medium-sized mammals such as squirrels and agoutis.

Contrary to expectation, minimal number of trapped rodents did not differ between habitats \((P = 0.16)\). Overall, 77.8% of captured rodents were trapped at the continuous forest \((n = 14)\), against 22.2% in forest fragments \((n = 4)\). Trapped individuals were mainly \(Heteromys desmarestianus\) and \(Peromyscus mexicanus\), with \(Peromyscus leucopus\) and \(Tylomys nudicaudus\) being rare.
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</tr>
<tr>
<td><em>Procyon lotor</em></td>
<td>Raccoon</td>
<td>Predator</td>
<td>0</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Table 3.1: Mammal activity in 2010 sorted by animal species. Values represent mean capture frequencies (number of photos/7 days).

### 3.3.2 Seed and fruit fate in the continuous and fragmented forests

Observations showed a large number of seeds damaged by rodents (n=150), particularly by squirrels, which destroyed the seed coat to consume the embryo. Fruits showing signs of decomposition and ant infestation after one week were still consumed. We observed no evidence of damage by arthropods on seeds.

Fate of fallen seeds significantly differed between habitats (Fig. 3.1b). We found that the number of seeds left intact was significantly higher ($Z = -0.50, P < 0.01$), as well as the number of seeds removed ($Z = -0.52, P < 0.01$). The number of seeds removed ($16.94 ± 2.20$) was higher...
compared to destroyed (0.88 ± 1.79) or intact seeds (5.19 ± 1.17) in the continuous and fragmented forests. Moreover, there was an interaction between seed fate and habitat type (Fig. 3.1b). Indeed, seed removal was dependent on habitat type with more seeds removed ($Z = 18.61$, $P < 0.001$) and more seeds left intact ($Z = 0.50$, $P < 0.01$) in forest fragments than the continuous forest. Seed density had no effect in seed fate ($Z = 0.002$, $P = 0.99$).

Similarly, fate of fallen fruits significantly differed between habitats. We found that the number of fruits removed was significantly higher ($Z = 3.34$, $P < 0.001$), than fruits eaten or left intact. More fruits were removed from the forest floor ($9.31 ± 0.84$) than eaten ($1.688 ± 0.37$), while no fruits were left intact. We found a significant interaction between fruit fate and habitat type (Fig. 3.1a). Fruit removal was dependent on habitat type ($Z = -0.52$, $P < 0.01$), with more fruits removed in the continuous forest ($10.63 ± 0.92$) than in forest fragments ($8.50 ± 0.75$).

We recovered several intact seeds from the experimental stations after the fruit pulp had been consumed. Fruit density had no effect on fruit fate ($Z = 0.002$, $P = 0.98$). Therefore, the results of this study show that while seed and fruit fate was independent of density, changes in faunal community lead to significant changes in fruit removal and seed predation patterns in forest fragments.
Fig 3.1: Fate of a) fruits and b) seeds of *Poulsenia armata* in the continuous forest and forest fragments of Los Tuxtlas in 2010.

3.4 Discussion

Loss of mammalian fauna is of special concern due to its significant impact on forest regeneration. Fragmented forests usually experience impoverishment of mammalian diversity, which leads to profound effects on frugivory and seed dispersal (Galetti *et al.* 2003) and subsequent seedling establishment. Trees that offer food to a variety of animals may experience ecological redundancy, buffering the negative effects of defaunation. *Poulsenia armata* appeals to a variety of mammals in the continuous forest and forest fragments, to the point that redundant
disperser assemblages appear likely. However, the variety of species interacting with *P. armata* significantly differed between habitats, altering seed predation and fruit removal patterns. Variations in the abundance and composition of seed predators and dispersers could limit seedling establishment, ultimately affecting long-term population dynamics.

In this study, changes in the faunal community led to significant changes in fruit fate of *P. armata*. Terrestrial frugivores preferred to remove fruits of *P. armata* rather than destroying them or leaving them intact. However, the amount of fruits removed was greater in the continuous forest than in forest fragments. Decreased animal activity and changes in species composition are plausible explanations for the differences observed in fruit fate. Additionally, many of the species observed in this study have been previously described as seed dispersers, but were recorded mainly in the continuous forest. Agoutis (*Dasyprocta mexicana*) are considered to be important seed dispersers for a wide variety of seeds in the Neotropics, as they do not destroy many of the ingested seeds and may enhance survival and germination by scatter-hoarding seeds (Forget 1990, Forget & Milleron 1991, Peres *et al.* 1997, Smythe 1978). Coatis (*Nasua narica*) have also been described as important seed dispersers, especially in anthropogenic landscapes, as they have better tolerance to habitat fragmentation than other species (Alves-Costa & Eterovick 2007). However, at our study site, coatis were recorded only in the continuous forest. The coyote (*Canis latrans*) was the only seed disperser recorded in forest fragments and, to our knowledge, this is the first report of this animal species feeding on fruits of *P. armata*. Coyotes have been identified as significant seed dispersers for several plant species in temperate zones and have the ability to perform long-distance dispersal (Willson 1993). The role of coyotes as possible seed dispersers in tropical forests has received little attention, especially in fragmented forests where they could potentially offset the negative effects of limited dispersal.
Seed predation may increase in defaunated areas due to an increase in the abundance of small rodents (Guariguata et al. 2002, Sanchez-Cordero & Martinez-Gallardo 1998); however this was not the case in this study. The idea of an ecological release of small mammals was not supported here, as we did not observe an increased number of rodents trapped in forest fragments. Increased seed predation in the continuous may be related to the presence of important seed predators, absent in forest fragments. While peccaries (Pecari tajacu), pacas (Cuniculus paca), and squirrels (Sciurus sp.) represented the main predators of P. armata in the continuous forest, skunks (Conepatus semistriatus), raccoons (Procyon lotor), opossums (Philander opposum) and armadillos (Dasypus novemcinctus) were possible predators in forest fragments. Peccaries are important seed predators of Neotropical forests and can negatively affect seed survival and subsequent seedling recruitment (Asquith et al. 1997). Spiny pocket mice (Heteromys desmarestianus) can also significantly affect seed survival by destroying seeds, similarly to squirrels, but also by leaving uneaten scatter-hoarded seeds (DeMattia et al. 2004). Seed predation has significant consequences on plant demography, which explains the differences observed on P. armata population structure between habitats, with a shift towards smaller individuals in forest fragments (Chapter 5).

Contrary to expectation, there was no evidence for predator satiation. Dense patches of fruits usually occur below reproductive adults of P. armata (pers. obs). It is possible that seed and fruit densities selected for this study were too low to satiate predators. However, another possibility is that other characteristics such as shape, texture and odor may be affecting food consumption rates (Haught & Myster 2008). Fruits of P.armata are characterized by an intense fermented odor that attracts several frugivorous mammals. Therefore, an apparent lack of density
dependence of seed and fruit removal could be the result of a high preference for this food source by many generalist consumers attracted to the experimental stations.

The fact that proportions of fruit removed were significantly higher than fruits left intact could be the result of ecological redundancy in forest fragments. When large and medium-sized mammals are severely reduced or completely absent, the remaining animals can play equivalent roles (Lawton & Brown 1993). Ecological redundancy requires density compensation or a functional behavioral response by competitors (Rosenfeld 2002, Walker 1992). Although, the remaining fauna in forest fragments could be compensating for the loss of the major frugivores, the animals detected in this study were less effective than the frugivorous mammals in the continuous forest. Based on the records of animals present in the continuous and fragmented forests at Los Tuxtlas, we hypothesized that the probability of seeds being dispersed would be higher in the continuous forest. This is consistent with field observations of P. armata regeneration patterns where denser aggregations of seedlings occur close to reproductive adult trees in forest fragments (Chapter 1).

Here we recorded the presence of animal species previously reported as absent at Los Tuxtlas forest in an earlier census conducted by Dirzo et al. (2007). It is possible that the mammal community at Los Tuxtlas was able to recover over time, or that the sites included in this study were not sampled before. While, our results suggest significant changes in the mammal fauna composition of forest fragments, we also found that the Los Tuxtlas area may not be as severely defaunated as previously described. Mammalian defaunation can result in an impoverishment of floristic diversity and an alteration of plant composition (Dirzo & Miranda 1990a, Dirzo & Miranda 1990b, Leigh et al. 1993, Wright et al. 2007). Recruitment of small-seeded species is predicted to decrease as human impact progresses, while large-seeded species
are expected to be over-represented in the seedling bank of defaunated forests (Beckman & Muller-Landau 2007, Dirzo et al. 2007, Mendoza & Dirzo 2007, Muller-Landau 2007). Many studies have documented how the loss of important seed predators has greater effects on large seeded tree species (Benitez-Malvido & Martinez-Ramos 2003, Donatti et al. 2009, Melo et al. 2010). We believe that plant-animal interactions are so complex that defaunation of forests may occur in different degrees, rendering impossible a generalization of this hypothesis. Additionally, the majority of removal studies have focused only on seeds while fruits have been not included, neglecting the effects generated by animals that are mainly frugivores and not granivores. Future removal studies should consider including fruits, as well as seeds, in order to improve our knowledge and predictions of the future of tropical forests.
4. UNDERNOURISHED SEEDS AND POOR SOIL CONDITIONS IMPACT SEEDLING PERFORMANCE OF *POULSENIA ARMATA* (MORACEAE)

4.1 **Introduction**

Plant reproductive success is inextricably dependent on the quantity and the quality of seeds that determine offspring persistence (Hanley *et al.* 2007, Jacquemyn *et al.* 2001, Jakobsson & Eriksson 2000). Many studies have shown a tradeoff between size and number of seeds (Baraloto & Forget 2007, Dejong & Klinkhamer 1989, Tsaliki & Diekmann 2010). Seed size is often described as an indicator of seed quality and a predictor of offspring fitness (Cheplick & Sung 1998, Li *et al.* 2011, Valencia-Diaz & Montana 2005) as evidenced by higher germination, offspring survival, and seedling competitiveness of large seeds when compared to small seeds of the same species (e.g. Howe & Richter 1982). Seed size varies within species or even within individuals (Jacquemyn *et al.* 2001, Vaughton & Ramsey 1998). Seed size variation is intricately connected to habitat and environmental quality dictated by resources available to parental plants at time of seed formation (Aguilar *et al.* 2012, Aguilar *et al.* 2006) and by transient climate conditions. The amount of nutrients available in seeds that are used during germination and initial seedling growth are partly set by environmental conditions (Jacquemyn *et al.* 2001, Li *et al.* 2011). This is the case of seed nitrogen (N) and carbon (C) content, both indicators of seed quality, that positively influence plant growth and mass accumulation of seedlings (Naegle *et al.* 2005, Soriano *et al.* 2011). Small seeds have a greater dispersal probability, but contain fewer resources for subsequent seedling establishment, survival and growth which is further affected by environmental conditions (Schupp 1995). Understanding
variation of seed size and quality in response to climate and land-use change is important because of the repercussions on early offspring survival and growth.

Degraded landscapes are often linked to a decrease in available resources to parental trees (Aguilar et al. 2006, Aizen & Feinsinger 1994). This is the case for fragmented plant populations, where limited pollination, increased inbreeding and/or changes in abiotic conditions may result in fewer seeds being produced (Aizen & Feinsinger 1994, Kramer et al. 2008). In some cases reduced seed quantity is also related to decreases in seed quality (Aguilar et al. 2012, Baraloto & Forget 2007, Gonzalez-Rodriguez et al. 2011, Tsaliki & Diekmann 2010, Yates et al. 2007), defined as decreases in seed mass (Henriquez 2004). Increased temperatures, reduced relative humidity and increased light are linked to forest fragments (Kapos 1989), which in turn can inhibit seed germination and result in higher rates of seedling mortality due to desiccation (Bruna 1999, Bruna 2002). Environmental conditions may directly affect progeny performance but also indirectly affect traits that are passed along the offspring by the mother plant, including seed mass, seed germination and seedling survival and growth (Donohue 2009). Alteration of soil structure and integrity associated with land-use conversion and fragmented forests may reduce the amount of resources available to plants for reproduction, possibly affecting seed performance (Renison et al. 2004). Plants may adjust to nutrient deficiency, especially nitrogen, by allocating a greater proportion of their biomass to the root system (Hermans et al. 2006). However, the effects of seed and soil quality on seedling establishment, hypothesized by many studies in fragmented landscapes, have rarely been tested in the field. To date, there is still a gap between knowledge of the effects of tropical forest fragmentation on seed quantity and quality and of the repercussions for seedling establishment.
The future of tropical forest in anthropogenic-modified landscapes is uncertain due to a constant increase in human population pressures (Wright & Muller-Landau 2006). Land use changes may trigger cascades leading to potentially irreversible alterations of ecosystem function and structure (Hobbs 2001), affecting the capacity of a system to undergo disturbance and still persist (resilience). Loss of biodiversity increases the risk of reduced resilience, and thereby potentially affects response of tropical forests to global change (Chazdon 1998). Obligate forest species, such as late-successional trees, are expected to become locally extinct as forest loss and fragmentation progress, while disturbance-adapted species (e.g. weeds, pioneer plant species) may increased in abundance reducing biological diversity (Gardner et al. 2009). Plant species may adjust to changing environments through plastic responses of key functional traits including morphology, physiology and/or reproduction (Nicotra et al. 2010), acting as a buffer against rapid changing conditions by providing rapid adaptation (Chevin et al. 2010).

Seedling performance of Poulsenia armata (Moraceae), a Neotropical late-successional canopy tree, is negatively affected by fragmented-related conditions at Los Tuxtlas forest in Southern Mexico (Chapter 2) that may also impact reproductive success and offspring performance of this tree species. At this site, only 16% of the original lowland forest remains after 30-40 years of conversion of pristine forest to pasture (Dirzo & García 1992, Mendoza et al. 2005) potentially affecting resilience of this system to future changes. Here we examined the impact of forest fragmentation on reproduction and offspring performance of P. armata in fragmented and continuous sites. If resources available to parental trees for reproduction are being reduced, we hypothesized: 1) small fruit crops, 2) low seed quantity and quality (i.e., seed mass and seed N and C content) and 3) poor seed and soil quality translated into reduced seedling performance (decreased survival and growth). We expected that seedlings with low
parental investment growing under poor soil conditions would allocate greater belowground biomass. For this study, we used stable isotopes to indicate environmental constraints on reproductive success and offspring performance (Dawson et al. 2002, Handley & Raven 1992). The use of these metrics in understanding changes in seed production and seedling performance in species from fragmented tropical forests has been very limited.

4.2 Methods

4.2.1 Study site and tree species

The study was conducted in the continuous forest and nearby forest fragments at the Los Tuxtlas Biological Station in Veracruz, southeastern Mexico (18º 30’N, 95º 04’W). This reserve is embedded in the 35,000 ha of pristine rain forest that forms part of the Los Tuxtlas Biosphere Reserve (Mendoza et al. 2005). The original vegetation of the study site is described as lowland tropical rainforest with a dry season from March to June and a wet season from July to February (Bongers et al. 1988). Soils at Los Tuxtlas area are of volcanic origin and are rich in N, P, K and organic matter (Bongers & Popma 1990), and are classified as sandy loam (Bongers et al. 1988). 

*Poulsenia armata* is a monoecious, shade tolerant, late successional canopy tree (Croat 1978) that is common to the forest of Los Tuxtlas. It occurs in moist and wet tropical forests from Mexico to Bolivia, reaching heights of 15 to 30 meters. Fruits are produced mainly April-June followed by a smaller fruiting period in October-November. *P. armata* has been described as a drought-sensitive plant species (Martínez-Garza et al. 2013a, b).

We established four 1 ha vegetation plots containing *P. armata* within the continuous forest of the Los Tuxtlas Biological Field Station, separated from each other by 0.5 – 2 km. We
set up four more 1 ha plots containing *P. armata* in four forest fragments separated by 500 meters to almost 2 km. This study included the forest fragments of Rancho Eugenia (19.4 ha), Playa Escondida (40 ha), Balzapote (34.6 ha) and Ruiz Cortines (≈20 ha), which have been isolated from the continuous forest for 30 to 40 years.

### 4.2.2 Data collection

We recorded fruit production during the reproductive periods from 2010 to 2012 for each adult tree within each experimental plot. For each reproductive adult, we measured diameter at breast height (cm), and crown area (m$^2$). We quantified fruit production by directly counting fruits on five randomly selected branches, estimating the average number per branch and multiplying by the total number of branches on the tree. An initial analysis revealed that the number of seeds per fruit did not differ between habitats ($F_{1,106} = 0.014, P = 0.905$). An average of 6 seeds per fruit was therefore used to calculate the mean number of seeds per reproductive adult (average number of seeds per fruit * total number of fruits per tree).

In 2012, we collected seed and soil samples for chemical analyses of quality. For this study, we focused on carbon, water and nitrogen as resources influencing plant performance and growth. We collected a total of 15 to 20 seeds from 25 reproductive adults (15 adults from fragments, 10 from continuous forest), and dried each to a constant weight at 105°C to obtain dry mass. Finally, we collected 10 soil cores randomly from each 1 ha plot (5 samples at 10 and at 20 cm deep), weighed and dried at 60°C until weight constancy. We calculated relative water content (RWC) for soil samples as: \([(W-DW)/W]*100\), where W represents the sample fresh weight at time of collection and DW the sample dry weight. Seed and soil samples were sent to
the University of Illinois at Chicago to determine the carbon and nitrogen stable isotope ratio
($\delta^{13}C$ and $\delta^{15}N$ respectively), carbon and nitrogen concentrations (% dry mass) and carbon-to-
nitrogen (C/N) ratios using a zero-blank elemental analyzer (Costech 4010, Valencia, CA)
coupled to an isotope ratio mass spectrometer (IRMS, Delta +XL, Finnigan, Bremen, Germany)
in continuous flow mode to a precision of 0.05 $^\circ/oo$ for $^{13}C$ and 0.2 $^\circ/oo$ for $^{15}N$. We calculated soil
C and N content (g) by multiplying C and N concentrations (% dry mass) by soil dry weight (g).
Then we divided the soil C and N content by the surface area of soil core (m$^2$) to obtain soil C
and N content per surface area. Several seed and tree parameters were estimated: (1) we
calculated the N invested per seed (mg) by multiplying seed mass by seed N content for the
continuous and fragmented forests, (2) total mass of trees (g) for both habitats was calculated by
multiplying seed mass by the total number of seed produced per tree, and (3) total N per tree
(mg) for both habitats was obtained by multiplying N invested per seed by the total number of
seeds produced per tree.

4.2.3 Germination and seedling growth

We collected fruits under reproductive adults, during the fruiting periods of 2010, 2011
and 2012, and randomly selected an equal number of seeds as part of a common garden
experiment (160 seeds each from trees growing in continuous and the fragmented sites). We
planted each seed in individual plastic bags at a growing house of the Los Tuxtlas Biological
Field Station. The objective was to determine if maternal seed origin had an effect on seed
germination and initial plant growth under controlled conditions. Because soil conditions might
also be a potential variable affecting germination and seedling growth, we used soil from both
the continuous forest and forest fragments in the experiment. Seeds were equally divided into
four treatments: 1) seeds from continuous forest grown in soil from continuous forest, 2) seeds from continuous forest grown in soil from fragments, 3) seeds from fragments grown in soil from fragments and 4) seeds from fragments grown in soil from continuous forest. After 30 days, we recorded the proportion of germinated seeds. Seedlings were then monitored for growth and survival from June 2010 to June 2012. We also recorded plant height and basal diameter. In July 2012, we harvested the surviving seedlings and recorded leaf area using the Portable Laser Area Meter CI-202 (Cid Bio-Science). We dried, each component at 60°C until constant weight and then weighed. To assert differences in seedling growth between habitats, we determined growth parameters (Table 4.1) and recorded the number of leaves produced after 2 years.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbreviation</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total dry mass</strong></td>
<td>TDM</td>
<td>G</td>
</tr>
<tr>
<td><strong>Root mass fraction</strong></td>
<td>RMF</td>
<td>gg⁻¹</td>
</tr>
<tr>
<td><strong>Stem mass fraction</strong></td>
<td>SMF</td>
<td>gg⁻¹</td>
</tr>
<tr>
<td><strong>Leaf mass fraction</strong></td>
<td>LMF</td>
<td>gg⁻¹</td>
</tr>
<tr>
<td><strong>Specific stem length</strong></td>
<td>SSL</td>
<td>Cm</td>
</tr>
<tr>
<td><strong>Leaf area</strong></td>
<td>LA</td>
<td>cm²</td>
</tr>
<tr>
<td><strong>Specific leaf area</strong></td>
<td>SLA</td>
<td>cm²g⁻¹</td>
</tr>
<tr>
<td><strong>Leaf area ratio</strong></td>
<td>LAR</td>
<td>cm²g⁻¹</td>
</tr>
</tbody>
</table>

*Table 4.1: Seedling growth parameters with their abbreviations and units*
4.2.4 Statistical analyses

We conducted all the analyses using the R environment (R development Core Team, 2013). We assessed the relationship between tree size and fruit production/mass using simple linear regressions. Since crown area was closely related to dbh ($r = 0.72$), we retained dbh as an indicator of tree size. We determined whether there was an effect of dbh and habitat type on the number of fruits produced per tree, individual seed mass (g) and seed mass per fruit (g) by using an ANCOVA. We also used an ANCOVA to determine any effects on the number of fruits produced and individual seed mass. We used Pearson correlation tests to describe any relationship between dbh and number of fruits, individual seed mass and seed mass per fruit. We also applied a Pearson test to describe the relationship between number of fruits produced and individual seed mass. Additionally, we looked for differences of tree dbh and crown area between habitats with the use of an ANOVA test.

We used linear models for quantitative response variables (seed mass, N and C content, N per seed, total mass, total N, and isotopic values). We applied generalized linear mixed models (GLMM; lmer function from the lme4 package, Bates & Maechler 2009), for binomial-distributed (e.g., germination success, seedling survival) or Poisson-distributed (number of fruits per tree) variables. We analyzed separately maternal seed origin and soil type and the interaction between both variables and included habitat as the fixed main effect with two levels (continuous forest or fragmented forest), plot ($n=8$) as a random effect nested within habitat and reproductive tree as a random effect nested within plot and habitat. Each random effect was compared against nested models using a Chi-square test. We used Wald-Z test for generalized linear mixed models to determine the significance of fixed effects and selected the best models by using the Aikake
Information Criterion (AIC) to compare models including all fixed and random effects and their interactions, against more simplified models.

Finally, we applied a MANOVA test to account for any differences in seedling growth due to maternal origin or soil type, and the interaction between both variables. Root mass fraction, root to shoot ratio, leaf area ratio, specific leaf area and specific stem length were log transformed.

4.3 Results

4.3.1 Fruit and seed production

The number of fruits produced per tree was significantly lower in forest fragments than in continuous forest (Fig. 4.1; $Z = -41.02$, $P < 0.001$). Seed production varied by year and habitat ($Z = -26.54$, $P < 0.001$). Fruit production in the continuous forest decreased by 30% from 2010 to 2011 by 80%. In the year of 2012, fruit production increased in both habitats. However, while fruit crops of 2012 were comparable to fruit production of 2010 in the continuous forest, the number of fruits per trees in the fragmented forest in 2012 represented 60% of the fruit production of 2010.

Results from the ANCOVA reveal that tree size (dbh) had a significant effect on the number of fruits produced per tree ($F_{1, 22} = 6.45$, $P = 0.02$) and on individual seed mass ($F_{1, 298} = 76.37$, $P < 0.001$). We found a significant correlation between tree size and number of fruits produced (Fig. 4.2a; $R = 0.57$, $t = 0.31$, $P < 0.01$) and seed mass (Fig. 4.2b; $R = -0.43$, $t = -2.14$, $P = 0.04$). Habitat type had a significant effect on individual seed mass ($F_{1, 298} = 31.51$, $P <$
0.001) and seed mass per fruit ($F_{1,298} = 4.14, P = 0.05$). Small trees produced fewer fruits with more seeds of low mass in the fragmented forest (Fig. 4.2). We found no significant effect on the number of fruits produced per tree and individual seed mass ($F_{1,298} = 1.54, P = 0.22$). Individual seed mass varied as a function of tree size (Fig. 4.2c; $R = 0.47, t = 2.4, P = 0.03$) but not of fruit production (Fig. 4.2d; $R = 0.1, t = 0.46, P = 0.65$).
**Figure 4.1:** Fruit production in the continuous (n = 19) and fragmented forests (n = 36) from 2010 to 2012. Values are means ± SE.
**Figure 4.2**: Relationships between tree size with (a) fruit production, (b) seed mass per fruit (g), (c) individual seed mass (g). Each dot represents adults at both habitats (n = 22) in the first and second panel, and seed mass (n = 298) in the third panel. Last panel indicates the relationship between individual seed mass and the number of fruit produced per tree.
4.3.2 Seed quality

Seed quality was significantly affected by forest fragmentation (Fig. 4.3a). Seed N and C content were significantly higher in the continuous forest ($F_{1,22} = 4.39, P = 0.04$; $F_{1,22} = 11.48, P <0.01$, respectively). Continuous versus fragmented habitat explain 90% of the variation in seed N content ($\chi^2 = 4.36, P = 0.04$) and 61% in the seed C content ($\chi^2 = 8.57, P <0.01$). Similarly, N content per seed was significantly higher in the continuous forest than the fragmented forest ($F_{1, 22} = 12.58, P <0.01$). The C-to-N ratio did not vary between the two habitats ($F_{1,22} = 2.58, P = 0.12$). Habitat type had no effect on isotopic values for $\delta^{15}$N ($F_{1,22} = 0.77, P = 0.39$) and for $\delta^{13}$C of seeds ($F_{1,22} = 0.01, P = 0.99$). Neither site nor parental tree explained any of the variation for $\delta^{13}$C ($\chi^2 = 3e-04, P =0.99$), or for $\delta^{15}$N ($\chi^2 = 0.83, P =0.36$). Finally, habitat type had a significant effect on total seed mass per tree ($F_{1,22} = 7.15, P = 0.02$) and total N per tree invested in total seed production ($F_{1,22} = 7.70, P = 0.01$). Total seed mass and N invested in seed production was almost two times higher in the continuous forest than in forest fragments (Fig. 4.3a).

Since DBH significantly differ between habitats ($F_{1,22} = 4.14, P = 0.05$), with trees in the continuous forest larger in dbh (147 cm ± 37), than trees from forest fragments (103 cm ± 53), we analyzed seed quality between trees of the same size (> 150 cm dbh). We found that seed mass significantly differ between habitats ($F_{1,14} = 5.92, P = 0.03$), with almost a 38% decrease in seed mass in forest fragments compared to the continuous forest for trees of comparable size (Fig. 4.3b). There were no significant differences between N ($F_{1,14} = 0.55, P = 0.47$), C content ($F_{1,14} = 2.63, P = 0.13$), and the C-to-N ratio ($F_{1,14} = 0.71, P = 0.42$). Differences between the amount of N per seed in continuous forest and fragments were marginally significant ($F_{1,14} = 3.23, P = 0.09$). Maternal seed origin had no effect on isotopic values for $\delta^{15}$N ($F_{1,14} = 18, P = 0.17$).
0.68) and for $\delta^{13}C$ of seeds ($F_{1, 14} = 1.06, P = 0.32$), indicating same potential sources of C and N for parental trees in the continuous and fragmented forests. Habitat had a significant effect on total seed mass per tree ($F_{1, 14} = 10.35, P < 0.01$) and total N per tree ($F_{1, 14} = 22.43, P < 0.001$), with a 33% decreased in total seed mass and a 78% reduction in the amount of N invested in fruit production in the fragmented forest (Fig. 4.3b)
Figure 4.3: Results of the seed quality analysis for all reproductive adults from 2012 in the continuous and fragmented forests, including (a) seed nitrogen content, (b) seed carbon content, (c) seed mass, (d) nitrogen per seed, (e) total mass per crop and (f) total N per crop sorted by maternal habitat.
Figure 4.4: Results of the seed quality analysis for individuals of same size in 2012 in the continuous and fragmented forests, including (a) seed nitrogen content, (b) seed carbon content, (c) seed mass, (d) nitrogen per seed, (e) total mass per crop and (f) total N per crop sorted by maternal habitat.
4.3.3 Seed N content tradeoffs and seed germination

The amount of nitrogen invested in a single seed was lower in trees from fragmented sites when compared to continuous forest ones (Fig. 4.3). We found a significant trade-off between seed quantity and quality; if trees from fragmented sites were to produce seeds of equal quality to those from continuous forests, seed production would decrease from about 50 seeds per tree to about 23 seeds per tree. Conversely, if trees from continuous forests were to produce seeds with the N content of trees from fragmented sites, trees in continuous forest could more than double their seed quantity production (195 to 495 seeds per tree). This seed quality trade off cause by habitat fragmentation affected seed germination. Maternal seed origin, but not soil type, had a significant effect on seed germination success \((Z = 2.93, P < 0.01)\), with 257 seeds that germinated, 55.25% were from the continuous forest while 44.75% were from the fragmented forest.

4.3.4 Soil quality

Soil C-to-N ratio was significantly lower in forest fragments at depths of 10 cm than at 20 cm, while soil C and N content remained unaffected at both habitats and different depths (Table 4.2). Site effects did not explain any of the variation in C-to-N ratio at 10 cm \((\chi^2 = 2.55, P = 0.11)\) or at 20 cm \((\chi^2 = 0.65, P = 0.42)\). Isotopic values for \(\delta^{15}N\) were higher in soils at 10 cm and 20 cm (Table 4.2) from the continuous forest when compared to soils from fragments, while isotopic values showed no significant degree of variability between habitats for \(\delta^{13}C\) (Table 4.2). Additionally, soils from the continuous forest accumulated more water (RWC) at deeper soils (20cm) than forest fragments (Table 4.2). Site effects did not explain the variation of RWC between habitats \((\chi^2 = 1.95, P = 0.16)\).
<table>
<thead>
<tr>
<th>Depth</th>
<th>Parameters</th>
<th>Continuous forest</th>
<th>Fragmented forest</th>
<th>Statistical tests</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-10 C g/m²</td>
<td>8.75±2.29</td>
<td>10.38±5.72</td>
<td>F = 1.4&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>0-10 N (g/m²)</td>
<td>0.85±0.19</td>
<td>0.94±0.48</td>
<td>F = 0.5&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>0-10cm C/N</td>
<td>19.19±0.90</td>
<td>10.89±1.10</td>
<td>F = 4.8&lt;sup&gt;*&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>δ¹³C (%/oo)</td>
<td>-27.13±0.66</td>
<td>-27.11±0.92</td>
<td>F = 0.004&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>δ¹⁵N (%/oo)</td>
<td>4.64±1.47</td>
<td>3.77±0.95</td>
<td>F = 4.9&lt;sup&gt;*&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>RWC (%)</td>
<td>20.13±6.26</td>
<td>17.63±8.16</td>
<td>F = 1.2&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>10-20 C g/m²</td>
<td>6.65±1.52</td>
<td>8.45±4.55</td>
<td>F = 2.8&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>10-20 N (g/m²)</td>
<td>0.70±0.13</td>
<td>0.78±0.40</td>
<td>F = 0.7&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>10-20cm C/N</td>
<td>9.44±0.55</td>
<td>10.65±1.18</td>
<td>F = 17.08&lt;sup&gt;**&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>δ¹³C (%/oo)</td>
<td>-26.51±0.65</td>
<td>-26.52±1.12</td>
<td>F = 0.0004&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>δ¹⁵N (%/oo)</td>
<td>5.68±0.74</td>
<td>4.17±0.89</td>
<td>F = 33.66&lt;sup&gt;**&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>RWC (%)</td>
<td>18.40±5.18</td>
<td>15.05±2.72</td>
<td>F = 6.45&lt;sup&gt;*&lt;/sup&gt;</td>
<td></td>
</tr>
</tbody>
</table>

Table 4.2: Carbon, Nitrogen and the isotopic composition of soil samples (n = 40) from the continuous and fragmented forests collected at 10cm and 20cm depth. Numbers indicate means ± SD. <sup>NS</sup> no statistical significance; <sup>*</sup> significant at P < 0.05; <sup>**</sup> significant at < 0.001.

4.3.5 Seedling performance

Early seedling survival was negatively affected in fragments (Figure 4.5). Survivorship in the growing house was significantly lower for seedlings from the fragmented forest grown in soil from forest fragments (Z = -26.54, P < 0.001).
Figure 4.5: Mean (± SE) survival of seedlings (n = 200) from the growing experiment sorted by maternal seed origin and soil condition.
Results of the MANOVA (Table 4.3) indicated that while seedling growth was not significantly affected by maternal seed origin ($F_{9, 200} = 1.31, P = 0.23$), soil condition had a strong effect ($F_{9, 200} = 4.81, P < 0.001$). Maternal seed origin significantly affected root-to-shoot ratio and specific stem length (Table 4.3). Seedlings from the continuous forest had higher root-to-shoot ratios but lower specific stem length than seedlings from the fragmented forest. Soil type significantly affected root-to-shoot ratios and stem mass and leaf mass fractions, and specific stem length and leaf area (Table 4.3). Seedlings growing in soil from continuous sites had higher root-to-shoot ratios and greater biomass allocation to leaves.

Seedlings grown in soil from forest fragments had more biomass allocated to stems and longer stems and seedlings with origin in fragmented forest did not allocate higher biomass to roots (Table 4.3), despite poor soil conditions. Total dry mass did not vary with maternal seed origin or soil condition (Table 4.3).
<table>
<thead>
<tr>
<th>Treatment</th>
<th>Parameter</th>
<th>Continuous forest</th>
<th>Fragmented forest</th>
<th>Statistical test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal seed</td>
<td>TDM (g)</td>
<td>8.76 ± 5.09</td>
<td>8.51 ± 5.34</td>
<td>$F = 0.44^{\text{NS}}$</td>
</tr>
<tr>
<td>origin</td>
<td>RMF (gg$^{-1}$)</td>
<td>0.26 ± 0.07</td>
<td>0.27 ± 0.07</td>
<td>$F = 1.30^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>LMF (gg$^{-1}$)</td>
<td>0.38 ± 0.12</td>
<td>0.39 ± 0.09</td>
<td>$F = 0.64^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>SMF (gg$^{-1}$)</td>
<td>0.36 ± 0.08</td>
<td>0.33 ± 0.06</td>
<td>$F = 1.69^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>R/S ratio</td>
<td>0.85 ± 0.28</td>
<td>0.76 ± 0.23</td>
<td>$F = 6.05^*       $</td>
</tr>
<tr>
<td></td>
<td>SSL (cm)</td>
<td>14.67 ± 7.35</td>
<td>26.17 ± 5.99</td>
<td>$F = 5.19^*$</td>
</tr>
<tr>
<td></td>
<td>LAR (cm$^2$g$^{-1}$)</td>
<td>11.95 ± 6.36</td>
<td>12.03 ± 6.11</td>
<td>$F = 0.49^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>SLA (cm$^2$g$^{-1}$)</td>
<td>36.07 ± 2.98</td>
<td>33.67 ± 2.86</td>
<td>$F = 0.12^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>Leaf number</td>
<td>5.79 ± 2.27</td>
<td>5.77 ± 2.07</td>
<td>$F = 0.002^{\text{NS}}$</td>
</tr>
<tr>
<td>Soil origin</td>
<td>TDM (g)</td>
<td>8.30 ± 4.80</td>
<td>9.16 ± 5.68</td>
<td>$F = 1.3^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>RMF (gg$^{-1}$)</td>
<td>0.26 ± 0.07</td>
<td>0.27 ± 0.07</td>
<td>$F = 6.7^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>LMF (gg$^{-1}$)</td>
<td>0.41 ± 0.11</td>
<td>0.35 ± 0.11</td>
<td>$F = 15.3^{**}$</td>
</tr>
<tr>
<td></td>
<td>SMF (gg$^{-1}$)</td>
<td>0.33 ± 0.07</td>
<td>0.38 ± 0.07</td>
<td>$F = 28.4^{**}$</td>
</tr>
<tr>
<td></td>
<td>R/S ratio</td>
<td>0.83 ± 0.27</td>
<td>0.74 ± 0.22</td>
<td>$F = 8.1^*$</td>
</tr>
<tr>
<td></td>
<td>SSL (cm)</td>
<td>15.73 ± 3.88</td>
<td>22.06 ± 3.20</td>
<td>$F = 9.9^*$</td>
</tr>
<tr>
<td></td>
<td>LAR (cm$^2$g$^{-1}$)</td>
<td>12.99 ± 6.56</td>
<td>10.57 ± 5.50</td>
<td>$F = 0.01^{\text{NS}}$</td>
</tr>
<tr>
<td></td>
<td>SLA (cm$^2$g$^{-1}$)</td>
<td>34.22 ± 2.57</td>
<td>36.28 ± 3.37</td>
<td>$F = 13.5^{**}$</td>
</tr>
<tr>
<td></td>
<td>Leaf number</td>
<td>5.97 ± 2.12</td>
<td>5.51 ± 2.24</td>
<td>$F = 2.3^{\text{NS}}$</td>
</tr>
</tbody>
</table>

Table 4.3: Mean ($\pm$ SD) seedling growth ($n = 200$) based on maternal seed origin and soil origin, organized by growth parameters. $^{\text{NS}}$ no statistical significance; * significant at $P < 0.05$; ** significant at $< 0.001$.

We found a strong interaction of maternal seed origin and soil condition on stem mass and leaf mass allocation, specific leaf area and leaf area ratio (Table 4.4). Greater biomass was
allocated to leaves by seedlings from and grown in soil from the continuous forest when compared to seedlings from the other treatments (Table 4.4). A post-hoc analysis also revealed greater biomass allocation to stems for seedlings from the continuous forest grown in soil from forest fragments (Table 4.4). Finally, seedlings from and grown in soil from forest fragments had thicker leaves (reduced SLA and leaf area) when compared to the other treatments (Table 4.4).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Continuous forest</th>
<th>Fragmented forest</th>
<th>Continuous forest</th>
<th>Fragmented forest</th>
<th>Statistical test</th>
</tr>
</thead>
<tbody>
<tr>
<td>TDM (g)</td>
<td>8.63 ± 4.81</td>
<td>7.81 ± 4.80</td>
<td>8.95 ± 5.52</td>
<td>9.43 ± 5.93</td>
<td>F = 0.7&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>RMF (g g&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.25 ± 0.06</td>
<td>0.28 ± 0.08</td>
<td>0.28 ± 0.07</td>
<td>0.27 ± 0.06</td>
<td>F = 2.3&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>LMF (g g&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.42 ± 0.11</td>
<td>0.40 ± 0.09</td>
<td>0.32 ± 0.12</td>
<td>0.38 ± 0.09</td>
<td>F = 6.7&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>SMF (g g&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.33 ± 0.07</td>
<td>0.33 ± 0.06</td>
<td>0.40 ± 0.07</td>
<td>0.35 ± 0.07</td>
<td>F = 5.3&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>R/S ratio</td>
<td>0.79 ± 0.25</td>
<td>0.89 ± 0.30</td>
<td>0.70 ± 0.18</td>
<td>0.79 ± 0.25</td>
<td>F = 0.04&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>SSL (cm)</td>
<td>16.24 ± 1.33</td>
<td>30.73 ± 4.69</td>
<td>12.30 ± 1.65</td>
<td>20.23 ± 5.60</td>
<td>F = 2.4&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>LAR (cm&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>12.67 ± 7.20</td>
<td>13.47 ± 5.49</td>
<td>10.89 ± 4.72</td>
<td>10.14 ± 6.43</td>
<td>F = 12.5&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>SLA (cm&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>30.98 ± 1.61</td>
<td>39.05 ± 3.52</td>
<td>43.66 ± 4.18</td>
<td>26.65 ± 1.40</td>
<td>F = 7.9&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Leaf number</td>
<td>6.14 ± 1.93</td>
<td>5.72 ± 2.37</td>
<td>5.26 ± 2.62</td>
<td>5.83 ± 1.63</td>
<td>F = 2.5&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Table 4.4: Mean (± SD) seedling growth (n = 200) based on the interaction between maternal seed origin and soil origin and, organized by growth parameters. NS no statistical significance; *significant at P < 0.05; **significant at < 0.001.
4.4 Discussion

Our results show a clear effect of habitat fragmentation not only in the reproductive potential of *Poulsenia armata* but also in the quality of seeds produced. *Poulsenia armata* trees from fragmented sites produce smaller seeds and invest a disproportionately lower amount of N for fruit production than trees from continuous sites. This trade-off could be a result of the distinct soil and environmental conditions of the fragments that limit resources available to parental trees. The lower quality seeds in fragments results in poor seedling performance and in changes in allocation patterns that may perpetuate a lower N uptake by this species when germinated and grown in fragmented sites. Changes in seedling survival and growth patterns are therefore impacted by parental investment and soil conditions that seem to be additive. This may indicate that maternal effects influenced by environmental conditions have strong effects on *P. armata* performance, anticipating further alterations due to climate change.

Interannual variability in fruit production suggest a strong relationship between allocation of resources to reproduction and climatic conditions as seen elsewhere (Lasso & Ackerman 2013). The year 2011 started with the climatic cycle of La Niña marked by historical droughts in Mexico, United States and West Africa (Lobato-Sanchez et al. 2012). Unfavorable environmental conditions coincided with sensitive stages of *P. armata* reproduction. Earlier phenological records from Los Tuxtlas area, including *P. armata*, show a peak in flower production during the wet season, followed by a major peak in fruit production between April and June (Dunn et al. 2010, Estrada et al. 1999). Flower production of 2011 was preceded by dryer conditions than any other year recorded in this study (see Appendix A); as a result fruit production was significantly lower in 2011 for both habitats. This indicates that *P. armata* is susceptible to fragmented-related environmental effects as evidenced by reduced fruit production.
in 2012 in trees from forest fragments. Sensitivity of *P. armata* to droughts was indicated at Los Tuxtlas area by strong seedling mortality and reduced growth during the severely dry season in 2007 (Martínez-Garza *et al.* 2011). Although annual precipitation of 2011 was higher when compared to years marked by unusual severely dry seasons (e.g. 2007), there was a considerable stronger seasonal variation of rainfall in 2011 (see Appendix A). Changes in seasonal patterns of precipitation have a stronger effect on plant reproduction, than total annual precipitation, especially for moisture-demanding species (Condit 1998) such as *P. armata*.

Plant growth (as an integrator of physiological performance) and tree size strongly influenced fruit production. Parental investment of *P. armata* seems to be limited by tree size, and the amount of fruits produced might be adjusted in response to available resources (see Figure 4.2). With fewer resources available, reproductive trees in fragmented forests experienced a trade-off between seed quantity and quality (N content). This trade-off favoring quantity over quality resulted in seeds with lower germination success and seedling performance in the fragmented forest. Our results were consistent with the idea that larger seeds within the same species result in more competitive seedlings due to greater metabolic reserves (Braza *et al.* 2010, Jacquemyn *et al.* 2001, Jakobsson & Eriksson 2000, Moles & Westoby 2004). Nonetheless, significant differences in offspring performance of *P. armata* are mediated not only by parental investment but also by environmental conditions encountered, in this case in fragmented forest. This is concordant with observation of seedling performance of *P. armata* in the field, where seedlings from the continuous forest showed better survival compared to the fragmented forest where daily temperature were higher (Chapter 2). Additionally, reduced soil nutrient content may also negatively impact offspring performance of *P. armata* in fragmented sites.
Soil resources might be decreasing in forest fragments as evidenced by lower C-to-N ratio and, perhaps, water content. Higher soil $\delta^{15}$N in the continuous forest suggest potential N losses via volatilization and/or denitrification as a result of higher microbial activity or symbiotic fungal communities (Evans 2001). This lost in the amount of soil nitrogen may have resulted in lower N allocation to seeds in trees from continuous sites; however, this was not the case. Individuals in continuous forest sites allocated more resources belowground (rooting depth, mycorrhizal associations) harvesting more N (Dawson et al. 2002). By allocating more resources to roots, seedlings amplify nutrient uptake and provide an advantage for the established seedlings (Breen & Richards 2008). Seedling survival and growth can be improved when grown on improved soil conditions and ambient conditions. However, this was not the case for P. armata seedlings as seedlings from fragments did not improve growth under continuous soils compared with native soils or seedlings from continuous forest. Results of this study suggest that seeds from the fragmented or continuous forests have limited plasticity for biomass allocation. This is consistent with the idea of restricted flexibility of late-successional species compared with species of variable and unpredictable environments (e.g. early successional species, pioneers) (Bazzaz & Pickett 1980). Reduced flexibility has been previously described for P. armata by exhibiting limited plasticity and acclimation when exposed to high irradiance environments (Strauss-Debenedetti & Bazzaz 1991). In this study, seedlings from the fragmented forest growing in soils from fragmented sites appear to be limited to produce enough roots to explore a larger volume of soil needed to compensate for the initial low N seed content. This impairs the ability of offspring from fragmented populations to acquire the necessary nutrients to grow like continuous forest seedlings in soil from continuous sites.
Changes in survival and growth may be an indication that Los Tuxtlas forest may have lost the capacity to cope with disturbance and change possibly affecting resilience to future perturbations. Another possibility is that *P. armata* may not be resilient to forest fragmentation; drought sensitivities for adults of a number of species, including this one, have been reported in Panama (Condit *et al.* 1995, 1996). By reducing seed production and the capacity of seeds to germinate, forest fragmentation may be limiting the seed to seedling transition, affecting *P. armata* ’s long-term persistence. If our results are applicable to other tree species with similar life histories, then we should expect further loss of diversity of the fragmented forest. As anthropogenic forest disturbance progresses, the ability to predict how species respond to changing environments becomes critical if we are to accurately assess the capacity of natural areas to recover and persist in human-modified landscapes.

### 4.5 Conclusion

Assessing the quantity and quality of seeds can give us an indication of the future for fragmented forests. Future studies on reproductive success and plant fitness should incorporate measurements of both seed quantity and quality in terms of seed mass and nutrient component. Evaluation of seedling performance in native and common garden conditions should also be performed for the evaluation of competitiveness change of the offspring. Reduced fruit production and seedling establishment is a serious indication of reduced population viability (Kolb, 2005). Forest fragmentation might be acting as a natural selection force favoring species with morphological and physiological traits that help to maximize nutrient intake in poor soil conditions.
5. POPULATION DYNAMICS OF A LATE-SUCCESSIONAL TREE IN THE FRAGMENTED FOREST OF LOS TUXTLAS, SOUTHERN MEXICO

5.1 Introduction

As burgeoning human populations and industrialization lead to increased deforestation of natural habitats, fragmented landscapes are becoming a common feature of tropical forests worldwide (Laurance & Bierregaard 1997). The investigation of fragmented tropical landscapes has severely increased in recent years (Harrison & Bruna 1999), with many studies documenting decreased biodiversity and species persistence due to habitat fragmentation (Benitez-Malvido 1998, Laurance et al. 1998, Laurance et al. 2000, Benitez-Malvido & Martinez-Ramos 2003, Arroyo-Rodriguez et al. 2007). Populations in fragmented habitats are prone to decrease in size to the extent of local extinction as they become more vulnerable to environmental (Bruna 1999) and genetic stochasticity (Kramer et al. 2008). Reductions in reproductive success (Aguilar et al. 2006), growth and survival (Bruna 2002) have been hypothesized as the main drivers of population decline in forest fragments. A few studies have focused only on the seed and seedling stages of fragmented plant populations (Benitez-Malvido 1998, Cordeiro & Howe 2001, Ashworth & Marti 2011) and are conducted over short periods allowing experimental manipulations in a more straightforward way than following adult individuals. Consequently, we still lack a basic understanding of the demographic mechanisms behind the declines of fragmented plant populations. Such an understanding can only be attained by examining the whole life cycle of the species.

Most of our knowledge on the effects of forest fragmentation on tropical plant population dynamics derives from matrix demographic approaches (see Bruna et al. 2009). Matrix
population models (Caswell 2001) have become a popular tool for describing population
dynamics for several reasons, including their relative simplicity and flexibility to analyze plant
population attributes such as population growth rates ($\lambda$), transient dynamics (Salguero-Gómez &
de Kroon 2010), or contributions to the life cycle of the species from the viewpoint of
conservation efforts (Hodgson et al. 2006). The latter is of utmost interest here, as it allows for
the evaluation of the relative importance of particular life-cycle stages (e.g. juveniles vs. adults)
or a vital rate (e.g. survival, growth, reproduction) through the use of elasticity analyses (Menges
2000). Briefly, elasticities, a technique in the family of perturbation analyses (de Kroon et al.
1986, de Kroon et al. 2000), measure the relative importance of a stage or vital rate by modifying
its value an infinitesimal amount and examining how much the population growth rate would
change. Despite their usefulness, projection matrix models have some limitations when dealing
with life cycles that are best described as a continuous variable such as size (de Kroon et al.
2000, Zuidema & Franco 2001). Integral projection models have recently emerged as a valuable
alternative in this context, as they allow for the modeling of population dynamics based on both
continuous and discrete state variables (reviewed in Easterling et al. 2000, Ellner & Rees 2006).

We explored whether and how forest fragmentation affects the population dynamics of a
long-lived, tropical tree species, *Poulsenia armata* (Moraceae), at Los Tuxtlas area (Southern
Mexico) using IPMs and perturbation analyses. *Poulsenia armata* is a widespread tree occurring
in Neotropical forests from Mexico to Bolivia. Therefore, this tree potentially offers intraspecific
comparisons over millions of km$^2$, allowing insights into variation in vital rates of species with
similar life history traits that may greatly differ from site to site and region to region.
Specifically, we tested for differences in population growth rate and population structure in
fragmented vs. continuous forest populations. Located in the southern part of the state of
Veracruz, Mexico, Los Tuxtlas is an area of great significance as it represents the northern most edge in the distribution of the tropical rain forest in the New World (Dirzo & Garcia 1992). However, railway and highway construction at the beginning of the 20th century have led to increased human population densities and anthropogenic activities, significantly affecting the natural vegetation of Los Tuxtlas; currently only 16% of the original forest persists in the form of an archipelago of small forest fragments (Estrada et al. 1997). Reduced recruitment and fertility have been underlined as major threats to plant persistence in fragmented forests (Aguilar et al. 2006). Though, survival and growth of larger individuals may contribute the most to population growth rate of long-lived trees (Pinero et al. 1984, Bruna et al. 2009). Consequently, if forest fragmentation resulted in effectively decreased adult survival and growth of P. armata, we hypothesized: (1) reduced P. armata densities in the fragmented forest compared to continuous forest, (2) lower population growth rates for fragmented populations of P. armata, and (3) high elasticity values of population growth rate to adult survival and growth. Alternatively, unfavorable changes to plant fecundity in fragments may severely limit plant recruitment leading to reduced population growth rate (Bruna 2003).

5.2 Methods

5.2.1 Study site and species

The study was conducted in the continuous forest and nearby forest fragments at Los Tuxtlas forest in the state of Veracruz, southeastern Mexico (18° 30’N, 95° 04’W, 500 m asl.). The original vegetation of the study site is lowland tropical rainforest (Guevara et al. 2004). Average temperature is 25°C in most of the study area, with slightly lower values (20-22°C) at higher altitudes (Guevara et al. 2004). Mean annual precipitation is 4900 mm, with a relatively
dry period in March-May (111.7 ± 11.7 [SD] mm/mo) and a rainy season in June-February (486 ± 87.0 mm/mo) (Estrada & Coates-Estrada 2002). The predominant land use in this area is conversion of the forest to grassland for cattle ranching (Dirzo & García 1992). The continuous forest of this study encompasses the 64-ha Los Tuxtlas Biological Station created in 1967, which is embedded in Los Tuxtlas Biosphere Reserve (640-ha) (Mendoza et al. 2005).

*Poulsenia armata* (Miq.) Standl. is a shade-tolerant, late successional canopy tree of up to 30 m height (Croat 1978). Individuals are monoecious and produce separate male and female inflorescences. Flowers are insect pollinated with thrips (Thysanoptera) as pollinators (Sakai 2001). Fruits are produced during May-June and October-November. Fruits hold seeds within a thin, smooth coating. Seeds are 7-9 mm long and 5-8 mm wide, and weigh 0.146 ± 0.017 [SD] g. Here, the life cycle of this species is classified in two main stages: juveniles (0-150 cm height) and adults (> 150 cm; Fig. 5.1a).

### 5.2.2 Data collection

In 2010, eight permanent 1-ha permanent vegetation plots were established in Los Tuxtlas forest. Four of these plots were haphazardly selected within the continuous forest (64-ha) based on the presence of individuals of *P. armata*, and established >500 m away from the edge of the forest. The other four 1-ha plots were established at the center of four forest fragments in the surrounding landscape. This study included the forest fragments of Rancho Eugenia (19-ha), Playa Escondida (40-ha), Balzapote (35-ha) and Ruiz Cortines (~20-ha); these fragments have been isolated from the continuous forest for 30-40 yr (Mendoza et al. 2005).
In the first census (May 2010), all living juveniles and adults were geo-located and individually tagged for posterior identification in 2011 and 2012. Every year, we quantified survival, growth and reproduction of the studied individuals, as well as recruitment of new individuals. In established juveniles, we measured basal diameter (cm), whereas in adults we measured dbh (diameter at breast height, at 1.3m; measured in cm). In May of 2011 and 2012, we checked for survival of established individuals, as well as the recruitment of new seedlings, identified by the presence of cotyledons. Seedlings were tagged and included in the study as small juveniles based on basal diameter. In total, 3195 and 3256 individuals of *P. armata* were recorded in the continuous and fragmented forests, from 2010 to 2012.

In order to estimate fecundity of adults of *P. armata*, we combined information from the permanent vegetation plots with data from a greenhouse experiment. During the reproductive season (May-June) of 2010, we collected a random sample of fruits from the continuous and fragmented forests for all reproductive adults. This allowed us to estimate the mean number of seeds per fruit as a function of adult size and habitat type. Pulp was carefully removed from seeds by rubbing them against a fine meshed screen under running water. All seeds were washed for 5 min in a dilute solution of sodium hypochlorite to avoid fungal infection. We then used the collected seeds and recorded their probability of germination over 30 d. Seeds of *P. armata* show no persistent dormancy and have been previously reported to germinate in <30 d (Rodriguez *et al.* 2000). A total of 144 seeds were collected from the continuous forest with 72 seeds planted in individual plastic bags with soil from the continuous forest and 72 seeds planted in soil from the fragmented forest. We applied the same treatment for seeds from the fragmented forest. Seeds were planted under the same conditions at the greenhouse of the Los Tuxtlas Biological Station. The objective was to determine effects of maternal habitat and soil conditions on the germination
probability of *P. armata* in a common garden experiment. These results were then included in our IPM to estimate the per-capita fecundity of adults (below) in the field. In the permanent vegetation plots, we also recorded the reproductive status for each individual as a binomial variable in 2010 and 2011. Finally, we estimated the per-capita fruit production by directly counting fruits on five randomly selected branches per reproductive individual in 2010 and 2011; we multiplied the mean number of fruits per branch by the number of branches to estimate fruit production for each individual.

### 5.2.3 Population structure and density

We tested for differences in population density by counting the number of individuals per plot and annual period, and standardizing by studied area (# ind/m²). We used a linear mixed effects model (*lme* function from the *lme4* R package), comparing continuous and fragmented forests from 2010 to 2012. We specified in our model habitat (continuous vs. fragmented) and vegetation plots (n =8) as fixed effects, and annual period as random effect. Additionally, we tested for differences in population structure of *P. armata* between habitats and annual periods using a two-way ANOVA. Juveniles and adults were analyzed separately to account for the differences in size measurements. All analyses were performed using R (version 2.15.3).

### 5.2.4 Demographic model construction

In order to determine the effects of forest fragmentation on *P. armata*’s population dynamics, we constructed integral projection models (IPMs) using modified code from the R library *IPMpack* (Metcalf *et al.* 2013). IPMs describe population dynamics by linking the size x
distribution of individuals at time \( t \), \( n(x,t) \), to their size \( y \) distribution \( n(y,t+1) \) the next studied period, \( t+1 \) (Easterling et al. 2000).

\[
n(y,t+1) = \int_{L}^{U} K(y,x)n(x,t)dx \quad \text{eqn. 1}
\]

Equation 1 describes how individuals alive in time \( t \) with a given size, \( n(x,t) \), will survive, grow and/or contribute with new recruits to the next yr \( t+1 \), resulting in a specific population structure \( n(y,t+1) \). \( K \) is the kernel that dictates such size-specific survival, growth and reproduction of individuals. This kernel is integrated across the range of possible sizes of all individuals, from \( L \) (minimum size) to \( U \) (maximum; see below) (Ellner & Rees 2006), and is typically decomposed into two sub-kernels: growth conditional on survival \( P \), and fecundity \( F \) (equation 2).

\[
K(x, y) = P(x, y) + F(x, y) \quad \text{eqn. 2}
\]

We made a slight modification to this approach due to the two-stage nature of the life cycle of \( P. \ armsa \) in (Fig. 5.1a). The sub-kernel of growth conditional on survival (equation 3) contains the survival probability \( \sigma(x) \) between time \( t \) and \( t+1 \), which here depends exclusively on the size of individuals \( x \) at time \( t \) (but can also depend on multiple covariates; see Merow et al. 2014), as well as the growth probability \( \gamma(x,y) \) to transition from any given size \( x \) to size \( y \) during such a period.

\[
P(x, y) = \sigma(x) + \gamma(x, y) \quad \text{eqn. 3}
\]

The sub-kernel \( F(x,y) \), on the other hand, informs on the size-specific per-capita contributions to the population via sexual reproduction. Specifically \( F \) calculates the amount and
size of new recruits in \( t+1 \) produced by reproductive individuals in time \( t \). In our specific case, the \( F \) sub-kernel is integrated by six vital rates (equation 4): probability of fruiting in yr \( t \) \( (\phi_1(x)) \), number of fruits produced per reproductive individual in yr \( t \) \( (\phi_2(x)) \), number of seeds per fruit \( (\phi_3) \), germination potential of a seed \( (\phi_4) \), probability of establishment \( (\phi_5) \), and the size distribution of seedlings in time \( t+1 \) \( (\phi_6(y)) \). Here, \( \phi_5 \) is defined as the number of seedlings at time \( t+1 \) divided by the number of reproductive trees in \( t \). We modeled \( \phi_5 \) and \( \phi_4 \) as constants, based on greenhouse experiments described above, while \( \phi_1(x) \) and \( \phi_2(x) \) were significantly predicted by size \( x \) at time \( t \); \( \phi_6(y) \) naturally depended on the size \( y \) of the new recruits entering the life cycle at time \( t+1 \) (see Appendix B for model specification). The latter three vital rates were incorporated in the IPM using generalized linear model, where \( \phi_1(x) \) was modeled using a binomial distribution, \( \phi_2(x) \) with a Poisson distribution, and \( \phi_6(y) \) with a negative binomial distribution to account for overdispersion in the data. For each vital rate parameterization, we use constant, linear, quadratic and cubic functions, and retained the model with the lowest AIC value that was consistent with our knowledge of the biology of the species, as we also did above with the vital rates of the sub-kernel \( P(x,y) \).

\[
F(x,y) = \phi_1(x) \times \phi_2(x) \times \phi_3 \times \phi_4 \times \phi_5 \times \phi_6(y) \quad \text{eqn. 4}
\]

Because there are two stages in the life cycle of \( P. \) armata, both of which were modeled based on continuous variables as size (\( i.e. \) log-basal diameter for juveniles, and log-dbh for adults), we built an IPM using a Goodman’s matrix framework (Goodman 1969, Horvitz & Schemske 1995), which can accommodate demographic dependencies of vital rates by more than one variable (\( i.e. \) Young 1985, van Groenendael & Slim 1988, Zuidema et al. 2009). We modified the overall \( K \) kernel to conform a \( 2 \times 2 \) Goodman’s matrix, as detailed in equation 5.
Our modification of the general IPM following a Goodman’s matrix framework resulted in four sub-kernels. The sub-kernel $P_{\text{Juv,Juv}}(x,y)$ models the survival ($\sigma_{\text{Juv}}(x)$) and growth of juveniles remaining juveniles ($\gamma_{\text{Juv,Juv}}(x,y)$) between times $t$ and $t+1$, using log-basal diameter as the state variable, after having contrasted via AIC scores the resulting models with those using juvenile height instead, which did not perform better (see Appendix B). The sub-kernel $P_{\text{Adu,Juv}}(x,y)$ models the survival ($\sigma_{\text{Juv}}(x)$) and growth of juveniles graduating (i.e. growing > 150 cm height) into the adult stage ($\gamma_{\text{Adu,Juv}}(x,y)$) between census times. This kernel was modeled using log-basal diam for juveniles in $t$ and log-dbh for those juveniles that became adults in $t+1$. The sub-kernel $P_{\text{Adu,Adu}}(x,y)$ encompasses the survival ($\sigma_{\text{Adu}}(x)$) and growth of adults ($\gamma_{\text{Adu,Adu}}(x,y)$) between time $t$ and $t+1$, using log-dbh as state variable. Finally, we modeled the contribution of adults to juveniles via the sub-kernel $F_{\text{Juv,Adu}}(x,y)$ (i.e. reproduction) which represents the per-capita contribution of adults of a given log-dbhs size in time $t$ to new juveniles of a given log-basal diameter size in time $t+1$.

A potential issue when defining the limits of integration in equation 1, is to inadvertently “evict” individuals near the size limits $L$ and $U$ of the integration in equation 1, as individuals may grow or shrink beyond the model size range (Williams et al. 2012). After optimization of mesh points in the IPM (see Appendix B), we used a 149 mesh point resulting in a $150 \times 150$ matrix for all sub-kernels ($P_{\text{Adu,Juv}}(x,y)$, $P_{\text{Adu,Adu}}(x,y)$, $P_{\text{Juv,Juv}}(x,y)$, and $F_{\text{Juv,Adu}}(x,y)$), and a size range for juveniles of 0.05-1.66 cm of log-basal diameter 0.66-10.39 cm log-dbhs for adults. The
resulting $K$ kernel had dimensions $300 \times 300$ when discretized into a matrix. The size mesh and integration range resulted in no eviction of individuals, and a robust estimation of population growth rate ($\lambda$), as checked with the function `convergeIPM` of `IPMpack` (Metcalf et al. 2013).

### 5.2.5 Differences in vital rates within habitats and annual periods

We tested the impact of forest fragmentation on the underlying vital rates in our models by examining whether and how the vital rates of juvenile survival and growth ($P_{\text{Ju},\text{Ju}}(x,y)$), juvenile graduation ($P_{\text{Adu},\text{Ju}}(x,y)$), adult survival and growth ($P_{\text{Adu},\text{Adu}}(x,y)$), and adult reproduction ($F_{\text{Ju},\text{Adu}}(x,y)$), all varied as a function of habitat type (continuous vs. fragmented) and annual period (2010-11, 2011-12). To do so, we applied two-way ANOVA tests and conducted separate analyses for juveniles’ and adults’ demographic processes. Reproduction was described by the probability of reproduction of adults ($\varphi_1(x)$), and the number of fruits produced per reproductive individual ($\varphi_2(x)$). Additionally, we applied paired $t$-tests to determine if plant survival and growth significantly differed between juveniles and adults.

### 5.2.6 Model output: population viability and contributions to the effects of fragmentation

We used the IPMs constructed for each habitat type and annual period to examine differences in population viability and their underlying demographic consequences of habitat fragmentation. We first calculated the deterministic population growth rate ($\lambda$). To compare effects of habitat and annual period on $\lambda$, we re-built IPMs and calculated the resulting $\lambda$ using ordinary non-parametric bootstraps with 999 iterations without replacement, and then tested for significant differences in $\lambda$ for habitats and periods using Kruskal-Wallis tests. To examine the
main drivers of $\lambda$ values, we calculated their elasticities to juvenile survival and growth ($P_{\text{Juv,Juv}}(x,y)$), juvenile graduation ($P_{\text{Adu,Juv}}(x,y)$), adult survival and growth ($P_{\text{Adu,Adu}}(x,y)$), and adult reproduction ($F_{\text{Juv,Adu}}(x,y)$). As we did with $\lambda$, we also ran 999 bootstraps followed by Kruskal-Wallis tests on the resulting elasticities to quantify significant differences among habitats and periods.

Having found striking differences in population growth rates between fragmented and continuous forests and annual periods, we implemented a Life Table Responses Experiment (LTRE) analysis (Caswell 2001, 2010) to explore the basis for such differences. The LTRE analysis, as formulated here (equations 6-9), helps us examine the demographic processes that most contributed to explain differences in population growth rates $\lambda$ as a result of habitat (fragmented or continuous forest) and annual periods (2010-11, 2011-12). The main effects of habitat and annual period and their interaction were calculated following Caswell (2001). The population growth rate of an IPM under a specific habitat and annual period is represented by equation 6.

$$\lambda^{(\text{habitat, period})} = \lambda^{(\ldots)} + \alpha^{\text{habitat}} + \beta^{\text{period}} + \alpha\beta^{(\text{habitat, period})}$$  \hspace{1cm} \text{eqn. 6}

Where $\lambda^{(\ldots)}$ is the dominant eigenvalue of the overall mean of all constructed IPMs, $\alpha^{\text{habitat}}$ is the main effect of habitat, $\beta^{\text{period}}$ is the main effect of annual period, and $\alpha\beta^{(\text{habitat, period})}$ their interaction. To determine the magnitude and direction (positive or negative) of the contribution of each vital rate, main effects habitat and annual period were estimated separately (equations 7 and 8).

$$\alpha^{\text{habitat}} = \sum (K^{\text{habitat}} - K^{(\ldots)}) \partial K^{\text{ref}}$$  \hspace{1cm} \text{eqn. 7}

$$\beta^{\text{period}} = \sum (K^{\text{period}} - K^{(\ldots)}) \partial K^{\text{ref}}$$  \hspace{1cm} \text{eqn. 8}
The main effects were decomposed into contributions from each demographic processes by multiplying the differences between each sub-kernel (i.e., $P_{Adu, Juw}(x, y)$, $P_{Adu, Adu}(x, y)$, $P_{Juw, Juw}(x, y)$, and $F_{Juw, Adu}(x, y)$) by the corresponding sub-kernel from the overall mean kernel ($K$) by the sensitivity from a kernel halfway between the kernel of interest and the overall mean kernel ($K_{ref}$) (Jongejans & de Kroon 2005). The interaction term was calculated following equation 9. This term indicates how much the population growth rate of a specific habitat $\times$ annual period combination departs from an additive model.

$$\alpha \beta^{(\text{habitat, period})} = \sum (K^{\text{habitat, period}} - K^{(\cdot)}) \partial K_{ref} - \alpha^{\text{habitat}} - \beta^{\text{period}}$$

eqn. 9

5.3 Results

5.3.1 Population density and structure

Contrary to expectation, forest fragmentation did not lead to lower population densities of $P. armata$ in the fragmented forest compared to the continuous forest ($t = 0.39, P = 0.70$) and population density did not differ between vegetation plots ($t = 0.25, P = 0.45$). However, we observed significant differences in the population size structure of juveniles (Fig. 5.2a, c) and adults (Figs. 5.2b, d) between habitats. Namely, there was a shift in the population size structure towards more frequent smaller individuals in the fragmented forest (0.47 ± 0.06 cm mean: [SE] log-basal diameter cm) compared to the continuous forest (1.04 ± 0.08 log-basal diameter cm, F = 843.29, P < 0.001). Additionally, we observed strong annual variation of the juvenile size structures in both habitats (F = 23.07, P < 0.001), with the yr of 2012 represented by smaller individuals (0.64 ± 0.06 log-basal diameter cm) than 2010 (0.72 ± 0.07 log-basal diameter cm) and 2011 (0.84 ± 0.08 log-basal diameter cm). The adult size structure remained constant
throughout annual periods \((F = 0.16, P = 0.086)\), but varied significantly between habitats \((F = 35.25, P < 0.001)\). Adults from the fragmented forest were on average smaller \((10.24 \pm 2.90 \log\text{-dbh cm})\) compared continuous forest \((20.68 \pm 3.95 \log\text{-dbh cm})\). Moreover, our estimates of Keyfitz’s \(\Delta\) for all the habitats and annual periods (Table 5.1), which assess the difference between the observed population size/stage structure and the structure that would be expected under stationary conditions, suggest that both populations are rather far from achieving long-term equilibrium \((\text{Keyfitz’ } \Delta < 0.4)\).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Annual period</th>
<th>(\lambda)</th>
<th>Keyfitz’ (\Delta)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continuous</td>
<td>2010-2011</td>
<td>(1.04 \pm 2.58 \times 10^{-5})</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td>2011-2012</td>
<td>(1.00 \pm 2.06 \times 10^{-8})</td>
<td>0.63</td>
</tr>
<tr>
<td>Fragmented</td>
<td>2010-2011</td>
<td>(1.19 \pm 1.43 \times 10^{-5})</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>2011-2012</td>
<td>(1.01 \pm 4.11 \times 10^{-6})</td>
<td>0.64</td>
</tr>
</tbody>
</table>

**Table 5.1**: Mean (± SE) population growth rates \((\lambda)\) for the annual periods 2010-11 and 2011-12 in populations of *Poulsenia armata* of continuous and fragmented forests at Los Tuxtlas. Values of \(\lambda \geq 1\), as obtained here, indicate demographic viability. Keyfitz’ \(\Delta\) reports how close to the observed size/stage structure of juveniles and adults in the population are to the stable stage distribution \(w\) (1: far from stationary equilibrium, 0: exactly as projected at stationary equilibrium conditions).

### 5.3.2 Population growth rates and stable size distribution

The population growth rates of all habitat types \(\times\) annual period combinations were \(\lambda \geq 1\), indicating demographic viability (Table 5.1). Population growth rate was significantly higher \((\chi^2\)
= 1802.81, P < 0.001) in the fragmented forest in 2010-11 when compared to the continuous forest in the same annual period (Table 5.1). In 2011-12, the population growth rate significantly decreased in the fragmented ($\chi^2 = 1790.31, P < 0.001$) and continuous forests ($\chi^2 = 1781.69, P < 0.001$) compared to 2010-2011 (Table 5.1).
**Figure 5.1:** Observed size structure (log scale) of juveniles of *Poulsenia armata* in (a) continuous forest and (b) fragmented forest, and of adults in (c) continuous forest and (d) fragmented forest in the years 2010 (black solid line), 2011 (grey dashed line) and 2012 (black dashed line). Total number of observed individuals during the study are depicted on the top-right corner of each panel.

5.3.3 Variation in demographic functions within habitat and year of transition

Most vital rates (*e.g.* survival, growth) of *P. armata* were appropriately described by linear and polynomial functions of individual basal (juveniles) and at-breast-height (adult)
diameter (Appendix B). Survival was strongly size-dependent for both juveniles (Fig. 5.2) and adults (Fig. 5.3). Moreover, a t-test revealed significant differences between life stages ($t = -9.62$, $P < 0.001$), with juveniles less likely to survive (mean survival $= 0.68 \pm 0.47$ SE) than adults (mean survival $= 0.95 \pm 0.23$). Juveniles of intermediate sizes had a higher survival probability than juvenile individuals of large sizes in all habitats × annual periods combination, except juveniles of fragmented forests in 2011-12 (Fig. 5.2d). Juvenile survival was also highly variable between habitats and annual periods (Table 5.2). Juveniles in continuous forest had greater survivorship (mean $= 0.78 \pm 0.41$) than in forest fragments (0.59 ± 0.30). Moreover, juvenile survival was higher in 2010-11 (0.73 ± 0.44) than in 2011-12 (0.64 ± 0.48). We found a significant interaction of habitat × annual period (Table 5.2), with lower survivorship of juveniles in the fragmented forest, and lower survival in 2011-12 than in 2010-2011 (Fig. 5.2). Similarly, adult survivorship varied between habitats and annual periods (Table 5.2). Adults in continuous forest had greater survivorship (mean $= 0.96 \pm 0.19$) than in forest fragments (0.90 ± 0.28) (Fig. 5.3). Moreover, adult survival was higher in 2010-11 (0.98 ± 0.14) than in 2011-2012 (0.90 ± 0.28).
<table>
<thead>
<tr>
<th>Life stages</th>
<th>Vital rates</th>
<th>Habitat</th>
<th>Annual period</th>
<th>Habitat × annual period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile</td>
<td>$\sigma$</td>
<td>$F = 138.57^{**}$</td>
<td>$F = 26.82^{**}$</td>
<td>$F = 12.65^{**}$</td>
</tr>
<tr>
<td></td>
<td>$\gamma$</td>
<td>$F = 100.67^{**}$</td>
<td>$F = 3.38^{*}$</td>
<td>$F = 2.72^{NS}$</td>
</tr>
<tr>
<td>Adult</td>
<td>$\sigma$</td>
<td>$F = 11.43^{**}$</td>
<td>$F = 21.19^{**}$</td>
<td>$F = 0.37^{NS}$</td>
</tr>
<tr>
<td></td>
<td>$\gamma$</td>
<td>$F = 4.73^{*}$</td>
<td>$F = 0.96^{NS}$</td>
<td>$F = 1.21^{NS}$</td>
</tr>
<tr>
<td></td>
<td>$\phi_1$</td>
<td>$F = 24.15^{**}$</td>
<td>$F = 0.26^{NS}$</td>
<td>$F = 0.29^{NS}$</td>
</tr>
<tr>
<td></td>
<td>$\phi_2$</td>
<td>$F = 5.05^{*}$</td>
<td>$F = 5.76^{*}$</td>
<td>$F = 0.01^{NS}$</td>
</tr>
</tbody>
</table>

Table 5.2: Results of the ANOVA tests showing differences between habitats and annual periods, and the interaction between both for juvenile and adult survival and growth ($\sigma$ & $\gamma$, respectively), juvenile graduation to adults and adult fecundity depicted by fruiting probability ($\phi_1$) and number of fruits per reproductive adult of *Poulsenia armata* ($\phi_2$). $^{NS}$ no statistical significance; $^{*}$ significant at $P < 0.05$; $^{**}$ significant at $< 0.001$. 
Figure 5.2: Fitted survival probabilities of juveniles of *Poulsenia armata* as a function of juvenile size (natural log transformed basal diameter measured in cm) from 2010-11 in (a) continuous forest and (b) fragmented forest and 2011-12 in (c) continuous forest and (d) fragmented forest. Line represents best-fitted model prediction and filled dots indicate survival probability between time $t$ and $t+1$ of juveniles at a given size $x$ at time $t$. 
Figure 5.3: Fitted survival probabilities of adults of *Poulsenia armata* as a function of adult size (natural log transformed DBH, cm) from 2010-11 in (a) continuous forest and (b) fragmented forest and 2011-12 in (c) continuous forest and (d) fragmented forest. Black lines shows best-fitted model prediction; filled dots indicate survival probability between time $t$ and $t+1$ of adults of a given size $x$ at time $t$. 
Juvenile and adult growth was also appropriately described by linear and polynomial functions of size in the previous year (see Appendix B). Adults were characterized by slow growth (0.03 ± 0.004 [SE] log-dbh cm/yr) compared to juveniles (0.20 ± 0.05 log-basal diameter cm/yr; t = -9.04, P < 0.001). Juvenile growth varied across habitats and differences were marginally significant among annual periods (Table 5.2, Fig. 5.4). Growth was higher in the continuous forest (0.78 ± 0.04 log-basal diameter cm/yr) compared to the fragmented forest (0.59 ± 0.05 log-basal diameter cm/yr), and for the annual period 2010-11 (0.73 ± 0.44 log-basal diameter cm/yr) than for 2011-12 (0.60 ± 0.48 log-basal diameter cm/yr). Interestingly, we observed reversion to smaller size (shrinkage) in some large juveniles, but mostly in the fragmented forest (Fig. 5.4d). Adult growth differed between habitats but not among annual periods (Table 5.2, Fig. 5.5). Growth was higher in the continuous forest (0.25 ± 0.06 log-dbh cm/yr) compared to the fragmented forest (0.17 ± 0.05 log-dbh cm/yr).
Figure 5.4: Growth of juveniles of *Poulsenia armata* as a function of juvenile size (natural log transformed basal diameter measured in cm) from 2010-11 in (a) continuous forest and (b) fragmented forest and 2011-12 in (c) continuous forest and (d) fragmented forest. The solid line shows best-fitted model prediction, while the dashed line represents the curve of zero growth during the time interval. Individuals above the 1:1 line increased in size and individuals below the line decreased in size (shrinkage). Filled dots indicate actual size changes of juveniles from a given size $x$ at time $t$ to a given size $y$ the next year.
Figure 5.5: Growth of adults of *Poulsenia armata* as a function of adult size (natural log transformed DBH measured in cm) from 2010-11 in (a) continuous forest and (b) fragmented forest and 2011-12 in (c) continuous forest and (d) fragmented forest. Lines show best-fitted model prediction (grey) and the 1:1 line (black dotted line). Filled dots indicate the probability of a juvenile of size $x$ at time $t$ to move to a different size $y$ during at time $t+1$. 
Adult fecundity was strongly size dependent, with the probability of fruiting \( (\phi_1(x)) \) and number of fruits produced per reproductive individual \( (\phi_2(x)) \) increasing with adult size (Fig. 5.6, Fig. 5.7). The relationship between fruiting probability and adult size was highly variable between habitats, but not among annual periods (Table 5.2). Probability of fruiting was significantly lower in the continuous forest (mean = 0.04 ± 0.01 SE) than in the fragmented forest (0.13 ± 0.03) (Table 5.2). Similarly, the number of fruits per reproductive adult varied among habitats and annual periods (Table 5.2). The number of fruits produced was greater from 2010-2011 (mean = 112.22 ± 17.50 fruits per adult) than from 2011-12 (mean = 70.83 ± 9.18 fruits per adult) and in the continuous forest (134.70 ± 16.0 fruits per adult) when compared to fragmented forest (mean = 61.67 ± 11.91 fruits per adult).
Figure 5.6: Probability of fruiting of *Poulsenia armata*, $\phi_t(x)$, as a function of adult size (natural log transformed DBH, cm) recorded from 2010-11 in (a) continuous forest and (b) fragmented forest and 2011-12 in (c) continuous forest and (d) fragmented forest. Black lines show best-fitted model prediction.
Figure 5.7: Number of fruits produced per reproductive adult of *Poulsenia armata*, $\phi_2(x)$, as a function of their size (natural log transformed DBH, in cm) observed from 2010-11 in (a) continuous forest and (b) fragmented forest and 2011-12 in (c) continuous forest and (d) fragmented forest. Black line shows best-fitted model prediction.
5.3.4 Elasticity and LTRE analyses

Elasticity values, which represent the effects of proportional changes in demographic processes of the IPM onto its population growth rate $\lambda$, varied significantly across habitats (Fig. 5.8). Adult survival and growth, integrated into the sub-kernel $P_{Adu,Adu}(x,y)$ (Fig. 5.1b), were of greater importance to $\lambda$ in both habitats during 2011-12, especially in the continuous forest ($\chi^2 = 1640.95$, $P < 0.001$; Fig. 5.8b). However, juvenile survival and growth, in the sub-kernel $P_{Juv,Juv}(x,y)$, made the largest contribution to population growth rate in the fragmented forest during the first annual period ($\chi^2 = 1645.92$, $P < 0.001$), while adult survival and growth had a stronger impact on $\lambda$ in the continuous forest ($\chi^2 = 1548.71$, $P < 0.001$; Fig. 5.8a). We found that graduation from juveniles to adults, $P_{Adu,Juv}(x,y)$, and adult reproduction, $F_{Juv,Adu}(x,y)$, had the lowest elasticities in both habitats (Figs. 5.8a and b). Finally, graduation from juveniles to adults had a larger relative effect on $\lambda$ in the fragmented forest in both annual periods than in the continuous forest (Fig. 5.8a; 2010-11: $\chi^2 = 1641.11$, $P < 0.001$; 2011-12: $\chi^2 = 1788.46$, $P < 0.001$). Similarly, adult fecundity had a stronger impact on $\lambda$ in the fragmented forest compared to the continuous forest (2010-11: $\chi^2 = 1637.9$, $P < 0.001$; 2011-12: $\chi^2 = 1781.13$, $P < 0.001$).
Figure 5.8: Mean (± SE) elasticity values of various demographic processes to the population growth rates ($\lambda$) of *Poulsenia armata* integral projection models fitted to data from populations in the continuous and fragmented forests during the study periods of (a) 2010-11 and (b) 2011-12. Elasticities were calculated for juvenile survival and growth ($P_{\text{Juva,Juv}(x,y)}$), juvenile graduation ($P_{\text{Adu,Juv}(x,y)}$), adult survival and growth ($P_{\text{Adu,Adu}(x,y)}$), and adult reproduction ($F_{\text{Juva,Adu}(x,y)}$). Asterisks indicate statistically significant ($P < 0.001$) differences for each demographic process within each habitat type.
Our LTRE analysis revealed that juveniles and adults did not contribute equally to the observed differences in population growth rates between habitats and annual periods (Fig. 5.9; Table 5.1). The largest contribution to such differences in $\lambda$ corresponded to adults, where positive contributions of adult fecundity during 2010-11 in the fragmented forest explained most of the variation of $\lambda$ between both habitats (Fig. 5.9a). Graduation from juveniles to adults had an intermediate positive contribution to $\Delta\lambda$ in the annual period of 2010-11. Differences in juvenile and adult survival and growth made lower contributions to $\lambda$, especially during 2011-12 (Fig. 5.0b).
Figure 5.9: Life Table Response Experiment (LTRE) analysis contribution of each demographic process to the differences in population growth rate $\lambda$ between the continuous and fragmented forests during the annual period of (a) 2010-11 and (b) 2011-12 using. The demographic processes are juvenile survival and growth ($P_{\text{juv,juv}}(x,y)$), juvenile graduation ($P_{\text{adu,juv}}(x,y)$), adult survival and growth ($P_{\text{adu,adu}}(x,y)$), and adult reproduction ($F_{\text{juv,adu}}(x,y)$).
5.4 Discussion

The lack of regeneration of tropical late-successional species is of critical concern for the long-term persistence of biodiversity in fragmented landscapes (Cole et al. 2011). Research to date has provided limited answers on how habitat fragmentation affects plant population dynamics. Here we present the first demographic analysis on the effects of forest fragmentation on the dynamics of a late-successional tree, *Poulsenia armata*, in the Mexican forest of Los Tuxtlas, an area of particular interest as it represents the northernmost distribution of tropical rainforest on the American continent. Though forest fragmentation did not consistently reduce population density, and it even resulted in higher population growth rates compared to pristine forests, the dynamics of fragmented populations of *P. armata* differed considerably when compared to populations in its control homologous.

While many studies in fragmented landscapes have documented decreases in population density (Jules 1998, Laurance et al. 1998, ; but see Bruna & Kress 2002), we found the opposite response for *P. armata* at Los Tuxtlas. Here, we report an astonishing increase in population growth rate in 2010-11 and 2011-12 for fragmented habitats compared to our control sites. Our study raising population growth rate values of $\lambda \approx 1$ coincided with reports of several studies on tropical tree demography (Pinero et al. 1984, Alvarez-Buylla 1994, Olmsted & Alvarez-Buylla 1995), indicating that populations in fragmented and continuous forests are viable. Naturally, negative consequences on the dynamics of fragmented populations could take years to become apparent, especially for long-lived tree species as *P. armata* (Martínez-Ramos & Alvarez-Buylla 1998, Zuidema et al. 2009). However, in this study, the population structure differed greatly between habitat types, suggesting an alteration of basic underlying demographic properties due to forest fragmentation. Of particular interest here is the shift in the population structure of *P.*
armata toward smaller sizes in fragmented patches. We argue for increase mortality and fewer individuals attaining adulthood in fragmented populations, as documented for Heliconia acuminata in a fragmented Amazonian forest, where populations are moving towards higher frequencies of smaller individuals (Gagnon et al. 2011). Additionally, we found that the observed size/stage structure obtained for P. armata differed from the expected structure at stationary equilibrium. This agrees with findings from previous manuscripts reporting plants populations being far from predicted stable stage distributions (Horvitz & Schemske 1995, Valverde & Silvertown 1998, Eriksson & Eriksson 2000, but see Williams et al. 2011). Important deviations from stable size distributions may occur in populations due to significant variations in vital rates through time due to environmental stochasticity (Doak & Morris 1999). Los Tuxtlas area is characterized by a recent history of intense anthropogenic activities (Dirzo & García 1992), affecting demographic parameters of P. armata, especially in the fragmented forest where a greater variation in vital rates was followed by the significant shift in size distribution.

Our study revealed that survival and growth of adults (and to a lesser extent of juveniles) were the most important demographic processes for the viability of P. armata in both habitat types. This finding is in agreement with our understanding of life history theory in long-lived organisms (Silvertown et al. 1993). However, we found that annual period, and not just habitat type, had an important effect on the demography of P. armata. Such an annual variability in demographic patterns was showcased by our life table response experiment analysis, and by the elasticity analysis, which together identified 2010-11 as a “good” annual period for juvenile and adult survival and growth, resulting in greater population growth rates than in 2011-12. Differences in population growth rates between both habitat types and annual periods were
mainly explained by the positive contribution of adult fecundity to $\lambda$ in the fragmented forest during 2010-11. Decreased population growth rate in 2011-12 was indeed the result of reduced survival and growth of juveniles in the fragmented forest, while in continuous forest decreased adult survivorship and growth led to decreased population growth rates. The fact that patterns of survival and growth oscillated similarly in the continuous and fragmented forests suggests that this variation may have been controlled by a larger-scale regional driver, likely the climate (Gagnon et al. 211). Significant decreases in juvenile survival and growth during 2011-12 coincided with a record drought induced by La Niña (Lobato-Sanchez et al. 2012). However, observations of lower survival and growth suggest that yr-to-yr variation of environmental conditions affects fragmented populations of $P.\ armata$ more severely than populations in a continuous forest. This pattern might also be the result of significant changes in microclimatic conditions in the forest fragments; positive contribution of fecundity to differences in $\lambda$ between habitats suggests that $P.\ armata$ exhibit different reproduction strategies in the fragmented forest, which could be a key factor for the persistence of this species. Caution should be taken when interpreting results of adult fecundity as seeds germination (included in the $F$ sub-kernel) may be affected by ingestion by mammals prior to germination (Traveset 1998), which was not accounted for in this study. Seed germination of $P.\ armata$ was enhanced for seeds recovered from feces of howler monkeys (Estrada & Coates-Estrada 1986), the primary seed dispersers of this species in this area (Estrada & Coates-Estrada 1984). However, seed germination depends also on abiotic conditions that seem to be more important in explaining differences observed in fecundity of $P.\ armata$. At Los Tuxtlas, altered microclimatic conditions negatively impacted reproduction of fragmented populations of $P.\ armata$, leading to a trade-off favoring seed quantity over quality and reducing offspring performance (Chapter 4). Increased seed mass
favors seedling survival and successful establishment under stressful environmental conditions, even translating into later stages (Moles & Westoby 2004), explaining our observations of reduced survival and growth in the fragmented forest.

Alteration of demographic processes could also be the result of changes in seed dispersal and predation driven by forest fragmentation (Gagnon et al. 2011). Burgeoning human populations in rural tropical regions have accelerated the fragmentation of these natural habitats, severely affecting for instance mammal communities such as birds (Estrada et al. 1997), primates (Harcourt & Doherty 2005), and large rodents (Chiarello 2000). We argue that this may be the case at Los Tuxtlas forest, where declines or local extinction in forest fragments have been documented for howler monkeys (Alouatta palliata) (Arroyo-Rodriguez & Mandujano 2006a). Loss of potential dispersers of P. armata results in limited seed dispersal in forest fragments, increasing the number of undispersed seedlings under reproductive adults (Chapter 2). Moreover, as forest area is reduced and fragmentation progresses, small forest-dwelling rodents may become main seed predators by increasing their abundance in disturbed forests due to competitor release (Arroyo-Rodriguez & Mandujano 2006a). Large-seeded species would be overrepresented on the forest floor because they are less preferred by small mammals (Dirzo et al. 2007), which seems to be the case for P. armata (Chapter 3).

Demographic analyses of dominant species are key to understanding not only population viability but also the conservation status of studied habitats (Hansen et al. 1999). The landscape at Los Tuxtlas has been severely altered by human actions, affecting ~80 percent of the remaining original vegetation, which is now heavily fragmented. Although the population structure of P. armata has been drastically altered in the fragmented forest, population growth rates did not decline. Our findings are consistent with previous work that primary arboreal
elements of unaltered forests are still present in large remnant patches at Los Tuxtlas (Arroyo-Rodriguez & Mandujano 2006b), suggesting that resilience of the fragmented forest may not have been compromised. The demographic attributes of *P. armata* may be promoting local adaptation in fragmented forest, vital to the future long-term persistence of this species.
6. CONCLUSION

The lack of regeneration of tropical late-successional species and the increase of disturbance-adapted species is of critical concern for the long-term persistence of fragmented landscapes. Declines of late-successional tree species have important implications for forest ecosystems such as decreased carbon storage and biomass (Laurance et al. 1997, Nascimento & Laurance 2004) that contribute to greenhouse gas emissions (Laurance et al. 1998). Nutrient cycling also be affected by faster decomposition rates and population turnover as smaller size and low wood density species (e.g. pioneer, invasive species) become more abundant. Additionally, changes in forest composition and structure significantly impact faunal communities, as some species (e.g. birds, large rodents) may be sensitive to reduced forest volume (Terborgh & Weske 1969). Despite the clear impacts of forest fragmentation on plant species, little is known of its consequences on the dynamics of late-successional tree species.

This study showed drastic effects of forest fragmentation on the dynamics of P. armata. Forest fragmentation not only significantly affected P. armata reproductive success by reducing seed quality (Chapter 2), but also lead to changes in regeneration patterns (Chapter 3) and population structure (Chapter 5) when compared to continuous forest. Changes in mammal communities in fragmented forest also affected regeneration of P. armata by decreasing fruit removal (Chapter 4), with significant effects on seedling establishment by limiting the colonization of favorable germination sites; however this was not tested here. Survival and growth of P. armata were negatively impacted in the fragmented forest with desiccation by warmer daily temperatures as the likely cause of mortality. Seedling survival and growth patterns were also impacted by low parental investment and poor soil conditions that seem to be additive. Sensitivity of this species to forest conversion and climatic variability dims its prospects in
highly fragmented landscapes, as negative synergistic effects of both factors are likely to increase over the foreseeable future.

The fact that population density and growth rate did not decline in the fragmented forest implies that despite the severe deforestation of Los Tuxtlas forest, this system appears to be resilient. The resiliency of tropical rainforests has been previously described (Lugo 1995), and is supported by evidence that primary forest is the result of anthropogenic activities dating back to pre-Columbian civilizations (Sanford et al. 1985, Gomez-Pompa 1987). Large remnant patches still possess great conservation value at Los Tuxtlas region (Arroyo-Rodriquez et al. 2009); they should be included in management plans. Another possible explanation for the observations of population density and growth rate is that fragmentation of the forest is a recent phenomenon in Los Tuxtlas forests. Slow-growing species may remain unaffected. However, reduced reproductive success and offspring performance suggest that conditions in forest fragments are detrimental for the regeneration of *P. armata* and are likely jeopardizing long-term persistence of fragmented populations. Developing a mechanistic understanding of how forest fragmentation affects plant population dynamics, as done here, will prove essential for the preservation of natural areas.
7. LITERATURE CITED


Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. Oikos 41:402.


APPENDIX A

Monthly precipitation data from 2007 to 2012, at Los Tuxtlas forest, were plotted with the use of the hydroTSM package in R. This package allows identifying dry and wet months and plots a matrix with color intervals representing monthly precipitation values as rows and years as columns. Monthly precipitation data were obtained from the station located at Los Tuxtlas Biological Station. Since seasonality of precipitation patterns have more severe effects on plant populations than total annual precipitation, we determined variation in precipitation around the annual mean using seasonality indices. These indices estimate variation of seasonal cycle relative to the annual mean and are calculated as follow:

\[
\text{Mean annual maximum value} - \frac{\text{Mean annual minimum value}}{\text{Mean annual value}}
\]

The year 2007 experienced not only a longer dry season compared to other reported years, but also decreased total annual precipitation. Despite this, precipitation during 2007 was marked by a greater seasonality.
Figure A1: Monthly precipitation (mm) data at Los Tuxtlas forest during the period of 2007 to 2012.
<table>
<thead>
<tr>
<th>Year</th>
<th>Annual precipitation (mm)</th>
<th>Seasonality indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>2727</td>
<td>0.19</td>
</tr>
<tr>
<td>2008</td>
<td>3336</td>
<td>0.23</td>
</tr>
<tr>
<td>2009</td>
<td>2889</td>
<td>0.24</td>
</tr>
<tr>
<td>2010</td>
<td>3295</td>
<td>0.24</td>
</tr>
<tr>
<td>2011</td>
<td>3353</td>
<td>0.12</td>
</tr>
<tr>
<td>2012</td>
<td>3738</td>
<td>0.20</td>
</tr>
</tbody>
</table>

*Table A1:* Annual precipitation data during the period of 2007 to 2012 at Los Tuxtlas forest. Variation of monthly precipitation data relative to mean annual value was determined by seasonality indices.
APPENDIX B

Juvenile basal diameter (cm) was selected as the state variable for model parametization as it was a better predictor of size than height (cm) as determined by the AIC values (Table B1). We determined the relationship between various vital rates and plant size ($x$) at the beginning of the annual period $t$ to $t+1$ using linear and polynomial regressions (quadratic and cubic). We retained the models with the lowest AIC values. Best fitted models were nonlinear in several cases and varied depending on habitat and annual period selected (Table B2).

Nonlinear relationships between plant size and vital rates have been recorded by other studies (e.g. Zuidema et al. 2010; Dahlgren & Ehrlen 2011). Even though the use of linear regression has been recommended to model size-dependent variation in survival and growth, tests for nonlinearity are recommended to make demographic models more realistic (Dahlgren et al. 2011).
<table>
<thead>
<tr>
<th>Annual Periods</th>
<th>Habitat</th>
<th>Height</th>
<th>Basal diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010-11</td>
<td>Continuous forest</td>
<td>3964.57</td>
<td>249.62</td>
</tr>
<tr>
<td></td>
<td>Fragmented forest</td>
<td>3782.06</td>
<td>3782.06</td>
</tr>
<tr>
<td>2011-12</td>
<td>Continuous forest</td>
<td>2776.23</td>
<td>358.74</td>
</tr>
<tr>
<td></td>
<td>Fragmented forest</td>
<td>3516.36</td>
<td>3516.36</td>
</tr>
</tbody>
</table>

**Table B1**: Akaike Information Criterion (AIC) values for *Poulsenia armata* juvenile size described by height (cm) and basal diameter (cm) for each habitat and annual periods.
<table>
<thead>
<tr>
<th>Annual Periods</th>
<th>Habitat</th>
<th>Stage</th>
<th>$\sigma(x)$</th>
<th>$\gamma(x,y)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Continuous</td>
<td>Juvenile</td>
<td>$y = -1.96 + 12.22x - 6.53x^2$</td>
<td>$y = 0.20 + 0.51x + 0.44x^2 - 0.17x^3$</td>
</tr>
<tr>
<td></td>
<td>Continuous</td>
<td>Adult</td>
<td>$y = -0.17 + 4.59x$</td>
<td>$y = 0.08 + 0.96x + 0.006x^2$</td>
</tr>
<tr>
<td>2010-11</td>
<td>Fragmented</td>
<td>Juvenile</td>
<td>$y = -0.98 + 5.46x - 2.12x^2$</td>
<td>$y = 0.09 + 0.92x - 0.07x^2$</td>
</tr>
<tr>
<td></td>
<td>Fragmented</td>
<td>Adult</td>
<td>$y = -0.17 + 4.59x$</td>
<td>$y = 0.02 + 0.99x$</td>
</tr>
<tr>
<td></td>
<td>Continuous</td>
<td>Juvenile</td>
<td>$y = -2.21 + 9.03x - 4.42x^2$</td>
<td>$y = 0.08 + 0.92x$</td>
</tr>
<tr>
<td></td>
<td>Continuous</td>
<td>Adult</td>
<td>$y = -26.87 + 80.99x - 73.91x^2 + 22.14x^3$</td>
<td>$y = 0.04 + 0.99x$</td>
</tr>
<tr>
<td>2011-12</td>
<td>Fragmented</td>
<td>Juvenile</td>
<td>$y = -0.66 + 20.7x + 5.10x^2 - 4.08x^3$</td>
<td>$y = 0.06 + 0.90x$</td>
</tr>
<tr>
<td></td>
<td>Fragmented</td>
<td>Adult</td>
<td>$y = 0.52 + 0.93x$</td>
<td>$y = 0.04 + 0.99x - 0.003x^2 + 0.004x^3$</td>
</tr>
</tbody>
</table>

**Table B2:** Parametization of survival $\sigma(x)$ and growth $\gamma(x,y)$ functions of *Poulsenia armata* used to construct projection kernels for each habitat and annual periods.
Limits of IPMs are defined by the number of bins used and the minimum and maximum size of individuals. We first built modeling the sub-kernels with 100 mesh points and the size range described in Rees and Rose (2002), where the limit was set at 0.9 times the observed minimum and 1.1 times the observed maximum size of our entire dataset (refer as Method 1). We included the \textit{diagnosticsPmatrix} function (see Metcalf \textit{et al.} 2013 for details) that provides a series of model diagnostic plots to determine whether the selected number of bins and minimum and maximum sizes were suitable for the IPM model. We determined that, while the selected size range was suitable for juveniles (see Fig. B1a, Fig. B2a, Fig. B3a and Fig. B4a), the size range was inadequate for adults (see Fig. B5a, Fig. B6a, Fig. B7a and Fig. B8a). Therefore, we adjusted the size limits of our sub-kernels to fit the actual range of sizes observed in the data for juveniles (minimum size = 1.7, maximum size = 3.9) and for adults (minimum size = 5.6, maximum size = 232.5) (referred to as Method 2). The selected range did not improve the previous observations on adults (see Fig. B5b, Fig. B6b, Fig. B7b and Fig. B8b), while juveniles remained unchanged (see Fig. B1b, Fig. B2b, Fig. B3b and Fig. B4b). However, when we increased the number of bins to 150 and multiply Model 1 by 2, only for juveniles, the size range resulted in subkernels that avoided accidental individual eviction for adults (see Fig. B5c, Fig. B6c, Fig. B7c and Fig. B8c). By increasing the number of bins to 150, juveniles remain unaffected (see Fig. B1c, Fig. B2c, Fig. B3c and Fig. B4c). Therefore, we selected this range size as well as increased the number of bins to 150 (Method 3) to model our IPMs.
Figure B1: Diagnostic plots for juveniles in the continuous forest from 2010-11 comparing lower and upper size limits and number of bins incorporated in the Integral Population Models, with limits defined by (a) 100 bins and a size range of 0.9 times the observed minimum and 1.1 times the observed maximum (Method 1), (b) 100 bins and a minimum size of 1.7 and maximum size of 3.9 (Method 2) and (c) 150 bins and a minimum size of 1.7 and maximum size of 3.9 (Method 3). Left panels depict current range (black) and extended range (red) and number of bins (blue) used to build Pmatrix, and plotted against each other in the middle panel. Finally, the last panel indicates if the extended size range and increased number of bins are suitable for the selected IPM model.
Figure B2: Diagnostic plots for juveniles in the fragmented forest from 2010-11 for (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.
Figure B3: Diagnostic plots for juveniles in the continuous forest from 2011-12 (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.
Figure B4: Diagnostic plots for juveniles in the fragmented forest from 2011-12 for (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.
Figure B5: Diagnostic plots for adults in the continuous forest from 2010-2011 for (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.
Figure B6: Diagnostic plots for adults in the fragmented forest in 2010 for (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.
Figure B7: Diagnostic plots for adults in the continuous forest from 2011-2012 for (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.
Figure B8: Diagnostic plots for adults in the fragmented forest from 2011-12 for (a) Method 1, (b) Method 2 and (c) Method 3. See figure S7 for detail explanation.