Fire, cattle and soil characteristics affect regeneration of *Attalea phalerata* in a forest-savannah mosaic

Iris Hordijk

February 2017

WAGENINGEN
UNIVERSITY & RESEARCH

Armonía
CONSERVACIÓN DE AVES EN BOLIVIA

Fire, cattle and soil characteristics affect regeneration of *Attalea phalerata* in a forest-savannah mosaic

MSc thesis by Iris E. Hordijk, MSc student Forest and Nature Conservation,
Wageningen University

February 2017

FEM 80436

Supervisor: Prof.dr.ir. L. Poorter, Forest Ecology and Forest Management Group,
Wageningen University

External supervisor: T. Boorsma Msc, Barba Azul Nature Reserve Coordinator,
Asociación Armonía, Santa Cruz, Bolivia

Table of contents

Summary

Justification The palm species *Attalea phalerata* shapes the forest-savannah mosaic in the Beni savannah in Northern Bolivia. *A. phalerata* is an ecosystem engineer, because it dominates the two principal landscape elements; the forest islands and gallery forest. *A. phalerata* is also a vital food and nesting source for numerous plant and animal species, such as the critically endangered blue-throated macaw. The population of this palm species is declining in the forest islands, due to low regeneration.

Aim In this case study on shifting landscape mosaic I examine the (a)biotic factors influencing the population structure and dynamics of *A. phalerata* in the forest islands and gallery forest. The conceptual model hypothesizes that landscape mosaic, density-dependent mortality, environmental conditions and disturbance affect the lifecycle of this palm species.

Study design To study the different habitat types of *A. phalerata* 91 plots of 10x20 meter were established. Data on habitat characteristics, as sand content of the soil, vegetation cover, cattle pressure and position in the landscape mosaic and data of 500 palms and 3700 juveniles on among others condition, fire damage and light availability were collected. Matrix projections were executed to predict population development in 50 years and a structural equation model was developed to reveal causal relations affecting the juvenile density.

Results Matrix projections show that in 50 years the landscape mosaic of the gallery forest is likely to remain stable, but that the forest islands tend to decline in size due to a decrease of juveniles in the forest island edge. Juvenile density is positively related to the condition of the juveniles, the amount of fruits, the bare soil surface, probably because of a reduced competition for resources, and sand content of the soil, which could be a measure for inundation or facilitate root penetration. Juvenile density is indirectly negatively affected by fire because it reduces the condition of the adult and so the fruit production. Juvenile density is also indirectly negatively affected by grazing, which reduces the condition of the juvenile.

Conclusions This study shows that even for *A. phalerata*, a species adapted to a human influenced and dynamic ecosystem, the lifecycle is mostly influenced by disturbance, such as fire and cattle grazing, followed by environmental factors, such as soil characteristics. The population is not resistant to a high cattle and fire disturbance, and soil characteristics, such as sand content and bare soil surface, are important for the juvenile density. To restore the regeneration and population structure on the forest islands it is recommended to reduce cattle pressure and fire frequency.

Keywords: landscape mosaic, *Attalea phalerata*, regeneration, population dynamics, fire, cattle

Introduction

Natural landscapes and how they change over time is directed by dynamic processes on different scales. The landscape is a composition of ecological communities expressed in patches, which together form the landscape mosaic (Watt, 1947). The biodiversity of a landscape is therefore formed by populations or individuals of different species within these patches. At the community level the species within and between patches interact with each other and are influenced by abiotic factors such as nutrients and water (Loreau, 2010; Naeem et al, 2012). Landscapes and species are influenced by human activity and with the high human population pressure in the Anthropocene this alterations become, especially in the tropical regions, more visible than ever (Hansen et al, 2005; Brook et al, 2006).

The palm family (*Arecaceae*) shows distinct spatial patterns of species distribution in landscapes and are often abundant across the (sub)tropical regions on this globe (Dransfield et al, 2008). Palms deliver important products for man, as food, medicine, fuel and construction materials (Balick, 1988; Sosnowska & Balslev, 2009) and are a keystone resource for pollinators and frugivores (Terborgh 1986; Zona & Henderson, 1989). It is identified that there is a knowledge gap on biotic interactions, especially competition and trophic interactions, and that often an important factor is not taken into account in studies on palm distribution in an ecosystem (Eiserhardt et al, 2011). In this case study on shifting landscape mosaic the (a)biotic factors influencing the population structure and dynamics of the palm species *Attalea phalerata* are investigated. *A. phalerata* is an ecosystem engineer, as it dominates the principal landscape elements (Yamashita & de Barros, 1997) and provides an important microhabitat and food source in the dynamic and human influenced Beni savannah of Bolivia (Pimentel & Tabarelli, 2004; Rios & Pacheco, 2006; Corrêa et al, 2012; Galetti & Guimarães Jr, 2013).

The Beni savannah is a landscape which is characterised by a high beta biodiversity promoted by a mosaic of different ecosystems. The ecoregion is therefore identified as a centre of plant diversity and endemism (Mayle et al, 2007). The Beni savannah is a mosaic of rivers, lakes, seasonally inundated savannah and wetlands, riverine gallery forest and forest islands on mounted areas (Mayle et al, 2007). The riverine gallery forest are forest patches next to the river on elevated areas formed by riverine sediment deposition. The forest islands are usually round shaped forest patches on elevated areas in the landscape, formed by anthropogenic influences or termite mounds (Denevan, 1966; Erickson, 1995).

The gallery forest and especially the forest islands are dominated by the palm species *A. phalerata* (Yamashita & de Barros, 1997). *A. phalerata* functions as an ecosystem engineer in the Beni savannah, as it provides a specific microhabitat and a food source for numerous plant, mammal and bird species (Pimentel & Tabarelli, 2004; Rios & Pacheco, 2006; Corrêa et al, 2012; Galetti & Guimarães Jr, 2013). *A. phalerata* has for example been identified as the critical factor for the survival of the endemic and critically endangered Blue-throated Macaw (Hesse & Duffield, 2000; Birdlife, 2015).

The Beni savannah is a seasonally inundated savannah, with an inundation period of eight months from October to May (Haase & Beck, 1989). It is classified as a hydromorphic climatic savannah which means that the savannah is mainly flooded by rainwater and receives limited sediment from the catchment, resulting in a nutrient poor soil (Junk et al, 2011). The forested parts of the savannah are not flooded during the wet season, as these areas are mounted (Mayle et al, 2007). Besides water in the wet season, human induced fire for natural pasture management is an important factor in this dynamic ecosystem in the dry season (Berkunsky et al, 2016).

For the past 12.000 years the Beni savannah has been influenced by human activity (Haase & Beck 1989; Erickson, 2000; Navarro & Maldonado, 2002; Lombardo et al, 2013). The savannah was inhabited by a dense population of pre-Columbian Paleo-Indians who constructed earth mounds, canals and fishing ponds (Denevan, 1966; Erickson, 2000). Nowadays, the main human influences are deforestation for cattle ranching infrastructure, protracted cattle grazing and burning of savannah by farmers to ensure fresh grass sprout for cattle (Killeen, 1991; Killeen et al., 2003; Berkunsky et al, 2016).

The dynamics in the Beni savannah ecosystem affect the population structure of *A. phalerata*. Currently, the population density of *A. phalerata* on the forest islands is decreasing and the population structure is changing due to a low regeneration rate (T. Boorsma, pers. obs.). If in the next 100 years the regeneration rate will not recover, the majority of the palms will disappear (Hennessy, pers.com). This will have consequences for the landscape mosaic as whole, and for the numerous plant animal species which depend on this palm. Unfortunately, the population dynamics of *A. phalerata* is poorly studied and understood in this region. Extensive research on the population structure and the factors influencing the abundance and regeneration of the palm is needed to analyse how the regeneration can be assured (Gould, 2013).

The aim of this study is to identify the current population structure of *A. phalerata* and determine which (a)biotic factors influence its population structure and abundance. The factors landscape mosaic, density-dependent mortality, environmental factors and disturbance are taken into account. The following research questions are formulated:
1. How do forest islands and gallery forest differ in the above mentioned (a)biotic factors and how do these factors affect the abundance and population structure of *A. phalerata*?
2. How do forest islands and gallery forest differ in population structure and dynamics of *A. phalerata*?

Factors influencing the life cycle of A. phalerata

The landscape mosaic, density-dependent mortality, environmental factors and disturbances are chronologically in this order likely to be the most important factors influencing the life cycle of *A. phalerata* from fruit to adult (Fig. 1).

Landscape mosaic According to the theory of island biogeography the smaller the island is, the higher the extinction rate and the more isolated the island is, the lower the immigration rate (MacArthur & Wilson, 1967). I hypothesize that smaller islands and forest fragments have a lower adult palm abundance, due to stronger edge effects such as wind intensity and inundation, and a higher chance of palm extinction because of a smaller population size (Williams-Linera, 1990; Souza & Martins, 2004). Also, more isolated forest islands are less frequently visited by potential pollinators and dispersers, and it is therefore expected that the immigration and regeneration rate will be lower (Frankham, 2005). At the edge of a forest there is a different microclimate and a higher disturbance frequency compared to the centre. Light availability and wind intensity are higher and trees are more exposed to inundation, fire and browsing by cattle at the forest edge (Williams-Linera, 1990; Camargo & Kapos, 1995; Cochrane & Laurance, 2002). I hypothesize that, despite the higher light intensity, at the forest edge there is a decreased population density due to an increased disturbance intensity compared to the centre.

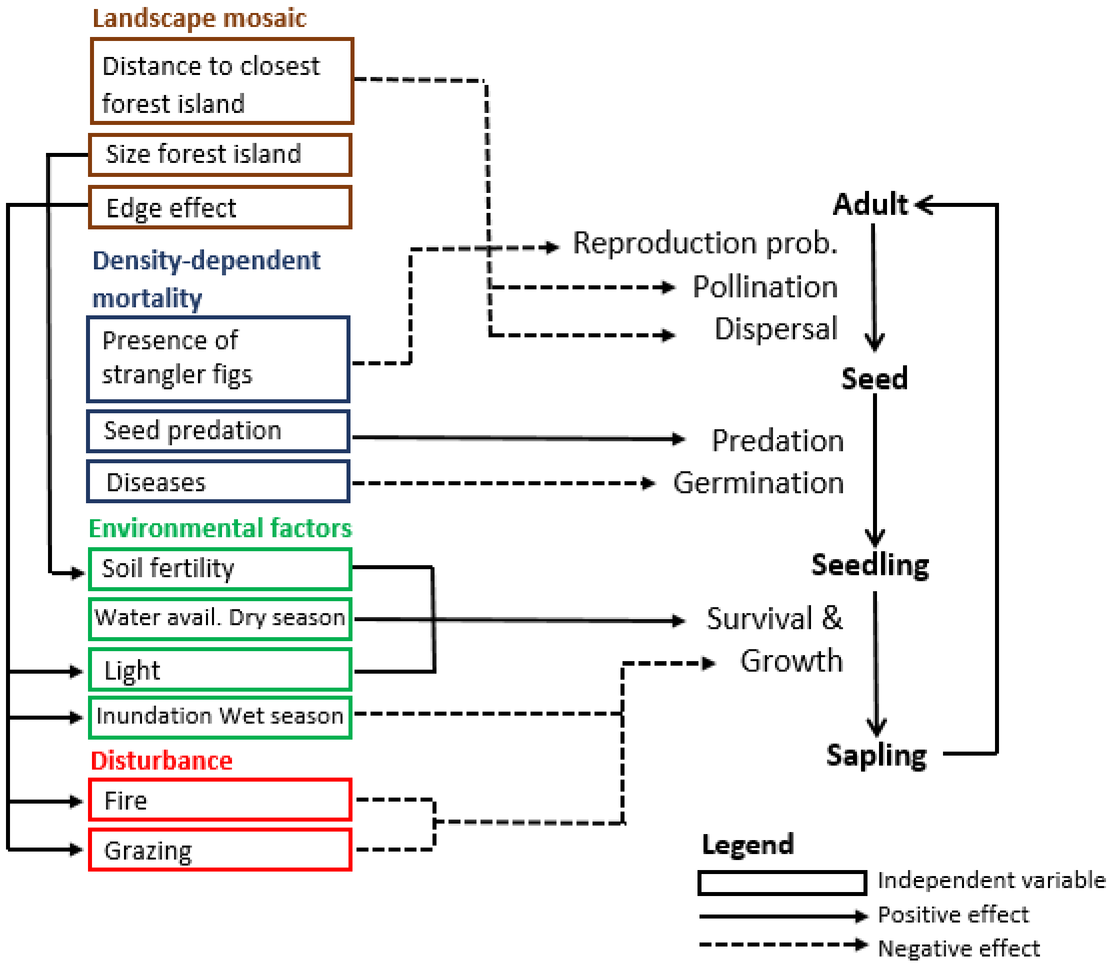

Fig. 1. Conceptual model shows effect of landscape mosaic, density-dependent mortality, environmental factors and disturbance on the life cycle of *A. phalerata*. At the right hand side the life cycle is displayed with the life stages seed, seedling, sapling and adult. In between the life stages the regeneration processes are placed. At the left hand side the abiotic and biotic factors are grouped in categories and with arrows the expected relation with the regeneration processes are visualised.

Density dependent mortality Density-dependent mortality is defined as the increased chance of being killed or affected by a host-specific enemy with a higher density of hosts present (Janzen, 1970; Connell, 1971). In this study the density-dependent mortality will focus on seed predation, presence of strangler figs and the occurrence of diseases. Seed predation by bruchid beetles (*Pachymerus cardo*) has a negative effect on the seed viability, is density-dependent (Salm, 2006; Giroldo et al, 2012) and occurs especially in large-seed palms such as *A. phalerata* (Salm, 2006; Giroldo et al, 2012; Quiroga-Castro & Roldán, 2001). The presence of strangler figs (*Ficus spp.*) do have a negative effect on the survival of adult *A. phalerata* as it competes for light, nutrients and eventually the palm is strangled (Daniels & Lawton, 1991). The presence of the strangler fig is mainly related to the amount and size of suitable hosts present (Athreya, 1999; Male & Roberts, 2005). Beside the strangler fig, there are density-dependent parasites and diseases present which can affect the survival of *A. phalerata* in different life stages (Gilbert & Webb, 2007). I expect a negative relation between the population density and seed predation rate, presence of strangler figs and diseases.

Environmental factors Environmental factors such as soil properties, inundation and light availability have an influence on the survival and regeneration of *A. phalerata*. This palm species prefers basic soils with a pH between 5 and 6, a low sand content and a relative higher content of available cations compared to other *Attalea* species. This indicates that the *A. phalerata* is either intolerant to high available aluminium concentrations or has high nutrient requirements (Haase, 1990; Grégoire, 2010). I therefore expect that a high nutrient content, alkalinity and a low sand content are positively related to the density of seedlings and palms. As for inundation, *A. phalerata* is perfectly suitable for a seasonally flooded environment because it is adapted to waterlogged soils, and it therefore occurs close to streams and in floodplains (Normand et al, 2006; Salm et al, 2015). The palm abundance and the proximity to the nearest river are expected to be positively correlated, because this palm is adapted to high water levels and needs sufficient water. *A. phalerata* is a pioneer species and therefore associated with a high light demand, this species has consequently a medium shade tolerance and the adult palms are expected to be the most abundant when sufficient light is available (Fredericksen, 1999; Giroldo et al, 2012). At the other hand shading stimulates germination because of the enhanced soil moisture, therefore more seedlings are expected in a more shaded environment as the gallery forest compared to the forest islands (Anderson et al, 1991).

Disturbance The factor disturbance such as human induced fire and cattle grazing affect palm regeneration. Farmers set fire to the savannah in order to fertilise the soil, and create grass with high nutrient concentration to provide high quality fodder for their cattle (Killeen, 1991; Berkunsky et al, 2016). The grazing pressure is high in the Beni savannah and I expect that this has a negative effect on the regeneration of *A. phalerata*, because seedlings and saplings are eaten and trampled by cattle (Yamashita & de Barros, 1997). A higher grazing pressure is expected in the forest islands, as these small forest fragments are surrounded by cattle grazed savannah. Adult palms of the *Attalea* genus are fire resistant, because the apical meristem is covered and well insulated by leaf bases which protects the palm against high temperatures during fire (McPherson & Williams 1998; Souza et al, 2000). In contrast, seedlings and saplings are negatively affected by the presence of fire because of their superficial meristem position (McPherson & Williams, 1998; Souza & Martins, 2004). Moderate fires do not affect germination, but intense fires strongly reduce germination by damaging the fruit (Anderson et al, 1991). In case the fire frequency is too high, the population is not able to recover (Hoffmann, 1999). Also, fire has a stronger affect in the smaller forest islands because the population growth rate is more negatively affected (Souza & Martins, 2004). I expect that fire frequency and intensity have a negative effect on seedling density and that the forest islands experience a higher fire frequency than the gallery forest.

Methods

Study area

The Beni savannah is located in the lowlands of the southwestern Amazon Basin, in the North of Bolivia. This flat lowland area covers 160.000 km^2 and is flanked by the Precambrian shield to the East and the Andes to the West (Mayle et al, 2007). The study area is located in the Barba Azul Nature Reserve, situated in the centre of the Beni savannah 13°45'44.50"S 66° 5'53.69"W, Beni department, Bolivia. Mean annual temperature in the Beni savannah is 26ºC and mean annual precipitation is 1800 mm/yr., the majority of the precipitation falls during the eight months wet season when the savannah becomes inundated (Haase & Beck 1989; Miranda, 2000). Fieldwork was conducted in August and September during the last two months of the dry season.

Biology of Attalea phalerata

The habitat of *A. phalerata* spreads from up to 1000 meter in the Brazilian highlands to the terra firme forests, seasonally flooded forests, semideciduous forests and forest islands in wet savannahs in the Amazon in Brazil, Peru and Bolivia (Moraes, 1989; Moraes, 1993; Henderson, 1994). *A. phalerata* is a single stemmed palm species, the stem can reach 10 meters in height and 100 cm in diameter (Moraes, 1996). The crown consists of 15-20 arching leaves and the staminate and pistillate inflorescence are placed in between the leaves, unisexual and occur on the same plant. The palm may flower throughout the year and the most important pollinators are nitidulid beetles of the genus *Mystrops*. The infructescences are pendulous along the stem with 350-500 fruits which have a yellow-orange colour when they are mature. Each fruits has 2-5 seeds, the endocarp is 4.6-5 cm long and has an elliptic shape (Moraes, 1996). The seeds germinate after three months, both removal of the mesocarp and shading, which enhances soil moisture, stimulate germination (Anderson et al, 1991). *A. phalerata* becomes reproductive when it is 7-10 years old and the stem is 0-1 meter tall. The palm can reach a maximum age of 100 years (Moraes, 1996).

Research design

The forested area in the Barba Azul Nature Reserve can be divided in riverine gallery forest and 25 forest islands with an average diameter of 50 meter. To study the different habitat types of *A. phalerata* 91 plots of 10x20 meter were established at least 60 meters apart in the centre and edge of gallery forest and forest islands; 25 random plots in the gallery forest centre, 25 plots in the gallery forest edge, 16 plots in the forest island centre and 25 plots in the forest island edge. The area from the forest edge to 10 meters into the gallery forest or forest islands was considered as edge as the *A. phalerata* reaches heights up to 10 meter (Moraes, 1996). The edge plots in the gallery forest and forest island were randomly placed North or South to avoid a bias caused by illumination or surrounding area. In case the diameter of the forest island was less than 40 meters, only an edge plot was established.

To study the transition zone between the gallery forest edge at the savannah side and the savannah, 25 transects were established. Each transect consist of three strips of 10x20 meter separated at least 60 meters directed North or South, depending on the position of the gallery forest. The three plots were randomly situated in the gallery forest centre, transition zone and the savannah. The forest islands do not have a transition zone, as these islands are elevated mounds in the landscape with a clear border.

Plot measurements

To quantify the landscape characteristics, the diameter of the forest islands were measured and the tallest point examined with a Nikon Forestry 550 clinometer. The distance to the nearest other forest island and the distance to the river for every plot was measured in Google Earth (Google Inc., 2016). The grazing intensity was inferred by measuring the number of dung piles and cattle resting places in each plot. To have a measure for competition in every plot the stem diameter at breast height (DBH) was recorded of trees with a DBH > 5 cm and the overall cover of bare soil, leaves, grass and shrubs was scored in percentages. To have an indicator of overall light availability the vegetation height was examined by measuring 10 times the vegetation height along the central line of the plot. In this study soil colour is used as an indicator of soil fertility; the darker the soil, the more organic matter it contains and the more fertile it will be (Jenkinson, 1988 in Craswell & Lefroy 2001). Therefore, at the central line 6 soil samples to 30 centimetres depth were taken with a regular closed hand auger. The soil samples were photographed in the shade and classified in five categories on soil colour according to the Munsell colour classification (Color, 2009). The soil sample in the centre was examined on sand content at 30 centimetres depth with a taste test in percentages and a precision of 20 percent (Forest Service British Columbia, 2016).

Palm measurements

For the 498 adults within the plots, an adult is defined as stemmed *A. phalerata*, the following characteristics were recorded: height was measured with a Nikon Forestry 550 clinometer, DBH, number of leaves, number of inflorescence and number of infructescence. To have a measure for fire intensity and the effect of fire on the adult, the fire scar height and width were recorded to calculate the percentage of the stem scarred. The canopy position was examined with the Dawkins crown position classes, which range from suppressed, intermediate, codominant to dominant (Jennings, 1999). The light availability of the adult was examined with the Dawkins crown illumination classes: 1. No direct light, 2. Lateral light, 3. Some overhead light, 4. Full overhead light, 5. Crown fully exposed (Jennings, 1999). As it is expected that the strangler fig (*Ficus spp.*) affects the condition of the adult, the dominance of the fig was scored in percentage total cover of the adult. The health of adult *A. phalerata* was scored as good, medium or bad based on the condition of the stem and the colour and uniformity of the leaves. Under each adult a 1 m^2 subplot was randomly established to examine the total amount of fruits and the amount of fruits infected by bruchid beetles (*Pachymerus cardo*).

To study the juveniles, defined as *A. phalerata* without a stem, four juvenile subplots of 5 by 5 meter were established in the forest island plots and two subplots were established in the gallery forest plots. In the field it became clear that two subplots were sufficient to give a good estimate of the number of seedlings present in the gallery forest plots, but that four were needed in the forest island plots due to the larger variation in juvenile abundance. For each of the 3699 juveniles the length of the longest leaf and the form of the leaves were noted as together, open or both (Appendix I). To evaluate the condition of the juvenile, the health was scored as bad, medium or good based on the colour and uniformity of the leaves. As a measure for light availability the canopy openness was examined with a spherical densiometer, Forestry Suppliers, Inc. model A.

Data analysis

Abiotic and biotic factors To explore how population characteristics, (a)biotic variables of forest islands and gallery forests were associated, a Principal Component Analysis was used (Appendix II, R package vegan [Oksanen et al, 2016]). From the PCA it became clear that soil colour and sand content are correlated (R^2=-0.17) and dung piles and resting places cattle are correlated (R^2=0.56). To reduce the amount of variables only sand content and dung piles are taken into account, as these can be quantified more precisely. To analyse how habitats differ in population density and (a)biotic variables a two-way Anova with interaction term was performed with habitat and centre as independent variables, using a Tukey HSD as posthoc test (R package stats). The residuals were tested for normality with a Shapiro-Wilk test and the homogeneity of variances was evaluated with a Levene's test. To normalize the data, the variables dung piles, bare soil surface, shrub cover and crown illumination were log10- transformed and the variables distance to the river, grass cover, amount of juveniles, crown position and amount of fruits per subplot were square-root transformed. Data on population characteristics, (a)biotic variables of the gallery forest centre, transition zone and savannah was analysed with a Kruskall-Wallis test with the Dunn test with Bonferroni correction as posthoc analysis. A parametric test was used, as the data was not normally distributed even after a transformation.

Based on the conceptual model (Fig. 1) and field observations a path model was developed, to unravel the mechanism behind the differences in population density between the forest islands and gallery forest. Three different models were developed, a model on plot level, a model on the individual level of the adult and the individual level of the juvenile. Models on different levels were developed to not only answer questions on plot level, but to have a model for the condition of the adult or juvenile on individual level as well. In the models on individual level, the plot number is used as a nesting factor. The variables were analysed with a generalized linear model from the Gaussian family, the regression coefficient was used to quantify the direction of the relationship in the model (lm.beta function from the R package QuantPsyc [Fletcher, 2012]). To test the overall correctness of the whole path model, a structural equation model was used. With structural equation modelling it is not only possible to test the hierarchical relations between variables, but also test the correctness of the whole model (SEM, as implemented in the R package Lavaan [Rosseel, 2012]). A SEM on plot level and a SEM on the individual level of the adults was developed. It was not possible to develop a sound SEM on individual level of the juveniles with the restricted amount of variables on individual level present. The SEM on plot level and individual adult level were merged together with a nested design, with the plot number as nesting factor. As the resulting pathmodels consisted of many variables, the SEM's were constructed starting with the relations to the most important dependent variable. This resulted in different SEM's, with different variables involved. The chosen SEM's were selected on a Chi-square p-value >0.05, the lowest Akaike's Information Criterion (AIC), a Tucker–Lewis index (TLI) >0.95 and a Root Mean Square Error of Approximation (RMSEA) <0.01 indicating an excellent model fit. All statistical analyses were carried out using R Studio v. 3.3.2 (R Development Core Team, 2011).

Population dynamics The population structure of *A. phalerata* was classified in 10 size classes according to leaf length and stem height, corresponding with ontogenetic stadia (Adapted from Paniagua-Zambrana & Moraes 2009, table 1). A matrix model was developed to make predictions on population development for the next 50 years (Appendix III), which is half the life span of *A. phalerata* (Moraes, 1996). The amount of seeds used in the transition matrix are derived from the average amount of germinating seeds per individual per size class. It was assumed that there are on average 3 viable seeds in a fruit not infected by bruchid beetles (Moraes, 1996; Anderson, 1991) and 3% of this seeds will germinate (Quiroga-Castro & Roldán, 2001). In this study the amount of fruits was measured in a 1m^2 plot below each adult. The dispersal radius around the adult is approximately 1.5 m, the amount of fruits was therefore extrapolated to 6,6 m^2; the surface of the dispersal area minus the average surface of the stem.

Table 1. The 10 size classes of *Attalea phalerata* used in this study, based on ontogenetic stage and stem size (Adapted from Paniagua-Zambrana & Moraes (2009))

Class name	**Class description**
Seedling 1 (S1)	Without stem, longest leaf <15 cm in length
Seedling 2 (S2)	Without stem, longest leaf 15 - 30 cm in length
Juvenile 1 (J1)	Without stem, longest leaf >30 cm in length
Juvenile 2 (J2)	Without stem, longest leaf >50 cm in length
Juvenile 3 (J3)	Without stem, longest leaf >100 cm in length
Adult 1 (A1)	Stem 0-1,5 m, longest leaf > 150 cm
Adult 2 (A2)	Stem 1,5 – 3 m
Adult 3 (A3)	Stem 3 – 5 m
Adult 4 (A4)	Stem 5 – 7 m
Adult 5 (A5)	Stem > 7 m

The 3 vital rates used in the projection are derived from data of the closely to *A. Phalerata* related *Orbignya phalerata* in the secondary forest Lago Verde, Mearim Valley of Maranhão in Brazil (Anderson, 1983). This site has a dry season of 5 months, the temperature ranges between 25 ºC to 27 ºC and annual rainfall is 1575 mm/yr (Anderson, 1983; Anderson et al, 1988). The climatic conditions are therefore comparative to our study site, as is the population structure. The matrix models of the forest islands, gallery forest and transition zone were projected in Microsoft Excel 2013 with the programme PopTools version 3.2.5 (Hood, 2010).

Results

The (a)biotic conditions and population abundance in the forest islands and gallery forest

Forest island and gallery forest The comparison between the forest island and gallery forest in (a)biotic conditions indicate that the forest islands are characterised by on average 11% more bare soil surface (ANOVA, p=0.0287) and 12% more grass cover (ANOVA, p=0.016). In the gallery forest the sand content of the soil is 14% higher ((ANOVA, p<0.001), leave cover is 27% higher (ANOVA, p<0.001), shrub cover is on average 7% higher (ANOVA, p=0.012) and the vegetation is 85 cm taller than in the forest islands (ANOVA, p=0.0015). The distance of the gallery forest plots to the river is on average almost 250 m larger than the forest island plots (ANOVA, p<0.001), as also gallery forests are found in old, dried up river arms, indicating that they currently occur in a drier environment. The amount of dung piles is on average 830% higher in the forest islands (ANOVA, p=0), suggesting a higher grazing pressure.

In terms of population abundance there is no difference in adult *A. Phalerata* per ha between the forest islands and the gallery forest (Fig. 2a). The overall canopy position is 13% higher in the forest islands (ANOVA, p=0.003), resulting in a more illuminated crown (ANOVA, p<0.001) and adults have a 17% better condition in the forest islands (ANOVA, p=0), although the percentage stem scarred from fire is 13% higher compared to the gallery forest (ANOVA, p=0.0029). The gallery forest contains on average 47% more fruits in the seedbank (ANOVA, p=0.0002) and there are 9 times more juveniles present (ANOVA, p=0) (Fig. 2b). Juvenile condition is 17% better in the gallery forest (ANOVA, p=0), despite the fact that they receive 8% less light than in the forest island (ANOVA, p=0.001). The diameter of the forest island or distance to the closest forest island did not have a significant effect on the juvenile, adult or fruit abundance in the forest islands.

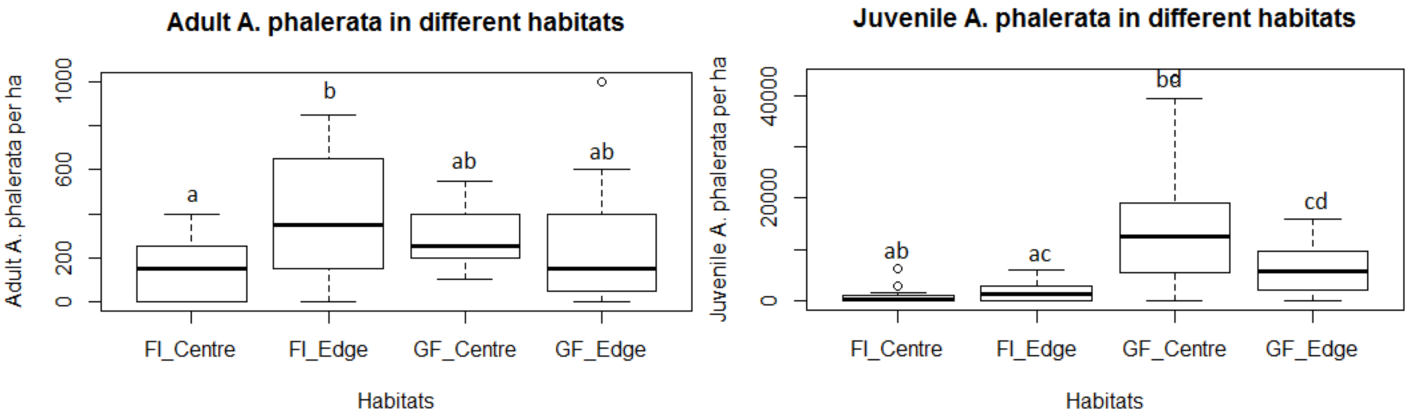

Fig. 2. a) The number of adult *A. phalerata* per habitat displayed in boxplots. b) The number of juvenile *A. phalerata* per habitat displayed in boxplots. FI is an abbreviation for forest island. GF is an abbreviation for gallery forest. Boxplots with a different letter differ significantly (Tukey, p<0.05).

Centre and edge habitat When the centre and edge habitats of both the forest islands and gallery forest are compared, then the condition of adults is 20% better (ANOVA, p=0), the basal area of trees is 5 times higher (ANOVA, p=0.012) and the grass cover is 9% higher (ANOVA, p=0.0014) in the edge, but there are 2 times more juveniles present in the centre (Tukey, p=0.025) (Fig. 2b). In comparison between the centre and edge of the forest island there are 3.7 times more adults present in the edge of the forest island (Tukey, p=0.018) and also the basal area of trees is on average 7.5 times higher in the edge (Tukey, p=0.04). In comparison between the gallery forest edge and centre, there is on average 14% more grass cover in the gallery forest edge (Tukey, p=0.0013).

Savannah transition zone The transition zone shows similarity with the gallery forest centre in sand content, bare soil surface, leave cover, grazing pressure and amount of juveniles. Compared to the gallery forest centre, the transition zone grass cover is 18% higher (Dunn, p=0.007), shrub cover is 4.6% higher (Dunn, p=0.03), the vegetation is on average 5.5 cm taller (Dunn, p=0.0018), there is a 4 times higher cover of trees (Dunn, p=0.0296) and half of the amount of adults is present (Dunn, p=0.003). The transition zone shows no similarity with the savannah according to the investigated (a)biotic factors. The savannah soil has 17% less sand content (Dunn, p=0), the vegetation is 4 times taller (Dunn, p=0.0025), and the grass cover (Dunn, p=0) and amount of dung piles (Dunn, p=0.0287) is 200% higher compared to the transition zone.

The (a)biotic factors influencing the A. phalerata population

The (a)biotic factors and the population structure of *A. phalerata* differs strikingly amongst habitats, and the underlying drivers can be explained using a structural equation model (Fig. 3). The condition of the adults has a positive influence on the fruit production, which has a positive relation with the amount of juveniles. The condition of the adults is explained by the percentage of stem scarred and the number of leaves, but does not have a relation with the density of adults. The models shows as well that the more fruits there are produced, the more fruits are infected by bruchid beetles. The amount of juveniles is explained, besides the amount of fruits, by the condition of the juvenile, bare soil surface and the sand content of the soil. Cattle pressure has a negative relation with the condition of the juveniles and affects indirectly the juvenile density. The density of the adults has a positive effect on the amount of juveniles, but this relation is not significant, resulted in a 10% higher AIC value and is therefore not included in the final model. In the best fitting model on plot level, without a nested design, this relation was significant (Appendix IV).

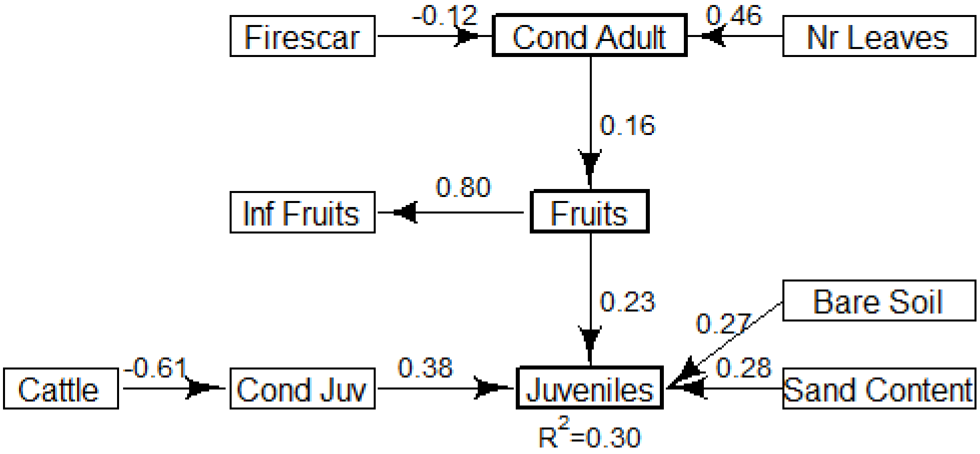

Fig. 3. Results of the best fitting structural equation model (N=91) indicating what (a)biotic factors affect the abundance of juvenile *A. phalerata*. The arrows are indicating a significant relation ($p<0.005$) and the numbers around the arrows are standardized path coefficients. This model explains 30% of the amount of juveniles present.

Population structure and dynamics of the forest islands and gallery forest

Current population structure In the gallery forest there are overall 7.5 times as much individuals as in the forest islands, because the gallery forest has in seedling class 1 to adult class 2 more individuals than in the forest islands (Fig. 4a). The forest island edge had, compared to the centre, more individuals in the seedling and adult classes, but less individuals in the juvenile classes.
The gallery forest edge had, compared to the centre, more individuals in the seedling and juvenile classes and adult class 4 and 5.

The population structure in 50 years The matrix projection indicates that in 50 years the total number of individuals in the gallery forest will increase with 8%, whereas in the forest islands it will decrease with 40% (Fig. 4b). Both the forest islands and gallery forest show an increase in seedling class 1 and adult class 1 and 2, except for the forest island edge. The gallery forest contains more individuals in the seedling and juvenile classes, whereas in adult class 4 and 5 there are more individuals in the forest islands.

In the transition zone between the gallery forest and the savannah there will be a 220% increase of individuals, caused by an increase in seedling class 1 and the adult classes.

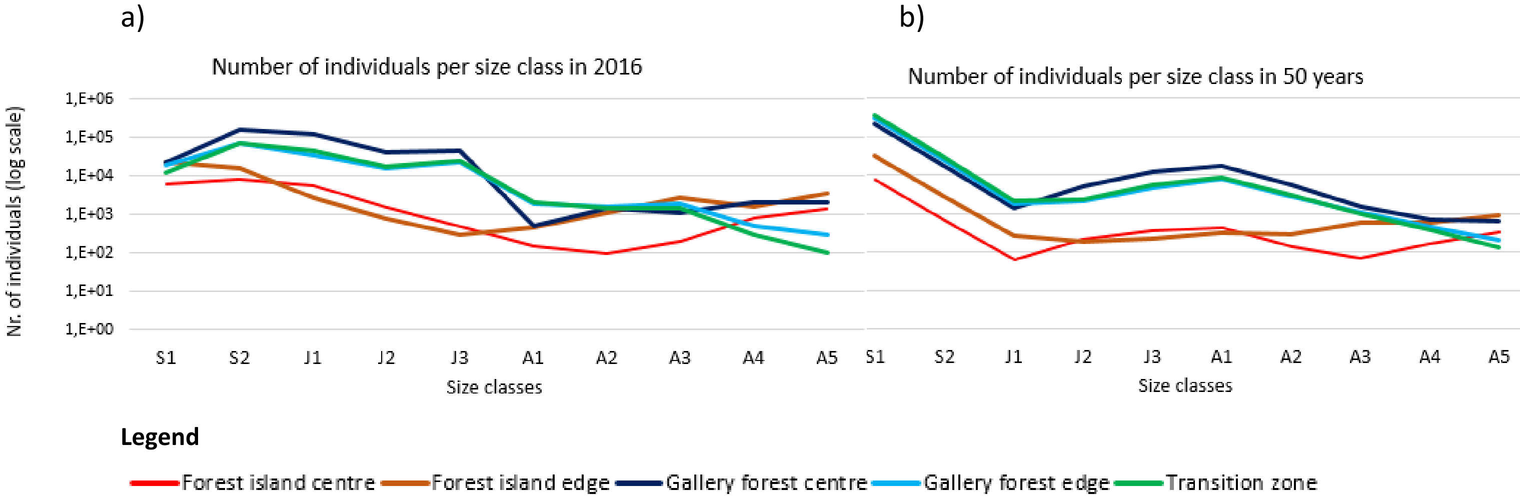

Fig. 4 a) The current population structure of *A. phalerata*, and b) The projected population structure in 50 years. The population structure is shown for five habitats: forest island centre, forest island edge, gallery forest centre, gallery forest centre and the transition zone. The population structure is divided in 10 size classes on a log10 scale.

Discussion

The aim of this study was to identify the current population structure of *A. phalerata* and determine which (a)biotic factors influence its population structure and abundance. The current population structure shows that there are almost 8 times more individuals in the gallery forest in comparison with the forest islands, especially for individuals with a stem height of <5 m. Matrix projections show that in 50 years the gallery forest is likely to remain stable, but that the forest islands tend to decline in size due to a decrease of juveniles in the forest island edge. Juvenile density is positively related to the condition of juveniles, the amount of fruits, the bare soil surface and the sand content of the soil. Juvenile density is indirectly negatively affected by fire and grazing. Here I will first discuss, following the order of the conceptual model, the differences of the (a)biotic factors between the forest islands and gallery forest and the effect of these factors on the population abundance. Second, I discuss what the population structure and dynamics of the forest islands and gallery forest implicate for the landscape mosaic.

Life cycle of A. phalerata is mainly influenced by cattle pressure, fire and condition of adults

In the conceptual model (Fig. 1) I hypothesized that in the lifecycle of *A. phalerata* a high adult density increases fruit production, which positively affect the juvenile density and finally the adult density. From the structural equation model (Fig. 3) it becomes clear that adult density has indeed a positive, but non-significant effect on the fruit production and that the amount of fruits is mainly influenced by the condition of the adults. Nevertheless, the higher fruit production in the gallery forest compared to the forest islands may be explained by the higher amount of adults in the gallery forest. As expected the amount of fruits do partly explain the juvenile density, although the juvenile density does not have a positive effect on the adult density, indicating a high juvenile mortality rate.

Landscape mosaic The distance to the closest forest island and the size of the forest fragment do not affect the population density, however in the centre habitats the juvenile density is higher and in the forest island edge the adult density is higher compared to the forest island centre.

I hypothesized that, in line with the island theory, smaller islands and forest fragments have a lower adult palm abundance, due to stronger edge effects and a higher chance of palm extinction because of a smaller population size (Williams-Linera, 1990; Souza & Martins, 2004). I also hypothesized that isolated islands have a lower regeneration rate due to less pollinators and dispersers (Frankham, 2005). However, I found that the ***size and distance between the forest islands*** in the landscape are in this study not related to the number of fruits, juveniles or adults present on the forest island. The variation in the landscape mosaic should be large enough to detect a relation, as the distance between the forest islands varied 25-fold (from 80 to 2030 meter) and the diameter of the islands 5-fold (from 20 to 100 meter). One reason for the lack of landscape effects could be that edge effect or environmental pressures such as grazing could be more important than the size or position of the habitat fragment (Laurance, 2008).

Pollination and seed dispersal do not seem to be a limiting factor on the life cycle of *A. phalerata*. The pollinators of *A. phalerata* are able to visit all the forest islands, even on the furthest forest islands fruits are found. Also, seed dispersers such as monkeys and several bird species are observed on all forest islands.

I hypothesized that at the ***forest edge*** there is a decreased population density due to an increased disturbance intensity compared to the centre. I found that within the forest islands there is a higher number of adults in the edge, whereas within the gallery forest there is no difference in adults between the centre and edge (Fig. 2a). Also, the condition of the individual adult is in general better in the edge, a possible explanation could be the better access to water at the edge during the dry season or higher nutrient availability trough trapped sediments (Junk et al, 2010). *A. phalerata* is associated with moist conditions in floodplains (Mayle et al, 2007; Normand et al, 2006) and has relatively high nutrient requirements (Haase, 1990; Grégoire, 2010). The average height of the forest islands is 1.3 m with a descending edge towards the savannah, whereas the gallery forest is not as elevated as the forest islands.

There are less juveniles present in the edge habitat compared to the centre, probably because higher grass, shrub and tree cover in the edge result in a stronger competition for nutrient and water resources (Williams-Linera, 1990; Svenning, 2001). Also, as the edge of the forest islands and gallery forest descend towards the savannah the seeds or seedlings could become inundated for a long period during the wet season resulting in anaerobic conditions (Veneklaas et al, 2005; Gurnell et al, 2007).

Density dependent mortality Diseases and strangler fig presence do not influence the population density, bruchid beetles do affect the viability of the fruits.

I hypothesized that seed predation rate, presence of strangler figs and diseases have a negative effect on the density of *A. phalerata* seeds and palms (Fig. 1). There is as expected a positive relation between the number of fruits and number of infected fruits by ***bruchid beetles*** (Fig. 3), because of density-dependent predation (Salm, 2006; Giroldo et al, 2012).

The condition of juveniles should be a reflection of the presence of ***disease*** and as the number of juveniles is positively rather than negatively related (Fig. 3), this indicates that there is no density-dependent mortality caused by diseases and that more vital juveniles may lead to a better survival and higher juvenile abundance. In contrast, the condition of the adult is not related to the number of adults, probably because the number of adults is not as directly affected by the condition of the individual due to an observed high resilience. The condition of the adult is positively related to the fruit production of the individual, therefore indirectly influencing the amount of juveniles (Fig. 3).

Strangler fig presence has neither a significant negative effect on the adult population (Fig. 3). The figs are removed by the reserve coordinator as a management intervention to protect the population of *A. phalerata*, which results in less strangler figs present at the time of data collection. During the fieldwork 19% of the adults hosted a fig, from which only 13% (12 individuals) had a fig cover of ≥50%. Strangler figs are reported to affect the host severely (Daniels & Lawton, 1991; Athreya, 1999; Male & Roberts, 2005) and the number of observations in this study is probably too small to draw a sound conclusion about the effect of the strangler figs on adult *A. phalerata*.

Environmental factors Light and proximity to nearest river do not affect the population density, a higher sand content of the soil enhances the juvenile density.

I hypothesized that a high nutrient content, alkalinity and a low sand content of the ***soil*** are positively related with the density of seedlings and palms, because this species has a suggested high nutrient demand (Haase, 1990; Grégoire, 2010). I found instead that a higher sand content has a positive effect on the amount of juveniles and has no effect on the amount or condition of the adults, probably soil fertility is not the limiting factor for the *A. phalerata* population in this ecosystem. Also, a higher clay and silt content could be a reflection of a longer inundation period (Wittmann et al, 2004; Junk et al, 2010) and a higher soil water retention (Leeper & Uren, 1993). *A. phalerata* occurs in floodplains, but only on elevated terrain (Moraes, 1996; Yamashita & de Barros, 1997; Balslev et al, 2012) and the seedlings are therefore not expected to survive inundation or waterlogged soil for a long period. A clayey soil could also inhibit root penetration, making it more difficult for seedlings to establish (Beck & Beck, 1983; Langstroth, 1996). The soil of the forest islands is lower in sand content compared to the gallery forest, which could be explained by the different origin as the majority of the islands are constructed by man and the gallery forest is established on sediment depositions

(Denevan, 1966; Erickson, 1995). The amount of bare soil surface has a positive effect on the amount of juveniles present. The higher bare soil surface probably diminishes the competition for resources with other plant species.

I hypothesized that the ***proximity to the nearest river*** has a positive effect on palm abundance, because the adult palm is adapted to high water levels and needs sufficient water. I found, however, that distance to river is not related to the amount or condition of juveniles or adults. Distance to river alone is probably not necessarily a good proxy for inundation during the wet season, due to the height differences caused by the landscape relief in the Beni savannah (Erickson, 2000; Mayle et al, 2007). Unfortunately, there is no data available on the height differences in the landscape in the study area.

I hypothesized that sufficient ***light*** enhances the adult density (Fredericksen, 1999; Giroldo et al, 2012) and in a more shaded environment, as the gallery forest compared to the forest islands, the juvenile density is higher (Anderson et al, 1991). I found that a higher canopy position or crown illumination are not related to the adult condition or adult density, probably because light is not the limiting factor for the adults in this ecosystem as nearly all adult crowns are in the forest canopy. The canopy openness above the juveniles is not related to the amount or condition of juveniles. The mean canopy openness above the juveniles is 30% with a standard deviation of 20%, thus the majority of the seeds do germinate in a shaded environment as expected (Anderson et al, 1991).

Disturbance Grazing pressure and fire negatively affects the juvenile density, but do not affect adult density.

I hypothesized that ***grazing*** pressure has a negative effect on the regeneration of *A. phalerata* (Yamashita & de Barros, 1997) (Fig. 1) and that the grazing pressure is higher in the forest islands, as these small forest fragments are surrounded by grazed savannah. Grazing has as expected a negative influence on the amount of juveniles by diminishing the condition of the juveniles through trampling, grazing and soil compaction (Langstroth, 1996; Endress et al, 2004; Shepherd & Ditgen, 2005; Mandle & Ticktin, 2012; Eaton et al, 2016;). Grazing pressure does not have a relation to the amount of adults, but is indeed higher in forest islands compared to the gallery forest.

I hypothesized that ***fire*** frequency and intensity have a negative effect on seedling density and that the forest islands experience a higher fire frequency than the gallery forest because the islands are surrounded by savannah, where the fire arises. I found that fire indeed negatively influenced the condition of the adult (Fig. 4), but did not have a direct effect on adult density. The fire disturbance is measured in fire scar percentage of the stem, which only affects the condition of the adult. *A. phalerata* is a fire adapted species, because the apical meristem is covered and well insulated by leaf bases which protects the palm against high temperatures (Feil, 1996; McPherson & Williams 1998; Souza et al. 2000). The adults in the forest islands do have a higher fire damage compared to the gallery forest as expected. There was no data available on the fire frequency of specific sites.

Implications of population dynamics for the landscape mosaic

In a natural and viable population, the amount of individuals decrease with increasing size class (Felfili, 1997). However, the population structure of *A. phalerata* in the forest islands and gallery forest shows in all habitats (i.e. edge and centre of forest island and gallery forest) less seedlings in the smallest size class (seedling class 1) compared to the next size class (seedling class 2). This population structure could also be a result of size dependent growth and mortality, individuals in seedling class 1 could grow faster or have a higher mortality rate than in seedling class 2 (Rose et al, 2009). This results in more seedlings in class 2, but does not necessarily imply a non-viable population. In the forest islands there are less juveniles and total number of individuals present compared to the gallery forest (Fig. 4a), which is probably caused by a higher cattle pressure, fire disturbance and lower sand content of the soil on the forest islands.

The landscape mosaic formed by the gallery forest will not drastically change in 50 years (Fig. 4b), in case the environmental conditions and disturbance frequency and intensity not alter. The amount of individuals in the adult classes stay stable and the amount of individuals in seedling class 1 increase. The landscape mosaic formed by the forest islands is expected to change in 50 years. The forest islands will decline in number of individuals, especially at the edge. This can have consequences for the diameter of the forest islands in this dynamic ecosystem, as the palms hold the soil together at the island edge (Junk et al, 2010).

The vital rates from a secondary forest are used for the forest islands and the gallery forest matrix projections. The recruitment and mortality rates in this ecosystem are probably higher than in a secondary forest, although this can compensate over time (Felfili 1993, 1995). The vital rates for the forest islands and the gallery forest are the same in this study, although it is expected that the forest islands have a higher mortality rate through the higher environmental stress (MacDougall & Kellman 1992; Kellman et al. 1994). It is expected that the edge habitats experience a higher level of competition compared to the centre due to the higher tree density, this phenomenon is not taken into account as well. It is therefore expected that the decline of the population density in the forest islands will be more severe than presented by the projection.

Management implications

A. phalerata is a robust species, associated with the dynamic floodplain forests (Normand et al, 2006; Mayle et al, 2007) and human settlements (Walker, 2008; Sosnowska et al, 2015). This species is able to recover from disturbances when these are not too frequent or intense. However, with the current population structure the forest islands will strongly diminish in palm abundance in 50 years. The Beni savannah is grazed by cattle and this grazing pressure has a negative effect on the regeneration of *A. phalerata*. With a decreased grazing pressure through rotation of cattle, the condition of the juveniles will improve and the amount of juveniles are expected to rise as observed in regions in the study area where cattle pressure is diminished (Giroldo & Scariot, 2015).

The fire frequency and intensity have a negative influence on the population structure of *A. phalerata*; fire results in a decreased production of fruits, which result in less juveniles. Fire damage is higher in the forest islands, probably because the islands are surrounded by savannah which is the main source of fire. The forest islands should be protected against a high fire intensity and frequency by fire management. Fire can be managed by establishing and maintenance of existing firebreaks, the suppression of fires and controlled burning of savannah (Wilgen et al, 2014).

Strengths and limitations of this study

The strength of this study is that it provides a comprehensive overview which factors may drive the population of *A. phalerata* and how these factors drive the population (Fig. 3). By using a landscape approach and focussing on key landscape elements (forest island and gallery forest) we may get a better insight in the role of this ecosystem engineer in landscape dynamics. Finally, by doing a suite of analyses and structural equations models the differences between the habitats and the most important factors influencing the population of *A. phalerata* are identified.

The limitation of this study is the fact that there is no detailed information on soil properties collected and that there is no information available on fire frequency and height profiles in the Beni savannah. Also, the vital rates used for the matrix projections are not the rates from the studied habitats, but are derived from literature. This was the first study at this site with the intention to monitor the plots and derive vital rates from the site itself.

Suggestions for further research

Research on the effect of different cattle densities, temporal variation in grazing (i.e., rotation of cattle) and fire management (i.e., fire frequency) could help to implement a sustainable management strategy that benefits cattle production but does not modify the landscape mosaic. Furthermore, it is unclear what the tipping points are in the population density; how many individuals are needed for a viable population and under which level the population is not able to recover. In the study area there are permanent plots established in the different habitats and vital rates from the study area could be derived for future projections of population development. As it appeared that the sand content has positive influence on the juvenile density, a more in depth research on the soil characteristics as pH, available aluminium and fertility would be beneficial in understanding the population behaviour in the ecosystem (Haase, 1990; Grégoire, 2010). Also, a detailed elevation and fire disturbance map could shed more light on the dynamics in the landscape mosaic.

Conclusions

This study shows that even for *A. phalerata*, a fire adapted species suitable for a human influenced and dynamic ecosystem, the lifecycle is mostly influenced by disturbances as fire and cattle grazing. Currently there are almost 8 times more individuals in the gallery forest in comparison with the forest islands, mainly caused by a difference in juveniles. It is expected that in 50 years the landscape mosaic of the gallery forest will remain stable, but that the forest islands will decline in population density. Especially the juvenile density in the forest island edge will decrease, possibly leading to a decrease in island size. The juvenile density is positively related with the condition of the juveniles, the amount of fruits, the bare soil surface and sand content of the soil. The juvenile density is indirect negatively affected by fire, which affects the condition of the adult and therefore the fruit production, and grazing, which negatively affects the condition of the juvenile. In the forest islands the grazing pressure and fire damage is higher, and sand content is lower compared to the gallery forest. With management measures decreasing the grazing pressure and fire frequency on the forest islands it is expected that the population of *A. phalerata* is able to recover and maintain its important role in the landscape mosaic of the Beni savannah.

Acknowledgements

This study is funded by the Alberta Mennega foundation, Bottelier Stipendium, Christine Buisman and Kronendak foundation. I would like to thank L. Poorter for supervising the entire project and the extended feedback, and T. Boorsma for the supervision regarding the preparation and fieldwork. I am grateful for the good cooperation with Fabian and Esther during the remote and sometimes challenging fieldwork.

References

Anderson, A. (1983). The biology of *Orbignya martiana* (Palmae), a tropical dry forest dominant in Brazil. Doctoral dissertation, University of Florida, Gainesville.

Anderson, A. B., Overal, W. L., & Henderson, A. (1988). Pollination ecology of a forest-dominant palm (*Orbignya phalerata Mart.*) in northern Brazil. *Biotropica*, 192-205.

Anderson, A. B., May, P. H., & Balick, M. J. (1991). *The subsidy from nature: Palm forests, peasantry, and development on an Amazon frontier.* Columbia University Press.

Andreazzi, C. S., Pimenta, C. S., Pires, A. S., Fernandez, F. A., Oliveira-Santos, L. G., & Menezes, J. F. (2012). Increased Productivity and Reduced Seed Predation Favor a Large-seeded Palm in Small Atlantic Forest Fragments. *Biotropica*, 44(2), 237-245.

Athreya, V. R. (1999). Light or presence of host trees: which is more important for the strangler fig?. *Journal of tropical ecology*, *15*(5), 589-602.

Balick, M. J. (1988). *The palm-tree of life: biology, utilization and conservation*. New York Botanical Garden.

Balslev, H., Durán, Z. P., Pedersen, D., Eiserhardt, W. L., Asturizaga, A. S., & Paniagua-Zambrana, N. (2012). Subandean and adjacent lowland palm communities in Bolivia*. Ecología en Bolivia*, 47(1), 7-36.

Barot, S., Mitja, D., Miranda, I., Meija, G. D., & Grimaldi, M. (2005). Reproductive plasticity in an Amazonian palm. *Evolutionary Ecology Research*, 7(7), 1051-1065.

Beck, S., & Beck, S. G. (1983). *Vegetationsökologische Grundlagen der Viehwirtschaft in den Überschwemmungs-Savannen des Río Yacuma (Departamento Beni, Bolivien)*. J. Cramer.

Berkunsky, I., Cepeda, R. E., Marinelli, C., Simoy, M. V., Daniele, G., Kacoliris, F. P., ... & Gilardi, J. D. (2016). Occupancy and abundance of large macaws in the Beni savannahs, Bolivia. *Oryx*, 50(01), 113-120.

BirdLife International. (2015). *Ara glaucogularis*. The IUCN Red List of Threatened Species 2015

Brook, B. W., Bradshaw, C. J., Koh, L. P., & Sodhi, N. S. (2006). Momentum Drives the Crash: Mass Extinction in the Tropics1. *Biotropica*, 38(3), 302-305.

Camargo, J. L. C., & Kapos, V. (1995). Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*, 11(02), 205-221.

Cochrane, M. A., & Laurance, W. F. (2002). Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology*, 18(03), 311-325.

Color, M. (2009). *Munsell soil-color charts with genuine Munsell color chips*. Munsell Color.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*, 298, 312.

Corrêa, C. E., Fischer, E., & dos Santos, F. A. (2012). Seed banks on Attalea phalerata (Arecaceae) stems in the Pantanal wetland, Brazil. *Annals of botany*, *109*(4), 729-734.

Craswell, E. T. & Lefroy, R. D. B. (2001). The role and function of organic matter in tropical soils. *Nutrient Cycling in Agroecosystems* 61, 7-18.

Daniels, J. D., & Lawton, R. O. (1991). Habitat and host preferences of Ficus crassiuscula, a neotropical strangling fig of the lower-montane rain forest. *The Journal of Ecology*, 129-141.

Denevan, W. M. (1966). *The aboriginal cultural geography of the Llanos de Mojos of Bolivia* (No. 24). National academy of sciences – National research council Washington DC Foreign research program.

Dransfield, J., Uhl, N. W., Asmussen, C. B., Baker, W. J., Harley, M. M., & Lewis, C. E. (2008). Genera palmarum. *Kew: Royal Botanic Gardens*, 410-42.

Eaton, D. P., Keuroghlian, A., Maria do Carmo, A. S., Desbiez, A. L., & Sada, D. W. (2016). Citizen scientists help unravel the nature of cattle impacts on native mammals and birds visiting fruiting trees in Brazil's southern Pantanal. *Biological Conservation*.

Eiserhardt, W. L., Svenning, J. C., Kissling, W. D., & Balslev, H. (2011). Geographical ecology of the palms (*Arecaceae*): determinants of diversity and distributions across spatial scales. *Annals of Botany*, mcr146.

Endress, B. A., Gorchov, D. L., & Noble, R. B. (2004). Non-timber forest product extraction: effects of harvest and browsing on an understorey palm. *Ecological Applications*, 14(4), 1139-1153.

Erickson, C. L. (1995). *Archaeological methods for the study of ancient landscapes of the Llanos de Mojos in the Bolivian Amazon* (pp. 66-95). Cambridge University Press.

Erickson, C. L. (2000). An artificial landscape-scale fishery in the Bolivian Amazon. *Nature* 408, 190-193.

Feil, J. P. (1996). Fruit production of attalea colenda (*arecaceae*) in coastal ecuador—an alternative oil resource?. *Economic Botany*, 50(3), 300-309.

Felfili, J. M. (1993). *Structure and dynamics of a gallery forest in central Brazil* (Doctoral dissertation, University of Oxford).

Felfili, J. M. (1995). Growth, recruitment and mortality in the Gama gallery forest in central Brazil over a six-year period (1985–1991). *Journal of tropical ecology*, 11(01), 67-83.

Felfili, J. M. (1997). Diameter and height distributions in a gallery forest tree community and some of its main species in central Brazil over a six-year period (1985-1991). *Brazilian Journal of Botany*, 20(2), 155-162.

Fletcher, T. D. (2012). QuantPsyc: Quantitative Psychology Tools. R package version 1.5. https://CRAN.R-project.org/package=QuantPsyc

Forest Service British Columbia (2016). Estimating soil texture in the field. FS238 HRE From: https://www.for.gov.bc.ca/isb/forms/lib/fs238.pdf

Frankham, R. (2005). Genetics and extinction. *Biological conservation*, 126(2), 131-140.

Fredericksen, T. S. (1999). Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. *Forest Ecology and Management*, 124(2), 263-273.

Galetti, M., & Guimarães Jr, P. R. (2013). Seed dispersal of Attalea phalerata (Palmae) by Crested caracaras (Caracara plancus) in the Pantanal and a review of frugivory by raptors. *Revista Brasileira de Ornitologia-Brazilian Journal of Ornithology*, *12*(21), 3.

Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences*, *104*(12), 4979-4983.

Giroldo, A. B., Nascimento, A. R. T., Silva, P. P. F., Júnior, P., & Viegas, G. (2012). Population structure and density of Attalea phalerata Mart. ex Spreng.(*Arecaceae*) in a semideciduous forest. *Revista Árvore*, 36(4), 637-645.

Giroldo, A. B., & Scariot, A. (2015). Land use and management affects the demography and conservation of an intensively harvested cerrado fruit tree species. *Biological Conservation*, 191, 150-158.

Google Inc. (2016). Google Earth (Version 7.1.7.2606) [Software]. Available from https://www.google.com/earth/download/ge/agree.html

Gould, R.W. (2013). Endangered and Threatened Wildlife and Plants; Listing the Blue-Throated Macaw. *Federal Register* 78(7): 2239-2249.

Grégoire, B. (2010). Le rôle des propriétés du sol dans la distribution des palmiers du genre Attalea (Palmae) et des cations échangeables de la région du Bas Tapajos (Amazonie brésilienne).

Gurnell, A., Goodson, J., Thompson, K., Mountford, O., & Clifford, N. (2007). Three seedling emergence methods in soil seed bank studies: implications for interpretation of propagule deposition in riparian zones. *Seed Science Research*, 17(03), 183-199.

Haase, R. (1990). Community composition and soil properties in northern Bolivian savannah vegetation. *Journal of vegetation science*, 1(3), 345-352.

Haase, R., & Beck, G. (1989). Structure and composition of savannah vegetation in northern Bolivia: A preliminary report. *Brittonia*, *41*(1), 80-100.

Hansen, J., Nazarenko, L., Ruedy, R., Sato, M., Willis, J., Del Genio, A., ... & Novakov, T. (2005). Earth's energy imbalance: Confirmation and implications. *science*, *308*(5727), 1431-1435.

Henderson, A. (1994). *Palms of the Amazon*. Oxford Press, New York

Hennessy, B (2015). Youtube video Barba azul nature reserve – Palm regeneration https://www.youtube.com/watch?v=vbFCmatfgrA

Hesse, A. J., & Duffield, G. E. (2000). The status and conservation of the Blue-Throated Macaw Ara glaucogularis. *Bird Conservation International*, 10(03), 255-275.

Hoffmann, W. A. (1999). Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology*, 80(4), 1354-1369.

Hood, G. M. (2010). PopTools version 3.2.5.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501 528

Jennings, S. B., Brown, N. D., & Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, 72(1), 59-74.

Junk, W. J., Piedade, M. T., Wittmann, F., Schöngart, J., & Parolin, P. (Eds.). (2010). *Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management* (Vol. 210). Springer Science & Business Media.

Junk, W. J., Piedade, M. T. F., Schöngart, J., Cohn-Haft, M., Adeney, J. M., & Wittmann, F. (2011). A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands*, 31(4), 623-640.

Kellman, M., Tackaberry, R., Brokaw, N., & Meave, J. (1994). Tropical gallery forests. *Research and Exploration*, 10, 92-92.

Killeen, T. J. (1991). The effect of grazing on native Gramineae in Concepción, Santa Cruz, Bolivia. *Trop. Grasslands* 25, 12-19.

Killeen, T. J., Siles, T. M., Grimwood, T., Tieszen, L. L., Steininger, M. K., Tucker, C. J., & Panfil, S. (2003). Habitat heterogeneity on a forest-savanna ecotone in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): implications for the long-term conservation of biodiversity in a changing climate. *How Landscapes Change* (pp. 285-312). Springer Berlin Heidelberg.

Langstroth, R. P. (1996). *Forest islands in an Amazonian savanna of northeastern Bolivia* (Doctoral dissertation, University of Wisconsin, Madison).

Laurance, W. F. (2008). Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biological conservation*, 141(7), 1731-1744.

Leeper, G. W., & Uren, N. C. (1993). *Soil science: an introduction*. Melbourne University Press.

Lombardo, U., Szabo, K., Capriles, J. M., May, J. H., Amelung, W., Hutterer, R., ... & Veit, H. (2013). Early and middle Holocene hunter-gatherer occupations in Western Amazonia: the hidden shell middens. *Plos one*, 8(8), e72746.

Loreau, M. (2010). *From populations to ecosystems: Theoretical foundations for a new ecological synthesis (MPB-46)*. Princeton University Press.

MacArthur, R. H., & Wilson, E. O. (1967). *Theory of Island Biogeography*. Princeton University Press.

MacDougall, A., & Kellman, M. (1992). The understorey light regime and patterns of tree seedlings in tropical riparian forest patches. *Journal of Biogeography*, 667-675.

Male, T. D., & Roberts, G. E. (2005). Host associations of the strangler fig Ficus watkinsiana in a subtropical Queensland rain forest. *Austral ecology*, 30(2), 229-236.

Mandle, L., & Ticktin, T. (2012). Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. *Journal of Ecology*, 100(4), 997-1008.

Mayle, F. E., Langstroth, R. P., Fisher, R. A., & Meir, P. (2007). Long-term forest–savannah dynamics in the Bolivian Amazon: implications for conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1478), 291-307.

McPherson, K. & Williams, K. (1998). Fire resistance of cabbage palms (Sabal palmetto) in the southeastern USA. *Forest Ecology and Management* 109: 197–207.

Miranda, C. L. (2000). La Reserva de la Biosfera Estación Biológica del Beni, Bolivia. *Biodiversidad, Conservación y Manejo de la Región de la Reserva de la Biosfera Estación Biológica del Beni, Bolivia*. SI/MAB, 4, 21-25.

Moraes, R., M.(1989). Ecología y formas de vida de las palmas bolivianas. *Ecología en Bolivia* 13:33- 45.

Moraes, R., M. (1993). Palmae. Pages 612-628 in T J. Killeen, E. García & S. Beck, eds. *Guía de Arboles de Bolivia*. Herbario Nacional de Bolivia-Missouri Botanical Garden. Quipus SRL, La Paz

Moraes, M., Borchsensiusa, F., & Blicher-Mathiesen, U. (1996). Notes on the biology and uses of the Motacu Palm (*Attelea phalerata, Arecaceae*) from Bolivia (1996). *Economic Botany*, Vol. 50, No. 4, 423-428.

Naeem, S., Duffy, J. E., & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, *336*(6087), 1401-1406.

Navarro, G., & Maldonado, M. (2002). *Geografía ecológica de Bolivia: Vegetación y ambientes acuáticos*. Centro de Ecología Simón I. Patiño, Departamento de Difusión.

Normand, S., Vormisto, J., Svenning, J. C., Grandez, C., & Balslev, H. (2006). Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecology*, 186(2), 161-176.

Oksanen, J., F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs and Helene Wagner (2016). vegan: Community Ecology Package. R package version 2.4-0. https://CRAN.R-project.org/package=vegan

Paniagua-Zambrana, N. Y., & Moraes, M. (2009). Hacia el manejo del motacú (Attalea phalerata, Arecaceae) bajo diferente tipo de cosecha (Riberalta, depto. Beni, NE Bolivia): Estructura y densidad poblacional. Revista GAB, 4, 17-23.

Pimentel, D. S., & Tabarelli, M. (2004). Seed dispersal of the palm Attalea oleifera in a remnant of the Brazilian Atlantic Forest. *Biotropica*, *36*(1), 74-84.

Quiroga-Castro, V. D., & Roldán, A. I. (2001). The Fate of Attalea phalerata (Palmae) Seeds Dispersed to a Tapir Latrine1. Biotropica, 33(3), 472-477.

R Development Core Team. (2011). R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rios, R. S., & Pacheco, L. F. (2006). The Effect of Dung and Dispersal on Postdispersal Seed Predation of Attalea phalerata (Arecaceae) by Bruchid Beetles. *Biotropica*, *38*(6), 778-781.

Rose, K. E., Atkinson, R. L., Turnbull, L. A., & Rees, M. (2009). The costs and benefits of fast living. *Ecology Letters*, 12(12), 1379-1384.

Rosseel, Y. (2012). Lavaan: an R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Salm, R. (2006). Invertebrate and Vertebrate Seed Predation in the Amazonian Palm Attalea maripa. *Biotropica*, 38(4), 558-560.

Salm, R., Prates, A., Simoes, N. R., & Feder, L. (2015). Palm community transitions along a topographic gradient from floodplain to terra firme in the eastern Amazon. *Acta Amazonica*, *45*(1), 65-74.

Shepherd, J. D., & Ditgen, R. S. (2005). Human use and small mammal communities of Araucaria forests in Neuquén, Argentina. *Mastozoología neotropical*, 12(2), 217-226.

Sosnowska, J., & Balslev, H. (2009). American palm ethnomedicine: A meta-analysis. *Journal of Ethnobiology and Ethnomedicine*, 5(1), 43.

Sosnowska, J., Walanus, A., & Balslev, H. (2015). Asháninka palm management and domestication in the Peruvian Amazon. *Human Ecology*, 43(3), 451-466.

Souza A.F., Martins F.R. and Silva Matos D.M. (2000). Detecting ontogenetic stages of the palm *Attalea humilis Mart. ex Spreng.* in fragments of the Brazilian Atlantic Forest. *Canadian Journal of Botany*, 78: 1227–1237.

Souza, A. F., & Martins, F. R. (2004). Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic Forest. *Biodiversity & Conservation*, 13(9), 1611-1632.

Svenning, J. C. (2001). On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *The Botanical Review*, 67(1), 1-53.

Terborgh, J. (1986). Keystone plant resources in the tropical forest. *Conservation biology: science of scarcity and diversity*. Sunderland, MA: Sinauer, 330–344

Veneklaas, Erik J., Adriana Fajardo, and Jaime Lozano (2005). Gallery forest types and their environmental correlates in a Colombian savanna landscape. *Ecography* 28(2), 236-252.

Walker, J. H. (2008). Pre-Columbian ring ditches along the Yacuma and Rapulo Rivers, Beni, Bolivia: A preliminary review*. Journal of Field Archaeology*, 33(4), 413-427.

Watt, A. S. (1947). Pattern and process in the plant community. *Journal of ecology*, 35(1/2), 1-22.

van Wilgen, B. W., Govender, N., Smit, I. P., & MacFadyen, S. (2014). The ongoing development of a pragmatic and adaptive fire management policy in a large African savanna protected area. *Journal of environmental management*, 132, 358-368.

Williams-Linera, G. (1990). Vegetation structure and environmental conditions of forest edges in Panama. *The Journal of Ecology*, 356-373.

Wittmann, F., Junk, W. J., & Piedade, M. T. (2004). The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *Forest ecology and Management*, 196(2), 199-212.

Yamashita, C., & de Barros, Y. M. (1997). The Blue-throated Macaw Ara glaucogularis: characterization of its distinctive habitats en savannahs of the Beni, Bolivia. *Revista Brasileira de Ornitologia-Brazilian Journal of Ornithology*, 5(7), 10.

Zona, S., & Henderson, A. (1989). A review of animal-mediated seed dispersal of palms. *Selbyana*, 6-21.

Appendix I Form leaves juveniles

The leaf form of the juveniles is classified as together, open or both. In figure 1 from Giroldo et al (2012) the ontogenetic stages are visualised (Fig.5). The leaf form in figure 1a is in this study classified as closed, figure 1b is classified as open.

Figure 1 – Ontogenetic stages of *Attalea phalerata* Mart. ex Spreng. (a) Established seedling, (b) Juvenile, (c) Virgin, (d) Reproductive plant, (e) Mature infructescence, (f) Fruit, and (g) Transverse section of fruit.

Fig. 5. Form leaves juveniles, from Giroldo et al (2012)

Appendix II Principal Component Analysis

The Principal Component Analysis (PCA) (fig. 5) shows that the differences between the habitats of the *A. phalerata* is mainly caused by the number of juveniles per ha and the basal area of trees expressed in m^2/ha. The first axis is mostly explained by the number of juveniles (component loading first axis 0,98, component loading second axis 0,22) and the second axis by the basal area of trees (component loading first axis -0,22, component loading second axis -0,98). The first two axis explain together 99,7% of the variation. The gallery forest centre and edge are aligned with the first axis, while the forest island centre and edge are aligned with the second axis.

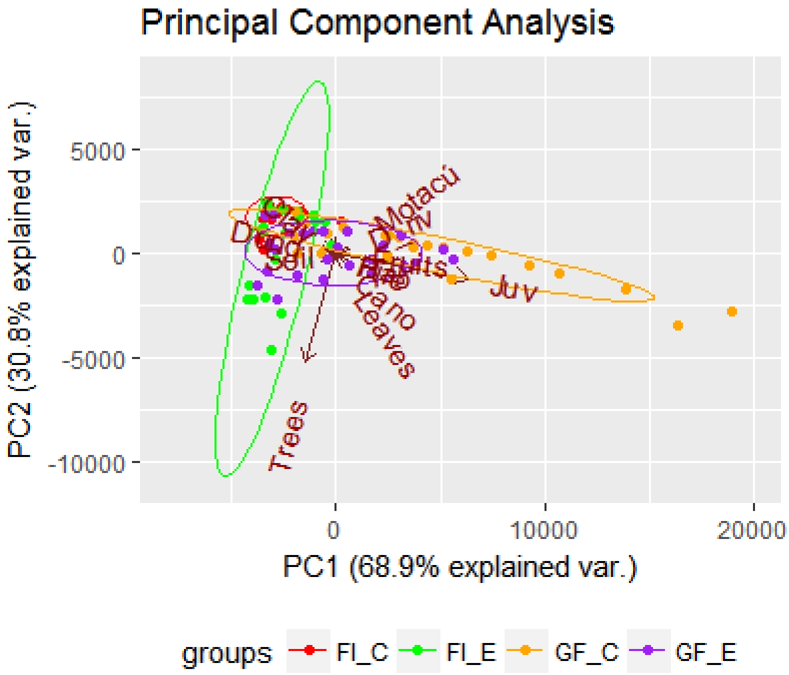

Fig. 6. The analysis is performed with all the available variables, in the figure the most important variables are visualised. This selection is based on the amount of variation of the first three axis is explained by the variable and the importance of the variable for further analysis.

Appendix III Transition matrix and population structure

Transition matrix forest island centre

Size class	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	0,8301	0	0	0	0	0	1,7	0	2,8	1,1
2	0,0135	0,8301	0	0	0	0	0	0	0	0
3	0	0,0135	0,8301	0	0	0	0	0	0	0
4	0	0	0,0135	0,952	0	0	0	0	0	0
5	0	0	0	0,032	0,952	0	0	0	0	0
6	0	0	0	0	0,032	0,9643	0	0	0	0
7	0	0	0	0	0	0,0132	0,9643	0	0	0
8	0	0	0	0	0	0	0,0132	0,9643	0	0
9	0	0	0	0	0	0	0	0,0132	0,9643	0
10	0	0	0	0	0	0	0	0	0,0132	0,9643

Population structure forest island centre

Size class	**Individuals per ha**
1	6406
2	8125
3	5781
4	1563
5	469
6	150
7	100
8	200
9	850
10	1350

Transition matrix forest island edge

Size class	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	0,8301	0	0	0	0	2,2	1,5	1,6	1,4	1,8
2	0,0135	0,8301	0	0	0	0	0	0	0	0
3	0	0,0135	0,8301	0	0	0	0	0	0	0
4	0	0	0,0135	0,952	0	0	0	0	0	0
5	0	0	0	0,032	0,952	0	0	0	0	0
6	0	0	0	0	0,032	0,9643	0	0	0	0
7	0	0	0	0	0	0,0132	0,9643	0	0	0
8	0	0	0	0	0	0	0,0132	0,9643	0	0
9	0	0	0	0	0	0	0	0,0132	0,9643	0
10	0	0	0	0	0	0	0	0	0,0132	0,9643

Population structure forest island edge

Size class	**Individuals per ha**
1	21700
2	16000
3	2700
4	800
5	300
6	450
7	1100
8	2650
9	1600
10	3650

Transition matrix gallery forest centre

Size class	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	0,8301	0	0	0	0	0,3	2	4,5	8,3	11,2
2	0,0135	0,8301	0	0	0	0	0	0	0	0
3	0	0,0135	0,8301	0	0	0	0	0	0	0
4	0	0	0,0135	0,952	0	0	0	0	0	0
5	0	0	0	0,032	0,952	0	0	0	0	0
6	0	0	0	0	0,032	0,9643	0	0	0	0
7	0	0	0	0	0	0,0132	0,9643	0	0	0
8	0	0	0	0	0	0	0,0132	0,9643	0	0
9	0	0	0	0	0	0	0	0,0132	0,9643	0
10	0	0	0	0	0	0	0	0	0,0132	0,9643

Population structure gallery forest centre

Size class	**Individuals per ha**
1	22600
2	163200
3	120600
4	43200
5	46600
6	500
7	1500
8	1100
9	2100
10	2050

Transition matrix gallery forest edge

Size class	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	0,8301	0	0	0	0	2,5	6,7	4,4	11	7,5
2	0,0135	0,8301	0	0	0	0	0	0	0	0
3	0	0,0135	0,8301	0	0	0	0	0	0	0
4	0	0	0,0135	0,952	0	0	0	0	0	0
5	0	0	0	0,032	0,952	0	0	0	0	0
6	0	0	0	0	0,032	0,9643	0	0	0	0
7	0	0	0	0	0	0,0132	0,9643	0	0	0
8	0	0	0	0	0	0	0,0132	0,9643	0	0
9	0	0	0	0	0	0	0	0,0132	0,9643	0
10	0	0	0	0	0	0	0	0	0,0132	0,9643

Population structure gallery forest edge

Size class	**Individuals per ha**
1	18000
2	69000
3	36200
4	15200
5	22400
6	1850
7	1650
8	1850
9	500
10	300

Transition matrix transition zone

Size class	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	0,8301	0	0	0	0	3,1	7,9	3,2	7,2	12,8
2	0,0135	0,8301	0	0	0	0	0	0	0	0
3	0	0,0135	0,8301	0	0	0	0	0	0	0
4	0	0	0,0135	0,952	0	0	0	0	0	0
5	0	0	0	0,032	0,952	0	0	0	0	0
6	0	0	0	0	0,032	0,9643	0	0	0	0
7	0	0	0	0	0	0,0132	0,9643	0	0	0
8	0	0	0	0	0	0	0,0132	0,9643	0	0
9	0	0	0	0	0	0	0	0,0132	0,9643	0
10	0	0	0	0	0	0	0	0	0,0132	0,9643

Population structure transition zone

Size class	**Individuals per ha**
1	12200
2	71800
3	45000
4	17200
5	25200
6	2100
7	1400
8	1450
9	300
10	100

Appendix IV Structural equation model on plot level

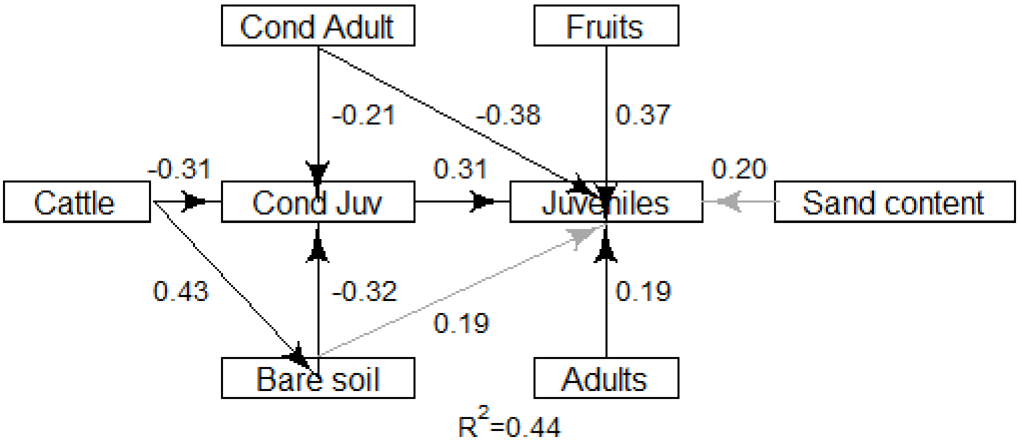

Fig. 7. The model with the best fit on plot level (N=91) shows that the amount of juveniles are explained by the amount of fruits, the condition of the juveniles, the amount of adult *A.phalerata*, the condition of the adults, the clay content of the soil and the bare soil cover. The condition of the juveniles are explained by the cattle pressure, the bare soil cover and the condition of adult *A. phalerata*. The black arrows indicating a significant relation ($p<0.005$) and the grey arrows a not significant relation. The numbers around the arrows are standardized path coefficients. This model explains 44% of the amount of juveniles present.