Population Dynamics of the Motacú (Attalea princeps)

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June 2018

FEM - 80424

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Summary

Justification: In the Beni Savannah a complex forest-savannah ecosystem has existed for hundreds of years, providing habitat for endangered and endemic species. Under influence of increasing cattle ranching this habitat has been changing, resulting in the decline of, among others, the Blue-throated Macaw that depends on the Beni savannah as a habitat and the Motacú palm as a food resource. Since little is known about the Motacú palm (*Attalea princeps*), the dominating palm tree in this ecosystem, research is needed to develop effective management for the protection of this ecosystem

Aim: This study aims to analyse how microhabitats, soil conditions and disturbance by cattle grazing and grass burning affect the regeneration and population dynamics of Attalea princeps.

Study Design: Research plots have been established in the two main forest types in the regions (gallery forests and forest islands), and their centre and edge, representing 4 habitats; gallery forest centre, gallery forest edge, forest island centre, and forest island edge with each other. These four habitats represent a disturbance gradient where the gallery forest centre is the least disturbed and the forest island edge is the most disturbed. The plots are 10x20m and are laid out in an East-West orientation (long sides facing North and South) to limit spatial differences. In total 93 plots have been established and measured.

In addition to the environmental conditions and soil characteristics I evaluated the first year effects of management interventions aimed at enhancing Motacú regeneration; the establishment of fences against cattle and firebreaks against fire.

Results: Multiple regression results show that regeneration density of seedlings (<50 cm tall) increases with the presence of fire (fire scars), and decreases with soil organic matter, bare soil surface, and canopy openness. The occurrence of a fire could have a positive effect through the removal of competing vegetation. Soil Organic Matter could have a negative effect on regeneration since it could increase the amount of waterlogging in the soil, hampering the growth of the regeneration. Bare soils are more prone to desiccation and high temperatures, leading to a lower regeneration.

Matrix models indicate that both grazing and fire have a negative effect on the recruitment of Motacú. Wilcoxon matched pairs tests indicated that individual fencing of islands benefits Motacú regeneration. The application of firebreaks can be useful as the regeneration is protected from fire, but positive effects of an occasional fire need to be identified to further enable regeneration on the forest islands.

Conclusion: Motacú regeneration needs a forest structure to be successful. A closed canopy and soil cover can protect the seedlings from desiccation in the dry season. Occasional fires can be beneficial to the regeneration of the Motacú, but under high frequencies (more than once every 7 years) seedling densities decline. Fencing treatments are necessary to protect the regeneration from cattle grazing.

Expanding these results to other forest systems we can say that removing or reducing the grazing disturbance benefits the recruitment of tree species. Concerning the fire disturbance the results are a little more diffuse, there are some positive effects of fire but frequency of fires should not be too high as regeneration needs a chance to grow up to adult trees. Therefore an optimal fire regime should be constructed for each ecosystem.

Keywords: Motacú, *Attalea princeps*, grazing pressure, fire pressure, population dynamics.

Introduction

Forest Fragmentation

Forest fragmentation is an increasing problem as human impact is ever increasing (Scariot, 1999). Due to forest fragmentation we have to deal with a loss of habitat for a lot of species and increasingly isolated (sub)populations. Since continuous forests will become more and more rare we will have to anticipate the effect to successfully protect and manage the remaining fragments (Howe, 1984; Laurance, 1991). Unfortunately long term effects of forest fragments are poorly understood since fragments of older than 100 years have to be studied to fully understand the impact of fragmentation (Laurance et al., 1998). But another reason to understand the dynamics in forest patches is that forest expansion may occur patch-wise (Favier, Chave, Fabing, Schwartz, & Dubois, 2004). So in reclaimed areas where forests develop fragmented forests may develop before continuous forests occur.

Traditionally the way to look at isolated populations like forest fragments was as isolated islands in a 'matrix' with no interaction between the island and the matrix (Kupfer, Malanson, & Franklin, 2006). However, in the case of forest fragmentation this view is unsuitable since quite a lot of interactions can actually occur (Kupfer et al., 2006). For example, a savannah can be more prone to fires than a continuous forests, so a forest fragment in a savannah matrix may be subject to more frequent fires than the continuous forest, or due to higher disturbance from the matrix a shift from successional species toward pioneer species may occur in the forest fragment (Laurance et al., 1998).

So it is important to understand the fragmentation effects to be able to protect them. An important thing to remember is that the fragmentation effects are larger as the fragment becomes smaller (Scariot, 1999). It was found that forest fragments have higher regeneration rates than continuous forests (Laurance et al., 1998). But this could be accounted to the fact that pioneer species were taking over the fragments and successional old-growth species were being outcompeted (Laurance et al., 1998). This could happen because of higher disturbance in the forest fragment and the fact that through lower taxonomic richness a fragment is more invasible than a continuous forest (Scariot, 1999). Another explanation is that smaller areas support smaller populations, which are more influenced by chance events and are more prone to go extinct (Arroyo-Rodríguez, Aguirre, Benítez-Malvido, & Mandujano, 2007; Kupfer et al., 2006). All in all the best predictor for fragmentation events was found to be fragment size (Arroyo-Rodríguez et al., 2007; Howe, 1984; Kupfer et al., 2006; Laurance et al., 1998; Scariot, 1999; Wright & Duber, 2001).

Other important things to consider when thinking about forest fragmentation is what happens in the matrix surrounding the forest fragments. As said before wildfires in the matrix also impact the fragment and through higher irradiance from the matrix forest fragments have been found to support higher vine and liana densities (Kupfer et al., 2006; Laurance et al., 1998). These effects can be called edge effects. These effects account for the fact that there is no sharp boundary between 'forest' and 'not forest' (Kupfer et al., 2006). Edge effects can be divided into three groups: Abiotic, direct biological, and indirect biological (Murcia C., 1995). Examples are higher solar irradiation (abiotic), changes in species composition (direct biological), and species interactions (indirect biological) (Murcia C., 1995).

A good system to research these interactions and edge effects would be forest-savannah ecosystems. These systems consist of savannah landscape with forested patches. Biodiversity in these systems is very high due to a high β-diversity, meaning that area's themselves are not very diverse but that there are large differences between areas (Furley, 1999; Mayle, Langstroth, Fisher, & Meir, 2007). These systems are considered to be very vulnerable, but little attention is being paid to them in conservation efforts (Junk et al., 2006). It has been estimated that only 20% of the South American Cerrado is undisturbed and only 1,2% is being protected (Cardoso Da Silva & Bates, 2002).
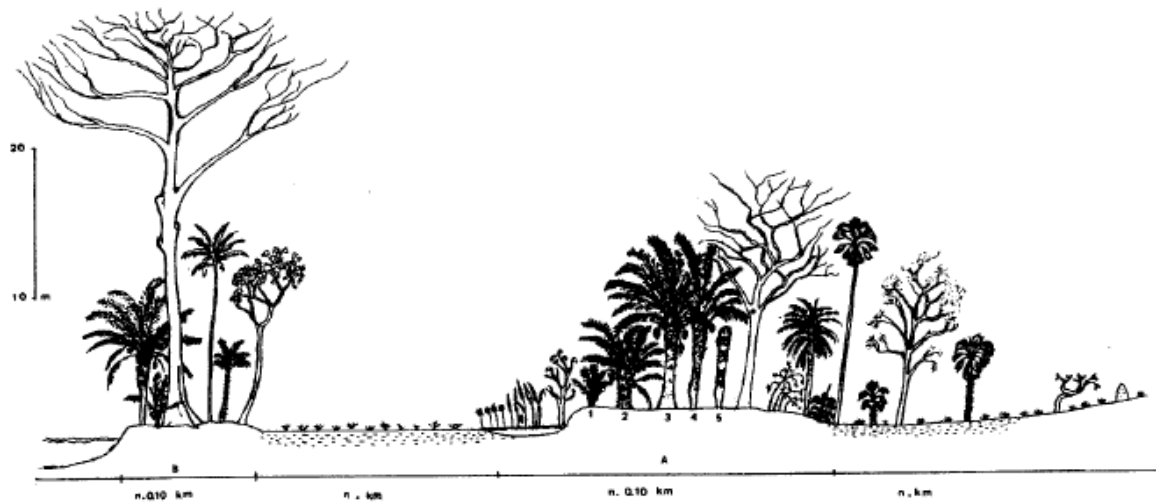
Beni Savannah

Figure 1, distribution of, from left to right, gallery forests, savannah, and forest islands in the Beni (Yamashita & de Barros, 1997).

An example of long-term forest fragments can be found in the Beni Savannah of Northern Bolivia. This area consists of an extensive savannah landscape interspersed with patches of forest (See figure 1) (Hamilton, Sippel, & Melack, 2002). These forests can be divided into two classes, forest islands and gallery forests. The landscape can be classified as a hyper-seasonal savannah, meaning that there are large differences between the dry and the wet season. In the dry season the system is subject to extreme drought while in the wet season the entire area is inundated due to extreme rainfall and bad drainage (Hamilton et al., 2002). Rainfall ranges from 1300 to 2000mm of which most falls from October to May (Hamilton et al., 2002; Langstroth, 2001). This annual inundation leads to pioneer vegetation able to handle with these disturbances. Due to the high and fast variability in circumstances there is little opportunity for successional vegetation to establish but vegetation is focussed on being able to adapt to these fast changes (Langstroth, 2001; Pott, Oliveira, Damasceno-Junior, & Silva, 2011). The successional (forest) vegetation is limited to the elevated patches in the area which are not subjected to the inundation (Hamilton et al., 2002; Junk et al., 2006; Mayle et al., 2007). As previously stated the forests in the Beni can be categorised into two groups with both a different history. Forest islands have developed on small elevations in the landscape. These elevations can be decaying termite mounds, but can also have an anthropogenic origin (Mayle et al., 2007; Yamashita & de Barros, 1997). Pre-Columbian Indians had constructed these mounds as living quarters and to practice agriculture during the wet season (Langstroth, 2001; Yamashita & de Barros, 1997). These anthropogenic forest islands are usually bordered by a water ditch (Yamashita & de Barros, 1997). The gallery forests are naturally occurring forests on the riversides. Since these areas are naturally elevated forest is able to develop here (Yamashita & de Barros, 1997).

Traditionally the Beni savannah was used as an agricultural area during the pre-Columbian times and after that by the Jesuits (Langstroth, 2001). But with the rubber boom in the Amazon large numbers of the population left the area (Langstroth, 2001). These days the most important economic activity is cattle ranching (Hordijk, 2017; Langstroth, 2001; Yamashita & de Barros, 1997). This ranching puts a stress on the forest systems. The cattle move to the forest islands during the wet season to escape the water. Here regeneration is eaten and trampled, resulting in hampered recruitment rates (Hesse & Duffield, 2000; Hordijk, 2017). Additionally there is a fire disturbance. There are naturally occurring fires and the system is adapted to this disturbance. But ranchers regularly burn the savannah to remove dead grass and make way for new, more nutritious grass to grow (Hordijk, 2017; Yamashita & de Barros, 1997). Since these fires are more frequent than the naturally occurring wildfires there is an increase in fire disturbance on the forest systems. This can become more worrying in the future when the climate becomes drier as a consequence of climate change, leading to more frequent and more intense fires (Mayle et al., 2007).

Motacú and the Blue-throated Macaw

The forests in the Beni savannah are being dominated by the Motacú palm (*Attalea princeps*) (Langstroth, 2001; Yamashita & de Barros, 1997). Due to its wide spread it is an important palm tree to a lot of wildlife, ranging from pollinators to frugivores and rodents (Barthlott, 1998; Fava, da Silva Covre, & Sigrist, 2011; Galetti & Guimarães Jr, 2013; Moraes, Borchsenius, & Blicher-Mathiesen, 1996; Quiroga-Castro & Roldán, 2001). A single tree can produce up to 90kg of fruit in a year with two ripening periods per year (Moraes et al., 1996).

Next to its large importance for wildlife the Motacú palm also has an important economic value. Fruits are used for consumption and oils is won for cosmetics. Furthermore Motacú leaves are frequently used for thatching (Moraes et al., 1996; Moraes, Sarmiento, & Oviedo, 1995).Due to this large economic value it is important to consider the effects of overexploitation. Moraes et al. (1995) found that palm species are being found further and further from human settlements as a result of overexploitation.

This effect is very concerning since the Motacú groves are the prime habitat of the endemic Blue-throated Macaw (BirdLife International, 2016; Jordan & Munn, 1993). The blue-throated macaw is a highly endangered endemic bird species with only up to 250 individuals left. It used to be a very abundant species, but under high poaching pressure and habitat decline their numbers dropped drastically (Bouzat & Strem, 2012; Hesse & Duffield, 2000; Yamashita & de Barros, 1997). At the moment only two verified populations are known (Bouzat & Strem, 2012). Since the Blue-throated Macaw is highly dependent on the Motacú palm forests it is important to protect these habitats.

It is known that the forest islands are disappearing as the result of increased human pressure (Hesse & Duffield, 2000; Hordijk, 2017; Yamashita & de Barros, 1997). There has been an increase in cattle ranching as new technologies made the area more accessible and new markets for beef opened up (Langstroth, 2001). The increased grazing pressure has led to a decline in recruitment (Hordijk, 2017; Yamashita & de Barros, 1997). Furthermore the application of fire to remove dead grass has increased the natural fire pressure and also contributed to a change in natural population dynamics (Hordijk, 2017; Yamashita & de Barros, 1997).

Despite all this still little is known about the Motacú, or even *Attalea* species in general and even discussions about taxonomy are still going on (Pintaud, 2008; Pintaud, del Castillo, Ferreira, Moraes, & Mejía, 2016). In the Barba Azul Nature Reserve (BANR) management experiments are going on to find the best management practices to protect the Motacú forests. One experiment is focussed on removing the grazing pressure and one is to remove the disturbances from human induced fires (Asociación Armonía, 2017; Friends of Barba Azul, 2017; Reserve, 2010)

Questions and Hypotheses

Since little is known about the soil requirements for Motacú soil samples have been taken in 2016 (Hordijk, 2017; Nissen, 2017). These have been analysed in the Netherlands. This allows us to ask the following question:

RQ1.　What environmental conditions and soil factors influence the regeneration of the Motacú?

The two most important disturbances of the Motacú palm are grazing and fire. Since 2016 the reserve has been experimenting with management measures to reduce these disturbances. This provided the opportunity to research the following questions:

RQ2.　What is the effect of fencing off forest islands on regeneration of the Motacú palm?
RQ3.　What is the effect of protection by firebreaks on the regeneration of Motacú?

To construct hypotheses for these questions a conceptual model has been made (See figure 2).
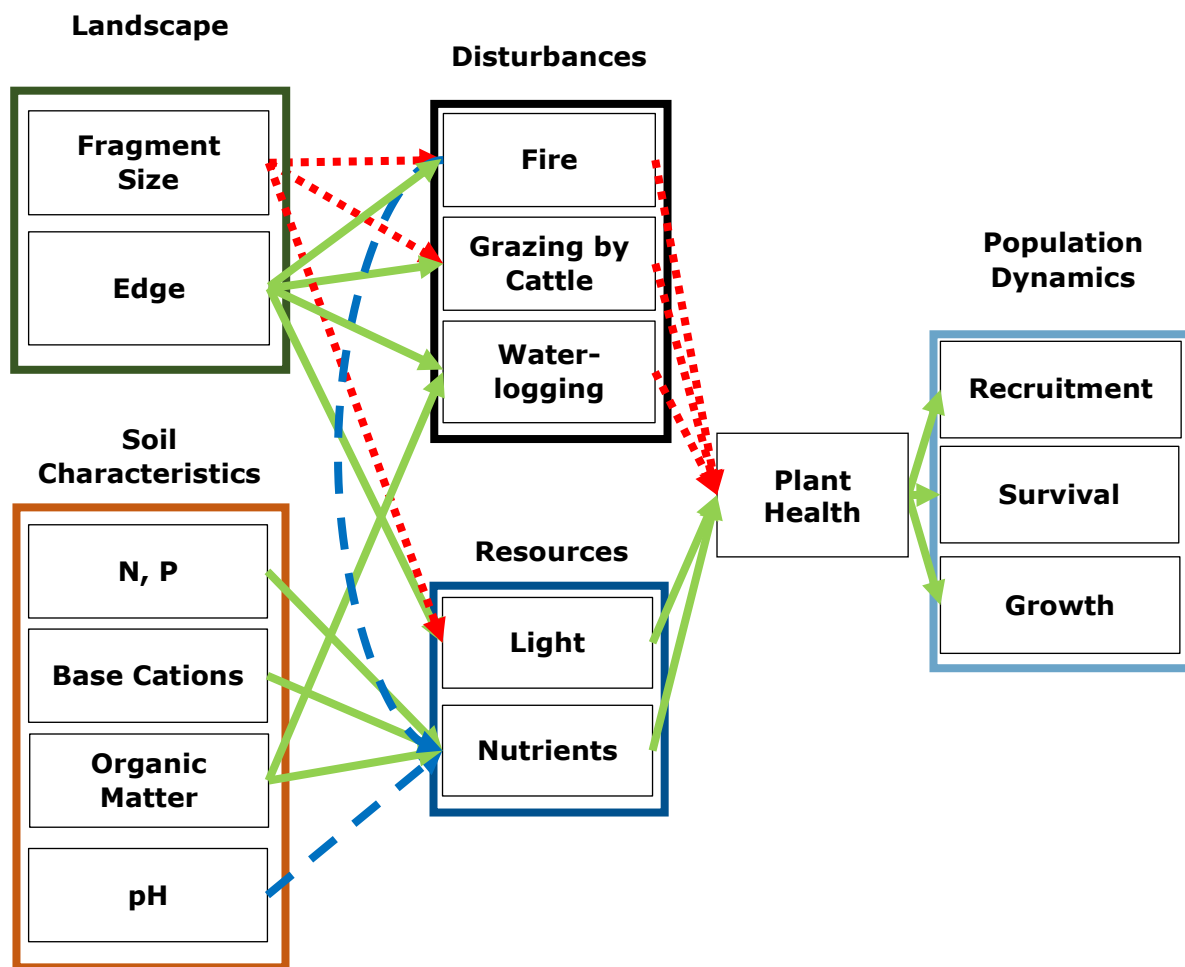
Figure 2, Conceptual model. Continuous green lines indicate positive effects. Dotted red lines indicate negative effects. Blue hatched lines can be either positive or negative.

 The driving variables behind the population dynamics can be grouped into landscape elements and soil characteristics. As stated before the most important landscape element explaining fragmentation effects is fragment size. For the soil characteristics it is expected that Soil Organic Matter (SOM), N and P content, Bas cations and pH are of influence. For the environmental conditions I expect environmental conditions related to edge habitats to have a negative effect on the regeneration. Thus canopy openness, grass and shrub cover, dung piles, and fire scar presence to have a negative effect. Whereas I expect a positive effect of environmental conditions more related to centre habitat like litter cover.

These driving factors influence the more direct factors of disturbance and resources availability. The disturbances are grazing, fire, and waterlogging. Grazing and fire are both negatively impacted by fragment size. Waterlogging is positively influenced by SOM since organic matter hold water really well and can result in anaerobic conditions even when soils are not inundated. The resources can be divided into Light and Nutrients. I expect that Fragment Size negatively influences light since larger fragments have relatively less edge and thus lower irradiation from the matrix. I expect the nutrient availability to be positively influenced by SOM, N and P content, and Base cations. pH and fire can have both a positive and negative effect. Nutrient availability is highest between a pH of 5 and 7, when pH values are outside of this range the nutrients are fixed and are no longer available for plants (see figure 3). Fire can have a positive effect on soil nutrients by liberating the nutrients from

standing biomass, but there is also a lot of loss through the evaporation of nutrients. Plant health is negatively influenced by the disturbances and positively influenced by the resources. Plant health has a positive effect on the population dynamics.
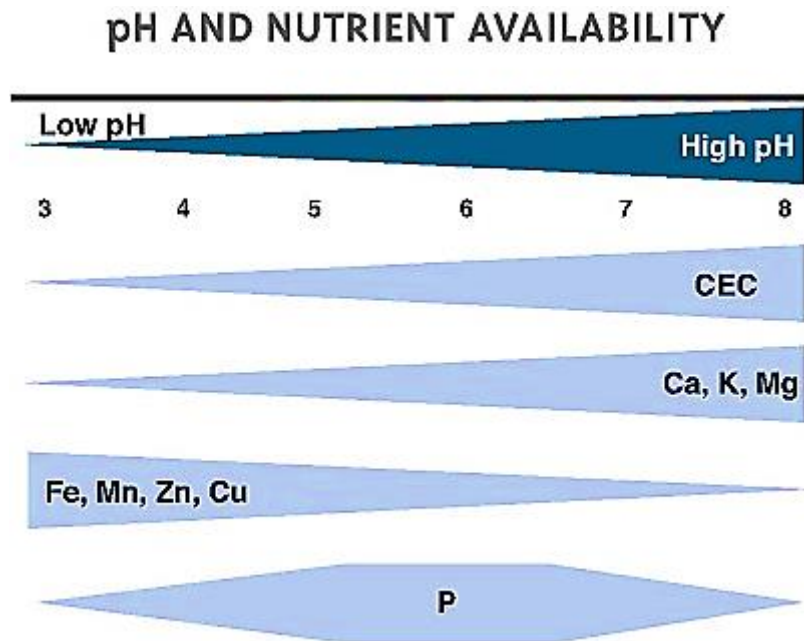

Figure 3, relation between pH and different nutrients.(Soil4teachers)

Following the conceptual model we can construct the hypotheses. RQ1 is related to the nutrients. I expect that the nutrients have a positive effect on recruitment rates since nutrients are positively related to plant health. SOM can still have some negative effects through the waterlogging effect, but I expect that this effect is overcome by the nutrient loads that come along with organic matter. For pH I expect an optimal range between 5 and 7.

RQ2 is related to the grazing pressure. Two fencing treatments have been applied to the forest islands and part of the gallery forests in the park. The first treatment is to fence off individual islands. The second approach is to fence an entire area and remove all cattle from this area, see methods for a further explanation. Since the fencing off an island or area removes the grazing pressure I expect regeneration here to increase compared to the control plots where no fence has been placed and grazing pressure is thus still available. I do not expect to find a difference between the two different fencing methods (fencing individual islands vs fencing an area). This is because the fences have been constructed in such a way that other animals can still cross the fence. Meaning that the only effect of the fence is to keep out the cattle.

RQ3 is related to the fire disturbance. By removing the stress that fire puts on the Motacú systems I expect that recruitment in the protected islands and gallery forests is increasing compared to the control plots where a firebreak has not been constructed. There are again two treatments, artificial firebreaks and natural protection by short-grass habitat or rivers. Since both treatments have the same function I do not expect a difference between the two treatments.

Methods

Research Area

The research has been conducted in the Barba Azul Nature Reserve (BANR). This area is located in the Beni Savannah in the north of Bolivia (See figure 4). The coordinates of the field station are 13°45'50S; 66°06,04W. The reserve spans 11,000 ha of seasonally inundated savannah. In this ecoregion the annual rainfall ranges from 13,000 to 20,000 mm per year, of which 80% falls between October and May (Langstroth, 2001). The savannah is interspersed with forested patches. These patches can be divided into two categories, forest islands and gallery forests. Forest islands are patches of elevated land where forests have been able to develop. These patches can be old termite mounds, or remnants of pre-Columbian mounds constructed by the native people (Mayle et al., 2007; Yamashita & de Barros, 1997). The gallery forests border the permanent river where the river bank has naturally elevated the landscape (Mayle et al., 2007; Yamashita & de Barros, 1997). Since these elevated areas are not inundated forests have been able to develop here. Over time these forests have developed to be important habitats for a variety of animal species, including the endemic blue-throated macaw (Hesse & Duffield, 2000; Hordijk, 2017; Meijer, 2017; Yamashita & de Barros, 1997).

Figure 4, location of the research area (red dot) (Friends of Barba Azul, 2017)

Study Design

In 2016 a series of permanent plots has been laid out to start a long term monitoring program for the Motacú Palm (*Attallea phalerata*) (Hordijk, 2017). For the current master thesis these permanent plots have been remeasured, these measurements have been carried out in October and November 2017. These plots have been divided over the two habitat types, gallery forest and forest island. In each habitat 25 locations had been selected and for each location a centre and an edge plot has been established. This theoretically would result in 100 plots. Since some forest islands were too small to construct both a centre and an edge plot only the edge plot has been constructed. This was the case for 9 forest islands. This results in 91 plots before the research started. When in the field it became apparent that one of the locations (forest island 17) could not be reached due to the appearance of a seasonal river. By request of the field supervisor, Tjalle Boorsma, an additional location has been made with both a centre and an edge plot (forest island26). This in the end resulted in 92 plots that have been measured, 42 forest island plots and 50 gallery forest plots. To limit spatial and irradiance differences edge plots have been established on either the north or the south side of a location

The nature reserve is under influence of two anthropological disturbances, fire and grazing by cattle. To estimate the effect of the disturbances management measures have been implemented in 2017. To remove the grazing pressure a fencing treatment has been applied. The natural reserve has experimented with two different techniques, the fencing off of an entire area and the fencing off of forest islands. In the northern and southern part of the reserve all cattle have been removed. In the eastern part of the reserve cattle are still being kept and forest islands have been fenced off. Smaller islands and the gallery forest in this part are still subjected to the grazing pressure. Furthermore two islands are positioned outside the reserve and are thus still subjected to grazing.

Firebreaks have been constructed to protect the reserve from fires in the surrounding areas. These fires can occur naturally as the result of lightning strikes, but more often they are lit by ranchers to remove old grass and make place for new, more nutritious grass for the cattle. Because of this we can test for the effect of fire on the regeneration of the Motacú palm. The firebreaks have been constructed along the borders of the natural reserve. Furthermore firebreaks have been constructed

within the reserve to limit the spreading of a fire originating within the reserve. In addition to this 'natural' firebreaks occur in the form of rivers (Omi in the south and Tiniji in the north) and the accompanying river edge shortgrass habitat. See figure 4 for the spatial distribution of the treatments.
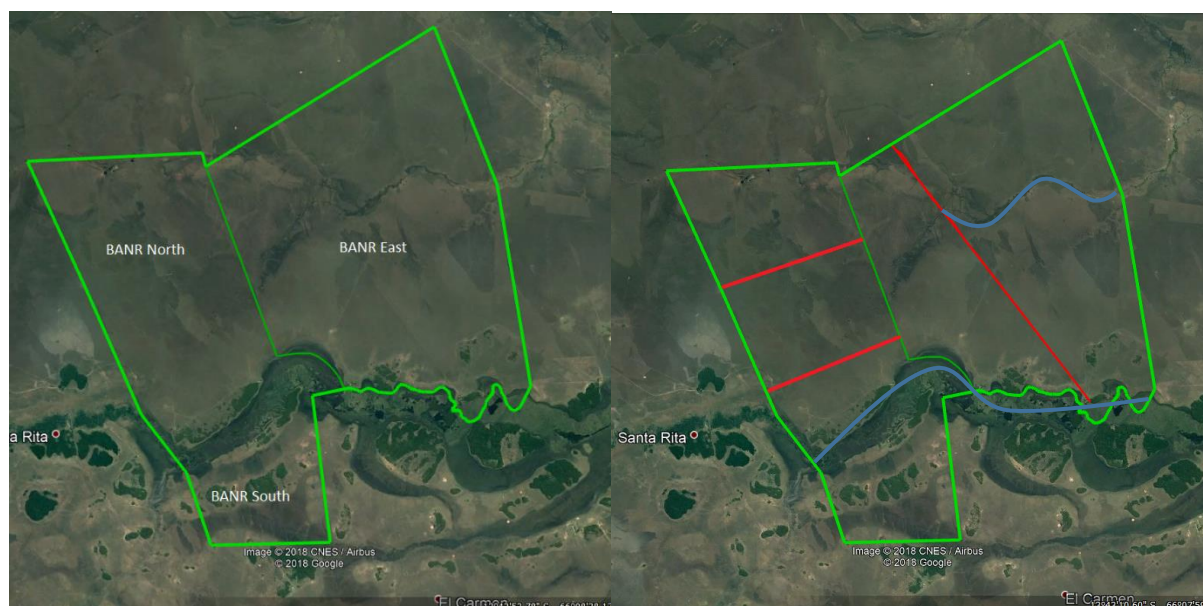

Figure 5, spatial distribution of the treatments. On the left the fencing treatment North and South all cattle were excluded. In BANR East individual islands have been fenced off. On the right the firebreaks. Green lines are the reserve borders which are firebreaks, red lines are firebreaks which run through the park, and blue lines are the natural firebreaks.

To limit the amount of spatial variation all plots have been laid out in an east-west orientation. Meaning that the 20m sides face the north and the south. To find the effect of environmental factors bare soil, grass cover, litter cover, palm cover, palm leaf cover have been measured.

All adult trees have been tagged in 2016 (Hordijk, 2017). To see how these trees developed they have been remeasured in 2017. For each adult the height, DBH, number of leaves, number of infructescence and inflorescence, health, canopy position and openness, fire scar presence, and ficus presence have been measured. Furthermore to estimate the seed bank per adult tree a seed plot of 1x1m has been established under each tree. See Appendix 1 for an overview of the variables measured

To find the amount of regeneration the plots have been divided into 8 subplots of 5x5m (See figure 5). To account for the higher variability in regeneration 4 subplots were measured in the forest islands where 2 were sufficient in the gallery forests. The two subplots used in the gallery forest were always in the corners marked with the wooden poles placed in 2016. The four subplots necessary in the forest islands were laid out in a zig-zag pattern (see figure 5).
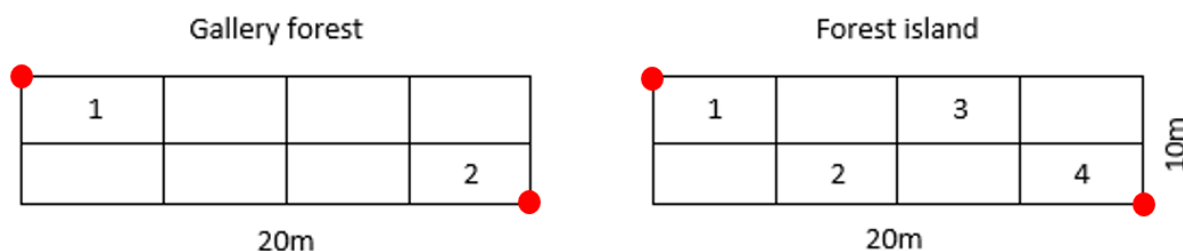

Figure 6, composition of the permanent plots. 10x20m divided into subplots of 5x5 for regeneration measurements. Red dots indicate the poles marking the plots in the field. Numbered subplots are the subplots that were measured.

To evaluate what variables had what effect on the tree performance mixed models were constructed for seed production, predation rate on the seeds, regeneration density, adult density, survival rate of the adults, growth (both absolute and as a ratio of tree height), and reproductivity. The independent variables in these tests are Size class in 2016, forest type, Centre/Edge, and the interaction between forest type and Centre/Edge. Plot was taken into account as a random variable.

To evaluate the population dynamics matrix models were made for the two forest types and Centre and Edge habitats, resulting in four matrix models. The individuals were classified following the criteria in table 1. To see what effect the grazing pressure and the fire pressure had matrix models were made simulating a forest island exposed to these disturbances. The vital rates for the model were taken from the height measurements from 2016 and 2017 for the adults. Since no individual seedlings and juveniles were tagged in 2016 vital rates for these classes had to be taken from Anderson (1983). The matrix models were run for 50 years using poptools in Excel (Hood, 2010). These 50 years correspond with half the life span of an adult Motacú palm (Moraes et al., 1996).

Table 1, division of the life stages for the matrix models and their criteria.

Name of category	Description category
Seed	Fertile seed
Seedling	No stem, longest leaf length <50cm
Juvenile	No stem, longest leaf length >50cm
A1	Stem <6m
A2	Stem >6m

Since little is known about the soil characteristics influencing Motacú palm regeneration soil samples have been taken in 2016 (Nissen, 2017). The samples were taken in the centre of the plot at 20-30cm depth. Using extraction methods available N-NO3, N-NH4, and P-PO4, CEC, Ca, Mg, and K have been measured. Furthermore pH, and % Organic Matter have been measured. To evaluate the effect of the different soil characteristics a spearman correlation has been done. To test for relations between the soil characteristics a categorical PCA has been done

Results

Habitat Analysis

Environmental circumstances of the different habitats

To see how the habitats differed in environmental conditions an ANOVA analysis has been done with a Tukey test as post hoc. No difference was found for bare soil surface and Palm leaf cover. For grass cover a significant difference was found between gallery forest centre and forest island edge with significantly more grass on the forest islands. The other two habitats, gallery forest edge and forest island centre, had no significant difference with any of the habitats. Shrub cover is significantly higher in the gallery forest edge, the other three habitats showed no difference. Canopy Openness was significantly higher in the forest islands, within the habitat there was no difference between centre and edge plots. See Appendix 2 for the boxplots of the tests.

Soil chemistry of the different habitats
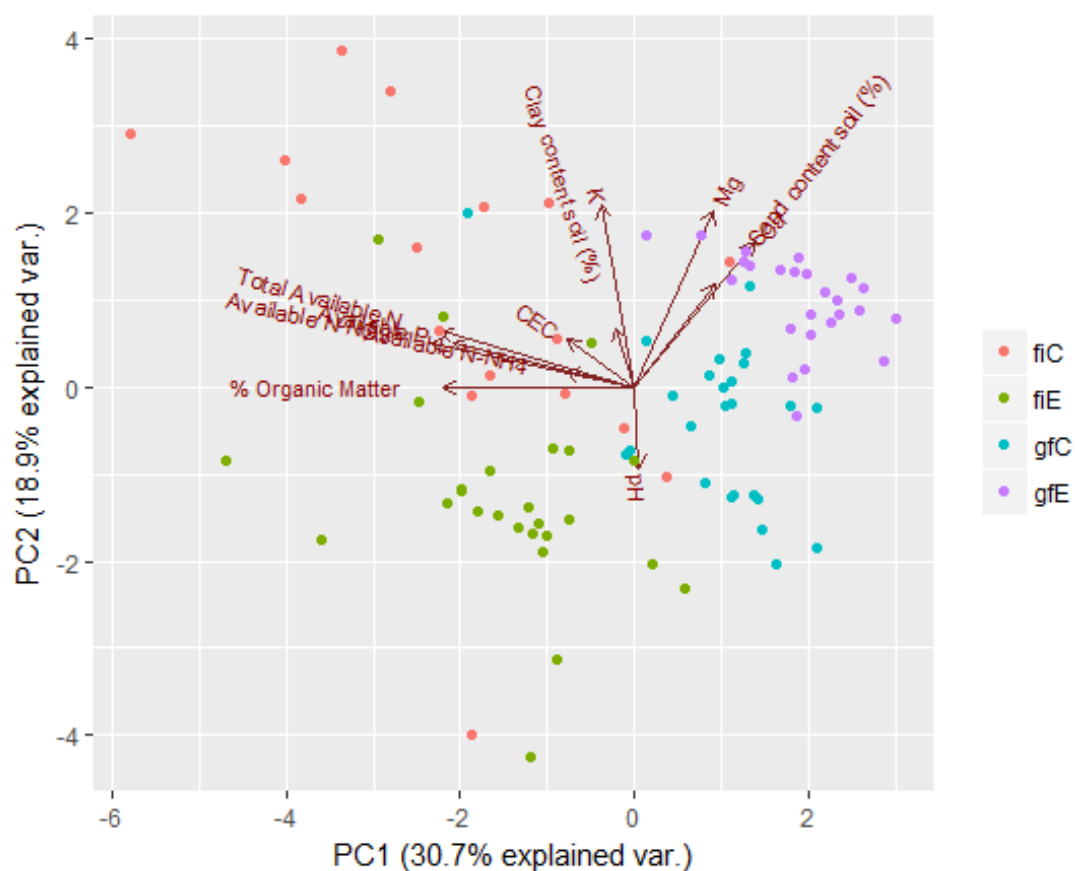
Figure 7, biplot of the PCA analysis of 12 soil variables in 93 forest plots in the Beni savanna. The regression scores of the plots are shown (red= forest island centre, green=forest island edge, blue=gallery forest centre, purple =gallery forest edge).

To evaluate how soil variables are associated a Principal Components Analysis (PCA) was done. From the PCA it showed that all macronutrients (the N forms and P) are linked with one another, and are also linked to Organic Matter. They are all linked to the first dimension. CEC is also linked to the first dimension which explains 30.7% of the variation. The second axis explained 18.9% of the variation and was related to soil texture and micronutrients (K, Mg, Ca, and CEC), with sand and clay content (see figure 5). It also shows that pH and the micronutrients are negatively related. Form figure 5 it shows that the forest islands have higher nutrient contents than the gallery forests. Regarding soil structure it seems that the gallery forests are sandier and the forest islands have a higher clay

content. These differences can be explained by the differences in history. See appendix 3 for the different soil values per habitat

To evaluate how soil characteristics affect the regeneration density of *A. princeps* correlations were done. Seedling density is negatively correlated with available P (R=-.34 p=.001), % Organic Matter (R=-.42, p=.000), and K (R=-.22, p=.003). Juvenile density increased significantly with Sand content (R=.24, p=.024) and Ca (R=.24, p=.019) and decreased strongly with available P (R=-.54, p=.000), and % Organic Matter (R=-.49, p=.000) and moderately with available N-NO3 (R=-.30, p=.003), total available N (R=-.24, p=.018) and clay content (R=-.24, p=.024). It should however be noted that % Organic Matter was positively correlated with clay content (R=.45, p=.000), available N-NO3 (R=.65, p=.000), total available N (R=.56, p=.000), available P (R=.75, p=.000), and CEC (R=.363, p=.000). So a lot of the negative correlations may instead be an indirect effect of the negative correlation with % Organic Matter.

To test for this direct effect a multiple linear regression was done using a forward selection method. From this test it was found that Organic Matter is the only explanatory soil factor (Seedlings: F=10.129, p=0.002, R=0.320; Juveniles: F=9.830, p=0.002, R=0.315). All other effects could be explained through the indirect effects of the Organic Matter. For both seedlings and juveniles the relation with organic matter was negative (Fig 8).
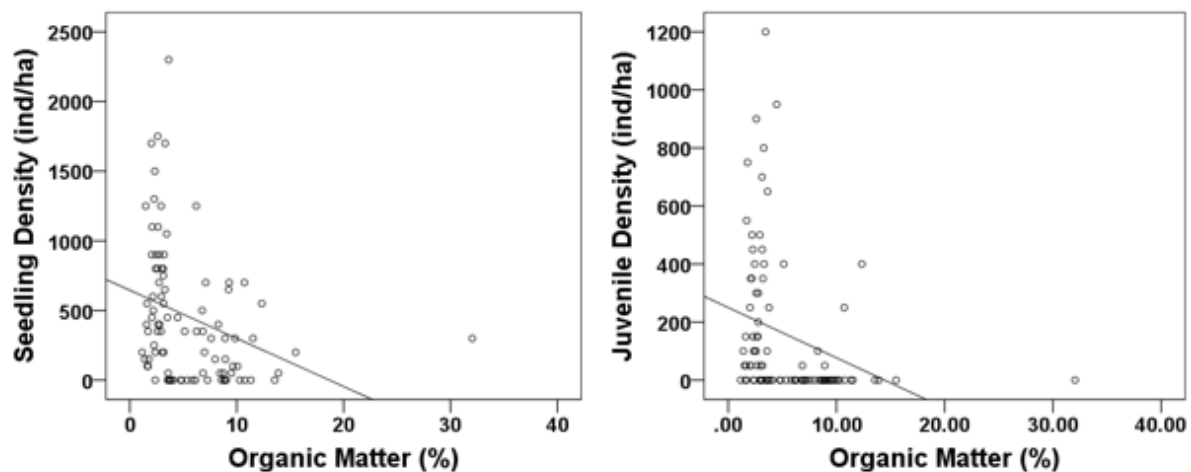

Figure 8, the effect of organic matter on the regeneration densities. What we see is a decline in density with an increasing organic matter content. Seedling density: R2=0.100, p=0.002; Juvenile Density: R2=0.092, p=0.002.

How regeneration is impacted by environment and protection treatments

To evaluate how environmental conditions affect regeneration density Spearman correlations were used (See table 2). A positive relation was found between amount of seedlings and amount of juveniles. Seedling density increased significantly with palm cover and decreased significantly with grass cover, amount of dungpiles, and canopy openness. For Juvenile Density a positive relation was found with shrub cover. Negative relations were found with amount of dungpiles, canopy openness, and grass cover.

To remove indirect environmental effects multiple regression analyses have been done using a forward selection method. From this it showed that seedling density is mainly determined by Canopy openness (B=-47.685, p=0.014), Average Firescar (B=34.494, p=0.014), and Bare soil surface (B=-5.235, p=0.049) (F=5.343, p=0.002, R=0.456). For the Juvenile density the only significant variable was found to be the amount of dung piles (B=-9.366, F=7.295, p=0.009).

To test whether fire and cattle exclusion increased the establishment and survival of seedlings, Wilcoxon matched pairs tests were carried out comparing the seedling density of 2016 with the densities of 2017 (Table 3). In contrast to the hypothesis, the densities of both regeneration stages declined significantly in all habitats. The only exceptions are seedling density in the Forest Island Centres and juvenile density in the Forest Island Edges. The latter one can be attributed to the fact that barely any juveniles were present on the forest islands.

For the fencing treatment it appeared that only in the individually fenced islands no decline was found. It should however be noted that in the area where cattle should have been excluded a group of 15 cows was still seen during the research.

For the firebreak treatment it appears that a firebreak, man-made or natural, has a negative effect since the unprotected islands showed no significant decrease, but the protected islands did. This could be supported by the almost significant relation between fire scars on adult trees and seedling density (See table 2) indicating that Motacú seedlings benefit from fire. However, the fires that have occurred in the park only affected one island with a single juvenile Motacú. So the effect of fire cannot be fully tested yet.

Table 2, Spearman correlation between regeneration density of seedlings (S) and juveniles (J) and environmental factors (N=93). Bold correlations are significant (P<0.05).

		Seedling Density	Juvenile Density	Bare soil surface	Grass cover	Shrub cover	Palm leaf cover	Canopy openness	Amount of dung piles	Average Firescar
Seedling Density	R	1	**0.596**	**-0.225**	**-0.256**	0.056	**0.263**	**-0.34**	**-0.239**	0.216
	p		0	0.031	0.014	0.597	0.011	0.003	0.022	0.056
Juvenile Density	R	**0.596**	1	-0.199	**-0.279**	**0.297**	0.176	**-0.308**	**-0.314**	-0.024
	p	0		0.057	0.007	0.004	0.093	0.008	0.002	0.832

Table 3, significances of the Wilcoxon paired samples test for forest type and centre/edge, fencing, and firebreak. Bold values are significant changes between 2016 and 2017. The changes over time ("differences") are calculated as the difference between 2016 and 2017

			Seedling Density	Juvenile Density
fi	Edge	Difference	**-8.56%**	4.81%
		p	**0.002**	0.680
	Centre	Difference	-28.03%	-1.96%
		p	0.183	0.317
gf	Edge	Difference	**-57.56%**	**-57.07%**
		p	**0.000**	**0.000**
	Centre	Difference	**-65.58%**	**-32.99%**
		p	**0.000**	**0.001**
Fencing	Unfenced	Difference	**-48.11%**	**-35.10%**
		p	**0.000**	**0.002**
	Individually Fenced	Difference	46.98%	-
		p	0.481	-
	Exclusion Zone	Difference	**-56.34%**	**-22.45%**
		p	**0.000**	**0.000**
Firebreak	No Firebreak	Difference	-43.48%	-20.00%
		p	0.068	0.317
	Firebreak	Difference	**-59.03%**	**-75.53%**
		p	**0.000**	**0.000**
	Natural Protection	Difference	**-30.85%**	**-20.06%**
		p	**0.000**	**0.001**

The effect of habitat on population dynamics

To evaluate what vital rates influenced the population dynamics of the adult *A. princeps* mixed models were run with several population components as dependent variables and habitat factors and size class independent factors. Plots were taken into account as a random factor (see table 4).

The seed production of an adult Motacú is influenced by Forest Type and Size Class (p=0.009 and p=0.000 respectively). In the higher size class (A2) seed production was higher than in the lower size class (A1) (See table 5). The seed production was also higher in the forest islands compared to the gallery forests. Centre/Edge and the ForestXCentre interaction had no significant effect (p=0.686 and p=0.591 respectively). Seed predation was not found to be significantly impacted by any of the factors.

Seedling density was significantly impacted by forest type (p=0.000), Centre/Edge (p=0.023), and the interaction ForestxCentre (p=0.000). The more regeneration was found in the gallery forests and in the centre habitats. For the interaction it was found that within the gallery forests more regeneration was found in the centre plots, but for the forest islands this effect was reversed; more regeneration was found in the edge plots.

Adult density was significantly affected by all factors. The A1 size class had a higher density than the A2 size class (p=0.005). Forest islands had higher palm densities than the gallery forest (p=0.006). In the Gallery Forest there are slightly fewer trees in the edge compared to the centre. In the Forest

Islands we see that this effect works the other way around; fewer trees are found in the centre compared to the edge (See figure 8). Growth is only influenced by size class (p=0.000), with palms in the smallest size class (A1) growing faster than palms in the larger size class (A2). The average survival was equal among all habitats except for Forest Island Centre that had lower survival (see figure 8). Reproductivity was higher in gallery forests compared to the forest islands (p=0.000). Again there is some kind of reversed edge effect on the forest islands, gallery forest edges have a lower amount of reproductive adults then the centre plots. But on the forest islands the lower reproductive values are in the centre habitat.
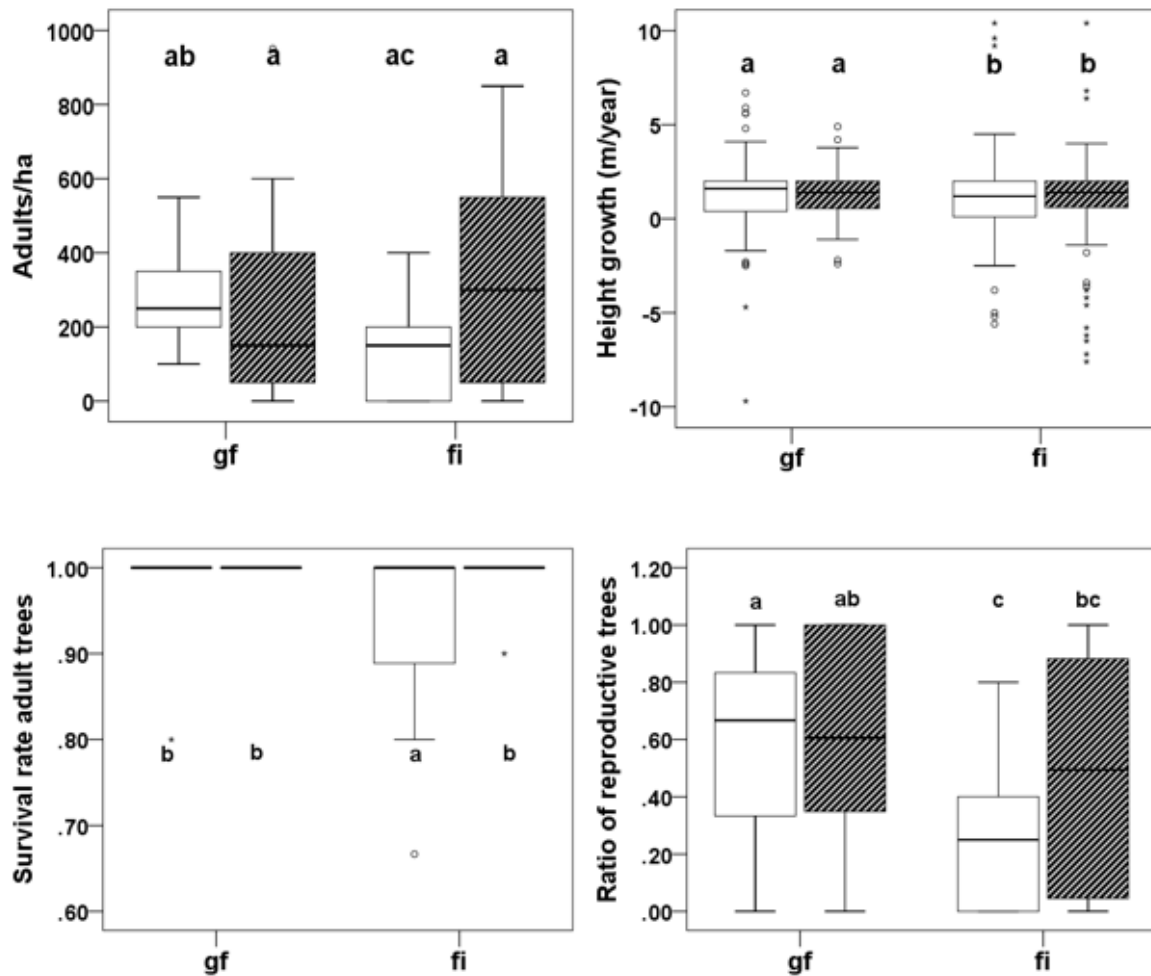

Figure 9, habitat effects on population dynamics of the adult Motacú palm tree in gallery forest (gf) and forest islands (fi). White boxes represent the centre plots and grey boxes represent the edge plots. The letters indicate significant differences between the habitats. Graphs have been constructed based on Mixed models and a Tuckey post hoc test (N=502).

When looking at the densities of the regeneration and the changes in these densities between 2016 and 2017 we see that regeneration is significantly higher in the gallery forest centres (See figure 9). The other three habitats have comparable seedling densities. Juvenile density is also highest in the gallery forest centre. It is followed by the gallery forest edge, forest islands did not have juveniles. When looking at the changes between 2016 and 2017 we see that the change in seedling density is not significantly different among the habitat types. For the juveniles the change is significant for the gallery forest edge. There seems to be no decline in the forest island habitats, however this may be due to the fact that no juveniles were present to begin with, so no decline could take place.
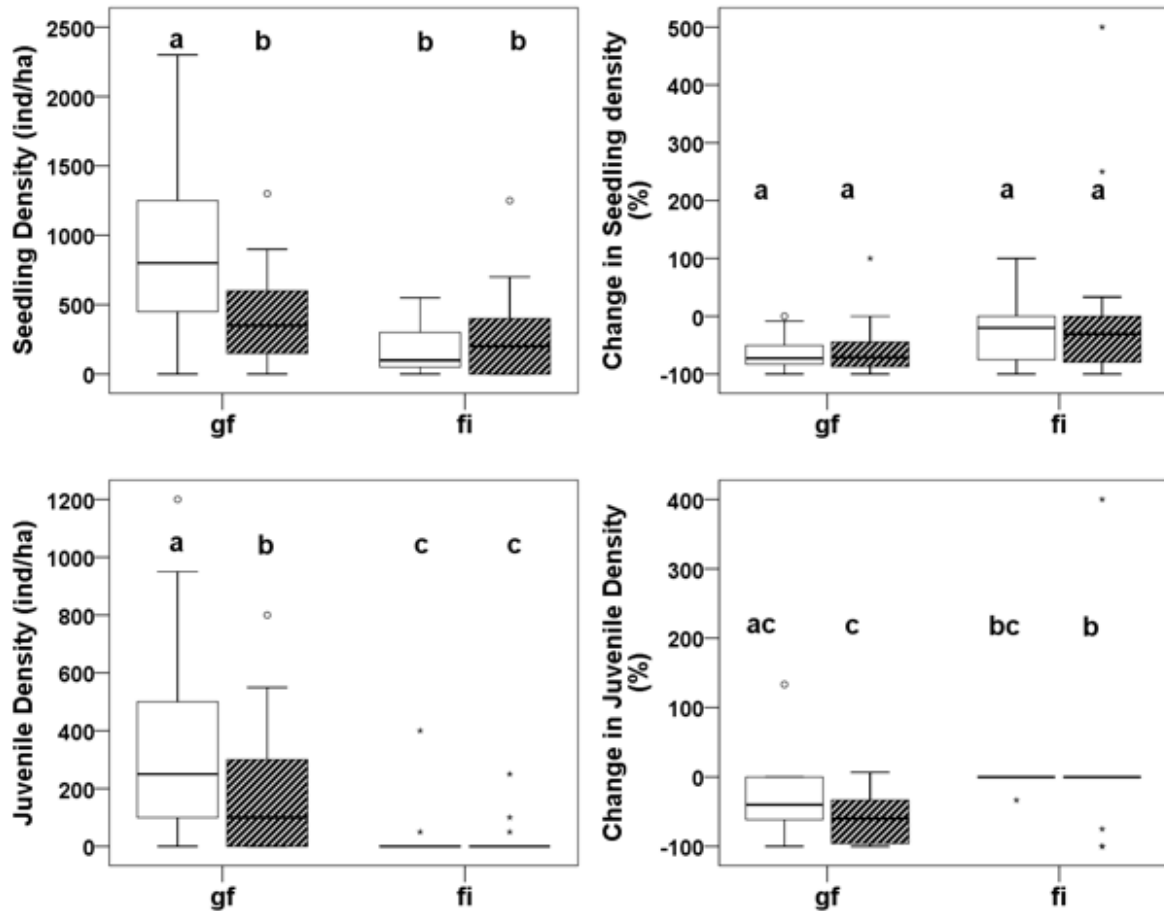
Figure 10, regeneration densities and changes between 2016 and 2017 for gallery forests (gf) and forest islands (fi). White boxes represent the centre habitat, grey boxes represent edge habitat. Letters indicate significant differences between the habitats. The letters indicate significant differences between the habitats. Graphs have been constructed based on Mixed models and a Tuckey post hoc test (N=93).

The counted seeds (seedbank) is significantly lower on the forest islands. Seed production however is higher in the forest islands (See figure 10). Since seed production is higher in the forest islands one would expect a higher seedbank in the forest islands. The lower seedbank that is actually found indicates a higher seed predation pressure in these forest island habitats.

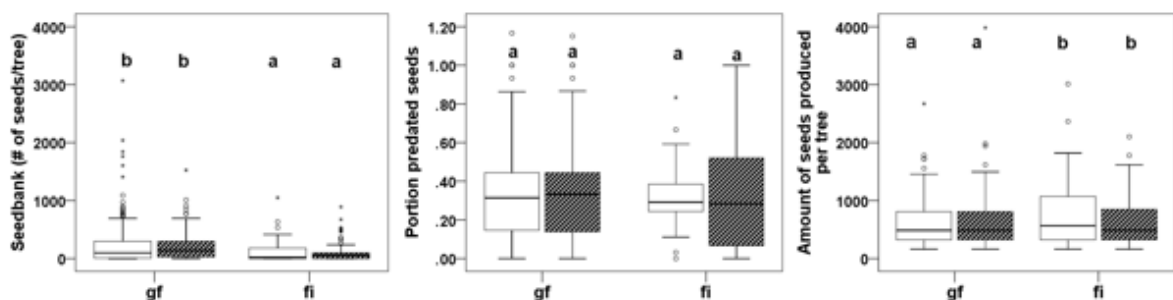*Figure 11, seedbank, seed production, and seed predation rate for the gallery forests (gf) and forest islands (fi). White boxes represent the centre habitats, grey boxes represent the edge habitats. Letters indicate significant differences between the habitats. The letters indicate significant differences between the habitats. Graphs have been constructed based on Mixed models and a Tuckey post hoc test (N=502).*

Table 4, Results of the Mixed Models. Here the significances are shown of whether a factor (e.g. forest type) has a significant effect on the population dynamic (e.g. seed production). Bold values are significant effects.

	Forest type	Centre	ForestxCentre	Fencing	Firebreak	Size class
Seeds						
Seedbank	**0.000**	0.364	0.954	0.393	0.641	**0.002**
Seed Production	**0.002**	0.179	0.612	0.060	0.143	**0.004**
Predation Rate	0.287	0.656	0.610	**0.001**	0.558	0.363
Seedlings						
Density	**0.000**	**0.014**	**0.001**	0.669	0.158	
% change S	0.781	0.469	0.780	**0.001**	0.883	
% change J	**0.015**	0.404	0.136	0.069	0.216	
Adults						
Density	0.800	0.092	**0.007**	0.495	**0.022**	
Survival rate	0.121	**0.023**	**0.043**	0.509	0.435	0.275
Growth	0.163	0.099	0.139	**0.000**	0.269	**0.000**
Reproductive	**0.000**	0.385	0.147	0.907	0.507	**0.016**

Table 5, mean values for the different population dynamics characteristics per forest type, treatment, and size class. Bold values are significant differences.

	Unit	Forest type		Centre		ForestxCentre				Fencing			Firebreak			Size class	
		GF	FI	C	E	GFC	GFE	FIC	FIE	Unfenced	Individually Fenced	Exclusion zone	Unprotected	Firebreak	Natural protection	A1	A2
Seeds																	
Seedbank	#/tree	**233.81**	**93.73**	221.88	134.08	256.97	205.86	123.37	85.02	158.90	62.77	191.75	125.68	199.07	178.82	**137.08**	**204.63**
Seed Production	#/tree	**699.69**	**631.67**	675.52	677.27	379.90	327.09	286.32	285.60	685.74	483.98	701.93	630.76	607.43	824.70	**747.62**	**532.08**
Predation Rate	Predated seeds/total seeds	0.29	0.26	0.32	0.30	0.25	0.28	0.16	0.23	**0.28**	**0.20**	**0.35**	0.28	0.34	0.30	0.32	0.29
Seedlings																	
Density	#/ha	**981.40**	**510.00**	**1284.00**	**608.00**	**1220.00**	**596.00**	**205.88**	**284.62**	492.59	150.00	762.96	390.00	818.33	513.79		
% change S	%	-62.15	-48.97	-67.87	-54.25	-65.58	-57.56	-28.03	-8.56	**-48.11**	**46.98**	**-56.34**	-43.48	-59.03	-30.85		
% change J	%	**-50.02**	**-38.33**	-37.31	-84.91	-550.00	-336.00	-11.76	-5.77	-301.85	0.00	-265.74	-10.00	-451.67	-153.45		
Adults																	
Density	#/ha	267.00	254.65	230.95	286.27	**290.00**	**244.00**	**144.12**	**326.92**	262.96	187.50	276.85	**410.00**	**328.33**	**213.79**		
Survival rate		1.00	0.98	**0.98**	**0.99**	**0.99**	**1.00**	**0.94**	**0.99**	0.98	0.96	1.00	0.98	1.00	0.98	1.00	1.00
Growth	m/year	1.41	1.60	1.54	1.47	1.42	1.40	1.90	1.52	**1.66**	**2.30**	**1.30**	1.67	1.60	1.11	**1.51**	**0.54**
Ratio of reproductive trees	Reproductive trees/total trees	**0.55**	**0.40**	0.52	0.46	0.60	0.50	0.31	0.43	0.49	0.49	0.48	0.39	0.51	0.56	**0.45**	**0.57**

Matrix Models

Matrix models have been made to analyse the population dynamics of *A. princeps*. Matrix models have been made for the four habitat types as survival was significantly affected by forest type and centre/edge; and reproductivity was significantly affected by forest type. To evaluate how grazing and fire impact the population dynamics matrix models have been made for a grazing and a fire scenario.

Table 6, finite growth rates (λ) in the four different habitats.

Habitat	λ
Gallery Forest Centre	1.054
Gallery Forest Edge	1.055
Forest Island Centre	1.010
Forest Island Edge	1.039

For all habitats the projected finite rate of increase (λ) was positive (see table 6). Since all the growth rates are more or less the same the eventual population increases look the same. The life stages J and A1 decrease in the first years, but after 4-5 years they start to increase. The other life stages start to increase immediately (see figure 11).
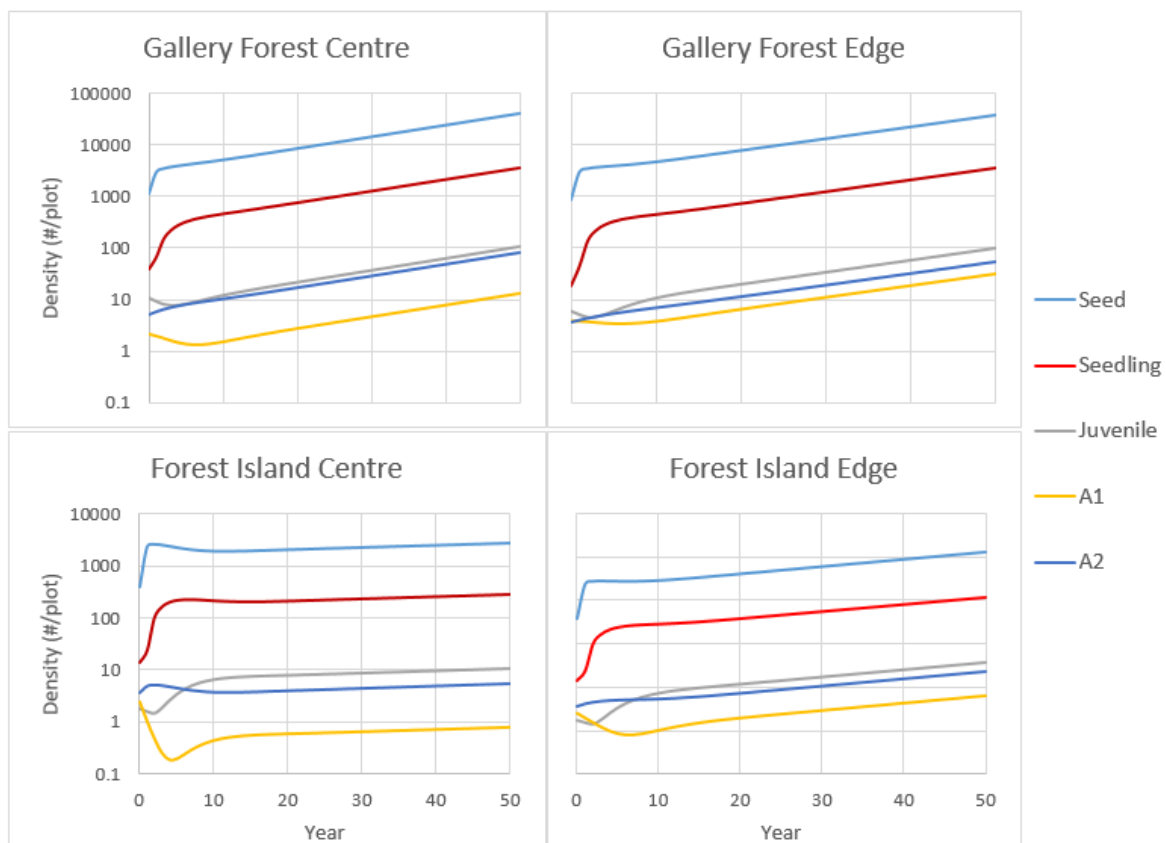

Figure 12, projected population development for the four habitats. Clear is how the juvenile (grey) and A1 (yellow) stage decline at first but after 2 years (juvenile) and 7 years (A1) start to increase again. Other life stages increase immediately.

Elasticity analyses were done on the four matrix models (See table 7). Elasticity analyses show how a population changes with small proportional changes in the vital rates. If we look at the elasticity rates we see that the survival of A2 is the most important vital rate. So changes in the vital rates for A2 survival have the largest proportional change in λ.

Table 7, elasticity values for the different vital rates for the different habitats. We see that the highest sensitivity values are for the rates indicating movement to the next stage. However, elasticity analyses point to the survival of A2 as the most important factor. The bold elasticities are the largest elasticities and thus the most sensitive vital rate to change.

Transition	Gallery Forest Centre	Gallery Forest Edge	Forest Island Centre	Forest Island Edge
Seed Stasis	0.007	0.007	0.01	0.009
Seed to Seedling	0.035	0.036	0.046	0.041
Seedling Stasis	0.057	0.058	0.084	0.069
Seedling to Juvenile	0.035	0.036	0.046	0.041
Juvenile Stasis	0.139	0.14	0.228	0.173
Juvenile to A1	0.035	0.036	0.046	0.041
A1 Stasis	0.063	0.217	0.028	0.104
Seed production A1	0.005	0.013	0.006	0.009
A1 to A2	0.03	0.023	0.04	0.032
A2 Stasis	**0.563**	**0.413**	**0.425**	**0.451**
Seed production A2	0.03	0.023	0.04	0.032

To test for the effects of grazing and fire on the population dynamics matrix models have been made simulating these disturbances on the system.

Effects of grazing on population dynamics

To simulate the effect of grazing the matrix model of a forest island (combining centre and edge) has been constructed. To test a worst case scenario survival at the seedling stage has been set to 0. Recruitment to the next stage (so Seedling to Juvenile) is kept the same. This is based on the assumption that seedlings are either eaten, or grow large enough to withstand the grazing pressure. For juveniles it is assumed that the smaller individuals still endure some negative effects from the cattle presence so survival has been set to half of the 'normal' survival in a forest island (0.420 instead of 0.840). For the other vital rates the vital rates of a forest island is used. This matrix resulted in a λ of 0.998, meaning that with grazing the population declines in the long run. What is clear from figure 12 is that the Juvenile stage drops immediately and stabilises around 0.7 individuals per plot. The A1 stage drops immediately and approaches 0.1 individuals per plot, this is probably a direct result of the lower recruitment from the juvenile life stage. After this stabilisation period both the life stages start decreasing in their abundance. The other three life stages (seeds, seedlings, and A2) increase initially but start declining after 3 years of grazing pressure.
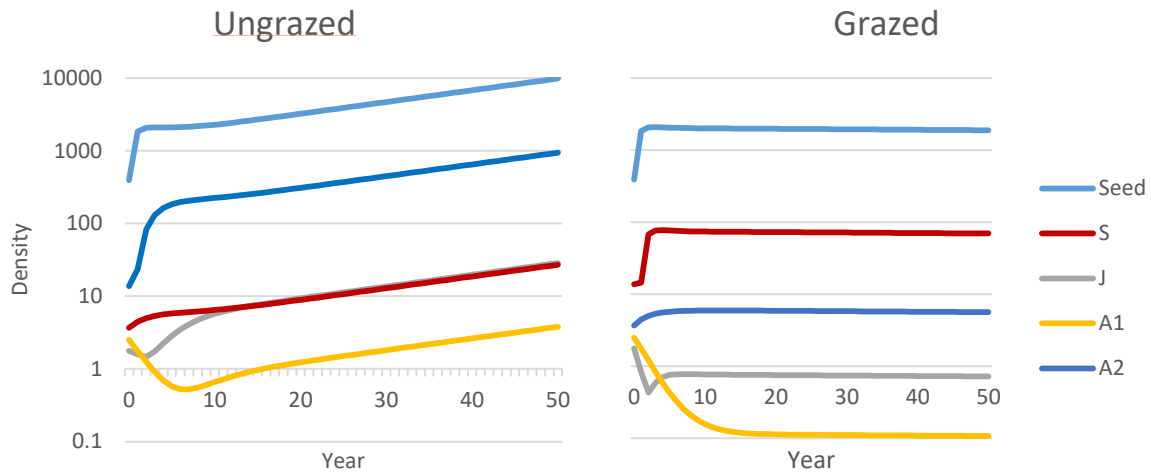
Figure 13, population development for an ungrazed (left) and a grazed (right) forest island. We can see that in the ungrazed scenario the Juvenile (grey) and the A1 (yellow) lifestages decline initially but increase after 2 and 7 years respectively. For the grazed scenario the Juvenile and A1 lifestages decline immediately. Other lifestages increase initially, but decline after ~4 years.

Effects of fire on population dynamics

To simulate a population dealing with fire pressure a series of matrix models was made. Since the forest islands are most impacted by a fire occurrence the vital rates of a forest island were used. It was assumed that a forest island had a fire occurrence every 5 years, which is less than estimated from the comparable Pantanal region where a fire frequency of once every 2-4 years is estimated (Furley, 1999). So a matrix model was run for 5 years and the final population structure was used as the initial vector for a new model with the seedling and juvenile stage set to 0, after the fire occurrence a 'normal' survival regime was used. This assumption was made since actual survival data was not available since no detrimental fires occurred between 2016 and 2017. This was repeated 15 times to get to a 75 year time period.

What we see is that all life stages decline with this fire intensity. In the first years no fire has occurred and the population increases along the same lines as an undisturbed forest island. Seeds, seedlings, juveniles, and A2 increase while A1 decreases. But after the fire occurrence has started (> 5 years) we see all life stages declining. However, this effect is strongly affected by the fire intensity used. If a fire occurrence of once every 7 years is used populations are able to recover sufficiently from the fire and we see the population increase again.
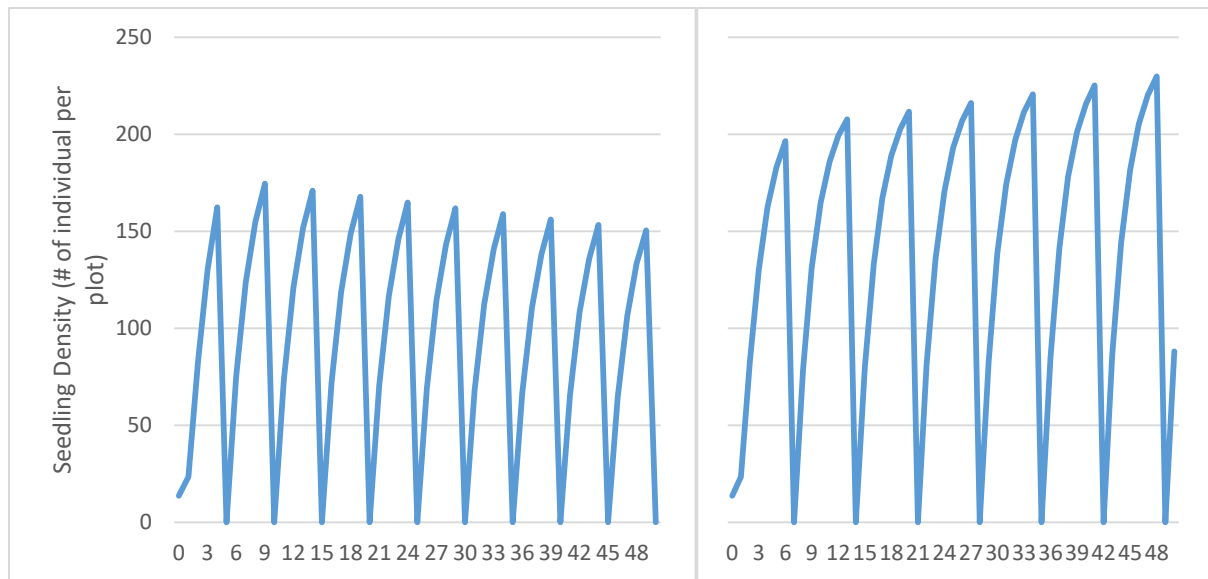
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Figure 14, seedling density development for a forest island with a fire frequency of once every 5 years (left) and once every 7 years (right). The lines were created by following the matrix projections over the years.

Discussion

The main question of this thesis was how the population dynamics of the Motacú is impacted by different environmental circumstances and disturbances in the ecosystem. For this I tested the effect of different habitats, soil characteristics, fire disturbance, and grazing disturbance. I will first discuss my findings according to the main research questions related to environmental conditions and soil characteristics, after that the effect of removing the grazing and fire disturbance will be discussed. I will conclude this chapter and the report with Management Implications and Concluding Remarks.

Analysis of the Population Dynamics

What was found is that the seedbank of the Motacú is significantly impacted by the size class of the Motacú. The larger size class (A2) has a significantly larger seedbank than the smaller size class (A1), while the seed production of the smaller size class was found to be larger than the larger size class.

It was found that that the A1 size class had the higher seed production per reproductive tree, but since the A2 size class had more trees that were reproductive average seed production for all trees was higher for the A2 size class. The larger seedbank under the large size classes can be explained by the higher seed production found for the large size class compared to the small size class.

The effects of habitats on Motacú regeneration and Population Dynamics

I hypothesized that forest islands and gallery forest would differ in population dynamics because there are differences in habitat characteristics. First there is the difference in abiotic soil conditions through the different histories of the habitats. Furthermore the amount of disturbance is different in the two habitats. The forest islands experience more disturbance and are more influenced by disturbances than the gallery forests. Since the Motacú palm is considered a forest species (Moraes et al., 1996) I expected more successful regeneration in the gallery forests compared to the forest islands. This hypothesis was correct for seed production and reproductive rate. The higher values were found in the gallery forests. Regeneration density was also higher in the gallery forests. However, the (negative) change in juvenile density was larger in the gallery forest than in the forest islands which contradicts the hypothesis. This may however be the result of not having any juveniles in the forest islands at all, making it impossible for the juvenile density to decline further.

Due to the same differences in disturbance I also expected differences between centre and edge plots. Due to the fact that edges are more disturbed than centres I expected centre plots to have a more successful regeneration (Moraes et al., 1996; Murcia C., 1995). This was the case for the gallery forests. On the forest islands however the effect was turned around, centre plots had lower regeneration than the edge plots. This 'reversed edge effect' can be explained by the behaviour of the cattle. When looking at the data of Hordijk (2017) it showed that the amount of dung piles was significantly higher in the forest island centres compared to the edges. When the cattle uses the forest island to rest they will concentrate in the centre of the island since it is the most driest and most protected part of the island, resulting in a highly disturbed centre and a relatively undisturbed edge.

To see what the driving factors were behind these differences multiple regression analyses were done. From this it showed that regeneration amount is mainly driven by Canopy Openness, Average Firescar, and Bare Soil; with Canopy Openness and Bare Soil having a negative effect and Fire Scar having a positive effect on regeneration density. Average Firescar was used as a measure to quantify the historical amount of fires in a habitat and is the average firescar cover on the adult trees. This could indicate that fire is needed to clear away competing vegetation since shrub and grass cover both had a negative correlation with regeneration density. However, a closed canopy and litter cover is needed for the seeds to germinate, possibly due to the dampening effect on soil desiccation (Breshears, Nyhan, Heil, & Wilcox, 1998).

Effects of soil characteristics on tree regeneration

At first I asked what the soil characteristics where that influenced Motacú regeneration. I expected positive relations between soil nutrients and regeneration and a pH optimum between 5 and 7.

It was found that the regeneration of the Motacú palm has a negative relation with clay content, available NO3, total available N, available P, organic matter content, and K. From the multiple regression it became apparent that Organic Matter is the only explanatory factor for regeneration densities. The effects of the other soil variables are explained by the indirect effect of organic matter content. Since organic matter is a good water retainer (Gupta & Larson, 1979) I think the presence of organic matter may result in waterlogging which may damage young plants as has been found in oil palm (Auxtero & Shamshuddin, 1991; Rivera-Mendes, Cuenca, & Romero, 2016). There was a positive relation between the number of Juveniles and sand content As sandy soils are generally well drained this may also indicate that avoidance of waterlogged conditions is important for palm regeneration (Tyler & Wheatcraft, 1990).

These findings are in line with what has previously been written in literature on the Beni, Pantanal, and forested patches in these areas, namely that the raised areas allow for forest vegetation to develop (Hamilton et al., 2002; Junk et al., 2006; Mayle et al., 2007).

Effects of cattle fencing on tree regeneration

As a second research question I asked what the effect of fencing off forest islands is on regeneration of Motacú palm. I hypothesized that the fenced off islands saw better regeneration since the grazing disturbance is removed in these Forest Islands. I did not expect a difference between the two ways of fencing (fencing an entire area vs fencing individual islands). As expected, the unfenced islands saw a decline in regeneration (See table 3). However, the area where cattle were excluded, but individual islands were not fenced, also experienced a decline in regeneration between 2016 and 2017 (table 3). The matrix model projections also indicate that adding grazing pressure to the current situation can lead to the decline of the population. This corresponds with previous research where fencing

positively impacted the survival of seedlings in tropical dry forests (Blackmore & Vitousek, 2000; Stern, Quesada, & Stoner, 2002; Wassie, Sterck, Teketay, & Bongers, 2009).

One should keep in mind that the fencing treatment was applied to the islands where Motacú was in general already well established whereas the unfenced islands were either outside the park, where grazing pressure could be very high in the wet season, or the unfenced islands were very small with little or no Motacú. This could have led to overestimations of the fencing effect. Moreover, the fencing treatment was not perfect, as a herd of cattle was still seen in the area where cattle should have been excluded. This could have resulted in some grazing pressure on the islands where no grazing was assumed. Despite these limitations I conclude that grazing has strong negative effects on population dynamics, and that the only efficient way to apply a fencing treatment to protect Motacú regeneration is to fence off individual islands.

Effects of fire breaks in tree regeneration

My third research question was 'What is the effect of protection by firebreaks on the regeneration of Motacú?' Since a firebreak removes the fire pressure on the system I hypothesised that forest islands which were protected by a firebreak saw a higher regeneration than the unprotected islands. I did not expect to find a difference between the artificial and the natural firebreaks which are present in the Reserve.

From the Matrix Models we can conclude that fire does have a negative effect on regeneration rates. This is however dependent on the fire frequency, once every 5 years led to declining seedling density while once every 7 years still resulted in increasing seedling density. Contrary to what was hypothesised it was found that average fire scar on adult trees had a positive effect on seedling density and that the islands which were protected by a firebreak saw a decline in seedling density between 2016 and 2017. The positive effect of average fire scar could come from the sudden increase in seed germination as fire increases canopy openness (Woods, 1989). Canopy openness however had a negative effect as soil desiccation increases with a more open canopy (Gerhardt, 1996), closing the canopy after a forest fire thus seems necessary to protect the seedlings from desiccating. It should be said that the Mixed Models only showed a significant difference for adult density between the different firebreak treatments. All other population dynamics were not influenced. This could be due to the fact that there is no effect, or that the effect does not show yet as this is the first year with a firebreak protection. It could be that the effect needs several years to manifest.

In the comparable Pantanal and Brazilian Cerrado it was found that seedling establishment was negatively impacted by fire whereas protection from fire can increase the woody component in a savannah (Furley, 1999; Hoffmann, 1996; Pivello & Coutinho, 1996). Therefore it is good to limit the amount of fires in the park and the construction of firebreaks is a good measure to protect the regeneration of Motacú. In circumstances where firebreaks are not possible or desired it is recommended to reduce the fire frequency of every 2-4 years to >7 years (Furley, 1999).

Strengths, limitations, and recommendations for further research

As with any research there were limitations to what could be done during the process. Due to the way the research was set up individual survival data of the seedlings could not be gathered. This limited the possibilities of constructing fully accurate Matrix Models. In the end literature was used to fill in the gaps in the gathered data in an attempt to get to functioning Matrix Models. This method however always reduces accuracy of the model.

Since biological processes in the Nitrogen cycle keep on running while storing soil samples the available nutrient loads in the soil samples may have been different in the soil samples than what would have been found in the field. These changes have not been accounted and corrected for while doing the analyses. This limits the amount of reliability of the analyses. Since available nutrient loads appeared not to have an effect this problem resolved itself. However, in future research these changes in available nutrient loads should be avoided by analysing the soils as fast as possible.

When doing the research it appeared that in the cattle exclusion zone a herd of 15 cows was still present. This has probably interfered with the measurements and the effect of the cattle exclusion zone can thus be different than is portrayed in this report. Continuation of this research program can give us definitive answers about the effect of cattle exclusion zones when this herd is removed from the park.

The strength of this research is that I've been able to compare an area where management is currently taking place. This allows for a real-time monitoring of the management effects, and allows for the management to adapt their management where and when necessary.

Since this project is intended to be a long-term monitoring program there is the opportunity to do a lot more research on the Motacú, Blue-throated Macaw, and gallery forests and forest islands in general. An obvious continuation of this research is to obtain individual survival data of the seedlings and juveniles to better construct the Matrix Models. Furthermore it might be interesting to investigate what drives the difference in reproductive rate between the different habitats. Another topic to investigate is the effect Organic Matter has on regeneration. Is it the effect of nutrient provision that organic matter has, or is it the effect of water retention? Answers to this question could allow for better targeted management of Motacú stands. Another topic of research could be how fires positively influence the Motacú regeneration. From the correlations and multiple regressions it showed that average fire scar had a positive effect on seedling density, but the mechanism behind this is not investigated.

Management Implications

This research showed that it is important to protect the regeneration of the Motacú palm from grazing. The Mixed Models and Matrix Models showed a negative effect of grazing, or positive effect of fencing, on the regeneration capabilities of the palm. Both the fencing of individual islands and using cattle exclusion zones could be fruitful, but since a cattle exclusion zone showed a decrease in regeneration density I would advise to use an individual approach to fencing. This decrease can be attributed to the fact that there was still a herd of cattle in the exclusion zone, but this also shows the weakness of the approach. In case of a herd entering the area all islands are at risk of being grazed while this is not the case when using an individual fencing approach. One last incentive for the farmer to use this technique is an economical incentive. When applying the cattle exclusion zone to Barba Azul North (See figure 4) 24.35km of fence had to be placed. If the individual fencing approach had been used only 1.12km of fencing would have been necessary.

Another important management measure in this research was the application of firebreaks. From the results a mixed effect shows. The multiple regression showed a positive effect of fire on regeneration, but from the matrix models it showed that a high frequency of fire can have negative effects on the regeneration of the Motacú. The Mixed Models showed no significant differences between the protected and the unprotected islands, but this can be attributed to the fact that fires have not burned the unprotected islands since the firebreaks have been constructed.

Taking all this into account I would advise to construct and maintain firebreaks to limit the amount of fires entering the forests. In addition I would advise to investigate through what effect fire enables regeneration. When this is known management can try to replace this effect and thus enable Motacú regeneration without experiencing the negative effects of fire. When the construction of firebreaks is not possible or desirable management should limit the fire frequency to once every 7 years, or even a lower fire frequency.

Concluding Remarks

The aim of this research was to find the effect of soil and environmental conditions on the population dynamics of the Motacú palm, as well as evaluating the effect of grazing and fire. After this research it can be concluded that organic matter has a significant negative effect while other soil factors seem to have less effect. From the environmental factors the regeneration densities are driven by canopy openness (negative), average firescar (positive), and bare soil surface (negative).

It was found that cattle exclusion has a positive effect on regeneration. The most effective way of regeneration protection seems to be an individual fencing approach where individual forest islands are fenced rather than an exclusion zone approach where a larger area is fenced and cattle are removed from this area.

Concerning the fire effect it is a bit harder to come to clear conclusions. There seems to be a positive relation between fire and regeneration as showed in the multiple regression. From the matrix models however a negative effect showed. It is therefore key to limit the fire intensity by constructing firebreaks and finding out what drives the positive effects of fire so that management can adapt their actions to this.

Acknowledgements

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Appendices

Appendix 1

Table 8, overview of where what variables were measured and why

| Where?	What?	Why?	How?
Plot			
	Amount of dung piles 2017	Quantify grazing pressure	Count
	Fencing treatment	Group habitats per treatment	Classification
	Firebreak	Group habitats per treatment	Classification
Per seedling/ Juvenile			
	Leaf Length	Classify into MM Stages	Measure with ruler
	Health	To have a measure of performance	Classification based on uniformity of leaves
Per Adult			
	Stem Height New (m)	To have a measure of growth combined with data of 2016	Measure with Nikon Forestry Pro
	DBH	To have a measure of growth combined with data of 2016	Measure with DBH measuring tape
	Distance to closest palm (m)	To have a measure of density	Measure with measuring tape
	# of leaves	To have a measure of health and productivity	Count
	# of inflorescence	To have a measure of fertility	Count
	# of infructescence	To have a measure of fertility	Count
	Health score new (d/b/m/g)	To have a measure of health	Classification based on leaf and stem uniformity
	Fire scar surface (cm2)	To quantify the fire disturbance	Measure with tape
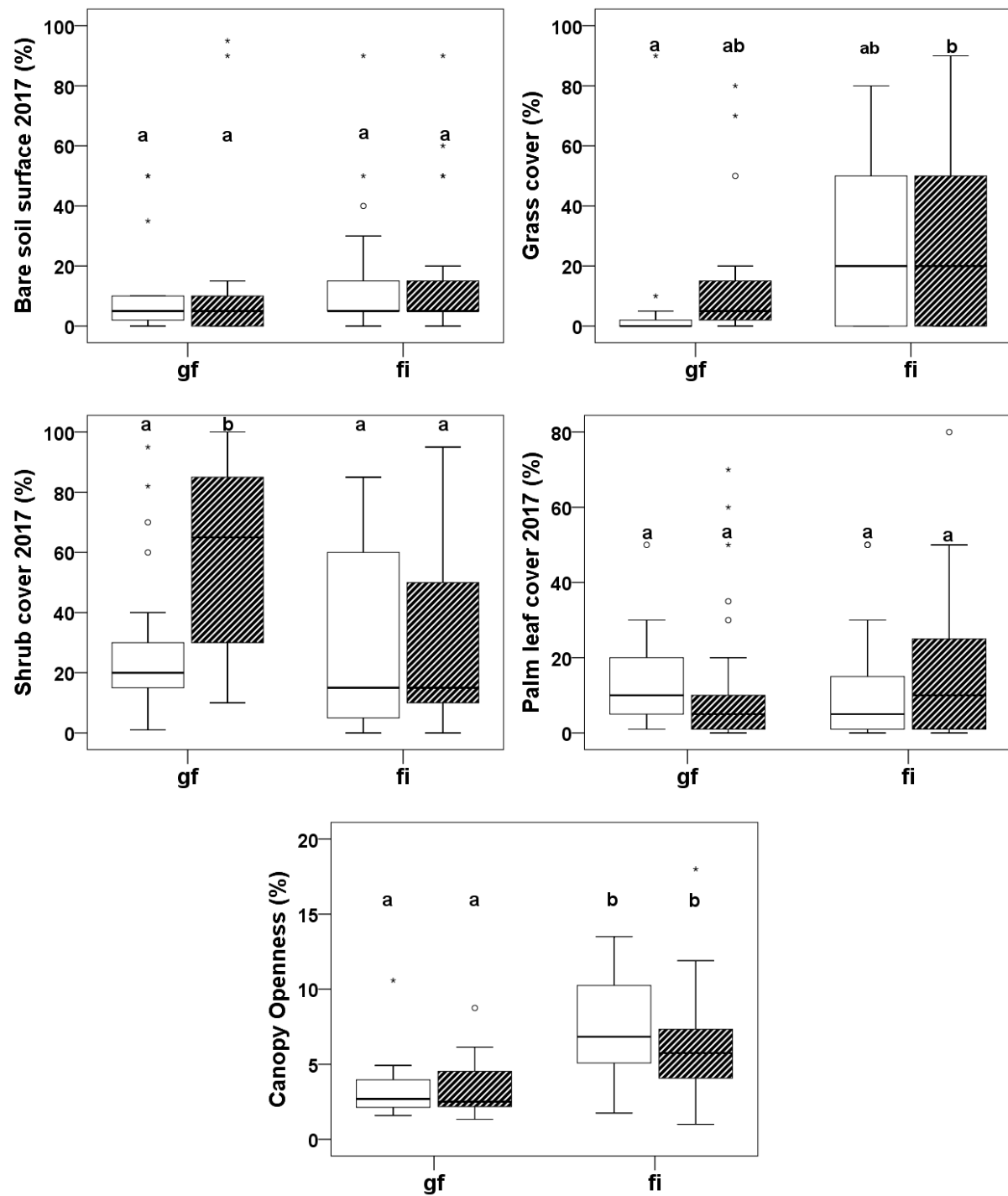
Figure 15, environmental variables of the different habitats. White boxes represent centre plots, grey boxes represent the edge plots (N=93).
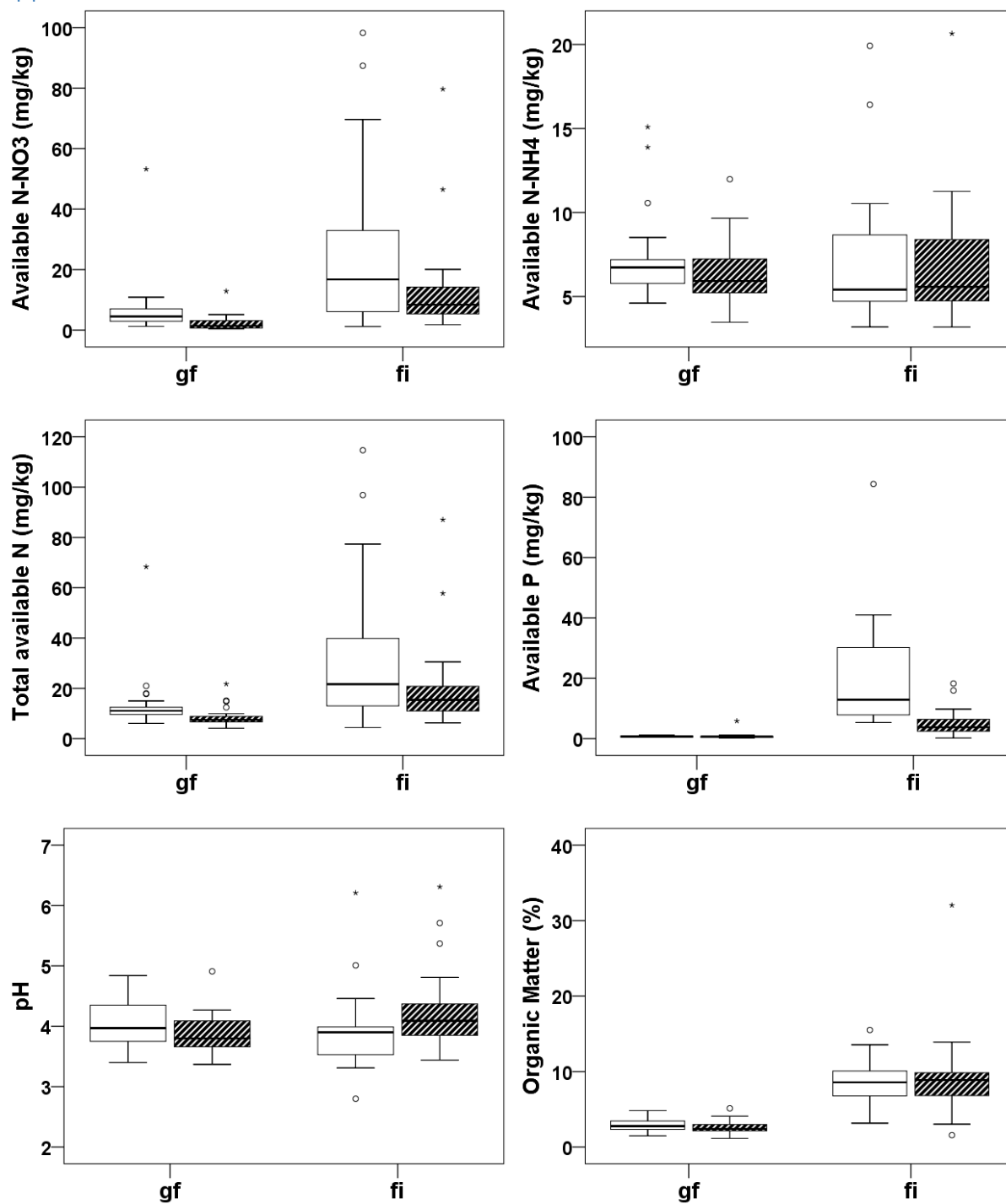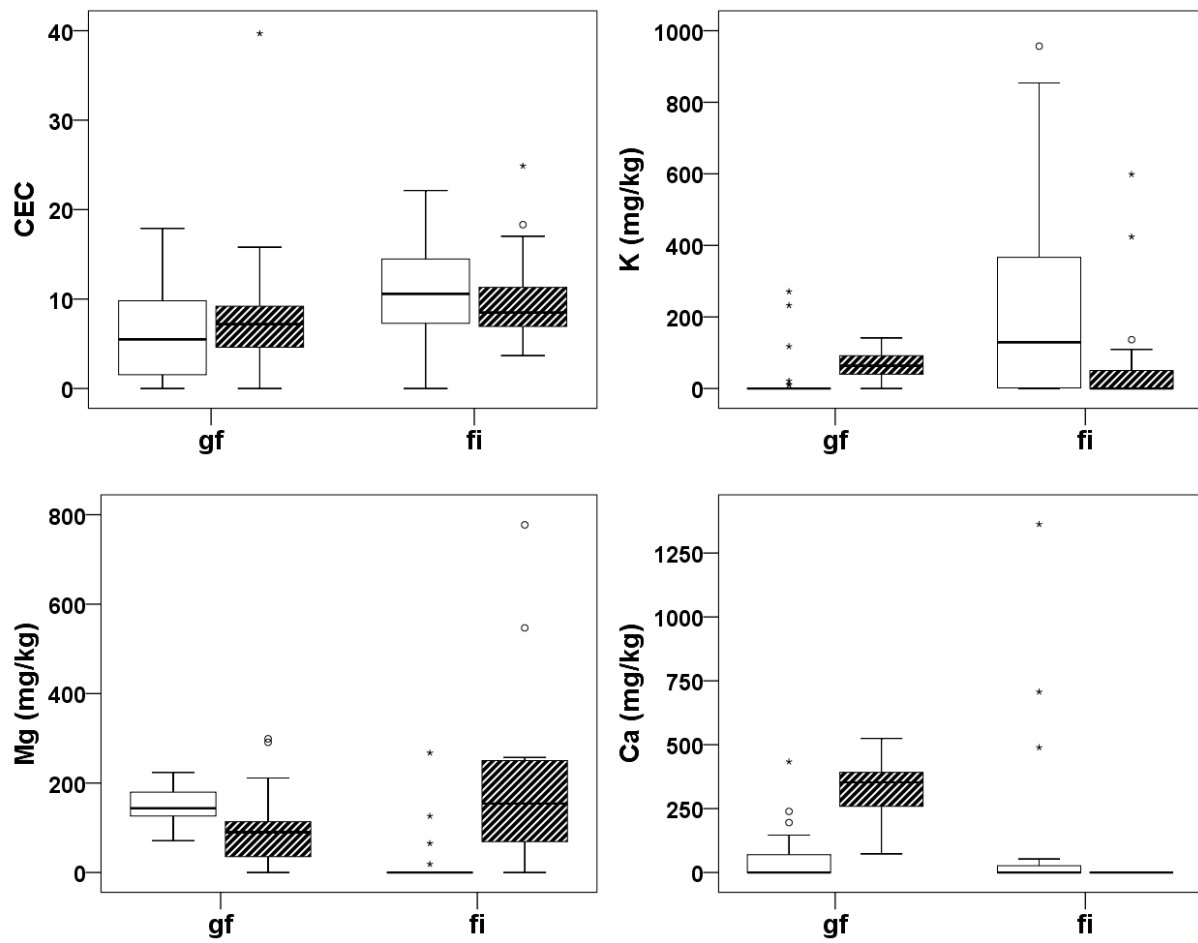
Figure 16, soil characteristics of the different habitats. White boxes represent centre habitat, grey boxes represent edge habitat (N=93.

Appendix 4

Transition	Gallery Forest Centre		Gallery Forest Edge		Forest Island Centre		Forest Island Edge	
	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity
Seed Stasis	0.043	0.007	0.043	0.007	0.056	0.010	0.049	0.009
Seed to Seedling	1.007	0.035	1.019	0.036	1.261	0.046	1.149	0.041
Seedling Stasis	0.092	0.057	0.093	0.058	0.130	0.084	0.110	0.069
Seedling to Juvenile	**6.176**	0.035	**6.252**	0.036	**7.734**	0.046	**7.048**	0.041
Juvenile Stasis	0.174	0.139	0.175	0.140	0.274	0.228	0.214	0.173
Juvenile to A1	0.756	0.035	0.765	0.036	0.946	0.046	0.862	0.041
A1 Stasis	0.098	0.063	0.253	0.217	0.074	0.028	0.144	0.104
Seed production A1	0.000	0.005	0.000	0.013	0.000	0.006	0.000	0.009
A1 to A2	0.101	0.030	0.253	0.023	0.070	0.040	0.131	0.032
A2 Stasis	0.593	**0.563**	0.435	**0.413**	0.465	**0.425**	0.483	**0.451**
Seed production A2	0.000	0.030	0.000	0.023	0.000	0.040	0.000	0.032