

The Blue-throated Macaw (*Ara glaucogularis*), a true palm specialist



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Table of Contents

Summary	iv
Introduction	1
History of the Blue-throated Macaw	2
Ecology of the Blue-throated Macaw	2
Aim and hypotheses.....	3
Methods.....	6
Study area	6
Data collection	6
Data analysis	8
Results: Resources	11
Landscape mosaic	11
Landscape disturbance	11
Results: Macaws.....	12
Predictors of macaw abundance	12
Resource competition.....	13
Discussion.....	15
Conclusion.....	21
Acknowledgements.....	22
References	23
Appendices.....	27
Appendix I	27
Appendix II Landscape mosaic	27
Appendix III Predictors of Macaw abundance	30
Appendix IV Macaw inventory and information on the forests	31

Summary

Justification. Habitat loss and fragmentation are the main drivers of worldwide biodiversity decline, and especially endemic species with a limited dispersal range are vulnerable to extinction. Using these endemic species as flagship species could offer possibilities for raising awareness and funding for conservation efforts. The endemic and critically endangered Blue-throated Macaw (*Ara glaucogularis*) is the flagship species of Bolivia and is suffering from habitat loss and degradation in the Beni savanna of Bolivia due to anthropogenic disturbance. It occurs only in the Beni savanna of Bolivia in riverine gallery forests and forest islands surrounded by savanna grassland and it is associated with the *Attalea phalerata* palm for food, roosting, and nesting.

Aim. The aim of this study is to get a broader understanding of the ecology of the Blue-throated Macaw by identifying what habitat conditions determine Blue-throated Macaw occurrence and abundance. In this study four concepts are described that can influence Blue-throated Macaw abundance, 1) landscape mosaic, 2) landscape disturbance, 3) resource availability, and 4) resource competition. The role of the sympatric Blue-and-Yellow Macaw (*Ara ararauna*) was also evaluated, as it occurs in the same area and it is thought to be a competitor for the Blue-throated Macaw.

Study design. To study the habitat characteristics of the Blue-throated Macaw, data on 498 palms and other tree species was collected from 91 plots in gallery forests and forest islands in the Barba Azul Nature Reserve. Data on Blue-throated Macaw and Blue-and-Yellow Macaw abundance and feeding behaviour was collected using point counts in both habitats (N=8 gallery forests, and N=25 forest islands).

Results. The two main habitat types -gallery forests and forest islands- in which both macaw species occur, differ clearly in structure and function. In the larger gallery forests, fruit availability of *A. phalerata* is 2.8 times higher and tree species richness is 1.6 times higher, than in the forest islands. Landscape disturbance in terms of fire has a negative effect on the condition of palms, which, in turn, negatively affects fruit production. The Blue-throated Macaw abundance shows a positive relation with *A. phalerata* fruit availability. The Blue-and-Yellow Macaw abundance shows a positive relationship with larger patch sizes and a higher species richness of trees. Observation data suggests that Blue-throated Macaw is a more specialist feeder, which mainly focuses on *A. phalerata* whereas the Blue-and-Yellow Macaw uses a higher variety of food sources. Resource competition in terms of food and roosting resources does not appear to play a large role in determining Blue-throated Macaw abundance.

Conclusions. The results confirm the hypothesis that the Blue-throated Macaw is a palm specialist, mostly associated with *A. phalerata*. I provide a comprehensive overview of the ecology of the Blue-throated Macaw as I show how its habitat is influenced by the landscape mosaic and disturbance, and I shed light on the knowledge gap on the association with *A. phalerata* and resource competition with the Blue-and-Yellow Macaw.

Keywords: *Ara glaucogularis*, *Ara ararauna*, *Attalea phalerata*, habitat use, resource availability, landscape disturbance

Introduction

In many parts of the world, habitat loss and fragmentation are taking place at alarming rates. These processes have a negative effect on the ecosystems and the biodiversity within these systems. Biodiversity is in decline, and habitat loss and fragmentation have been determined to be one of the most important drivers (Dirzo & Raven, 2003; Kerr & Deguise, 2004; Butchart et al., 2010). As species populations become smaller and isolated, stochastic events increase their vulnerability and consequently populations become more prone to extinction (Caughley, 1994; Hedrick et al., 1996). This is the case with endemic species inhabiting limited ranges, which makes them extra vulnerable. To use them as flagship species could offer possibilities for raising awareness and funding for conservation efforts (Leader-Williams & Dublin, 2000; Walpole & Leader-Williams, 2002). Often, charismatic species such as the giant panda are used as flagship species that easily appeal to many people (Leader-Williams & Dublin, 2000). Birds can also be used as flagship species and with regard to the different groups of animals, birds represent one of the best known and researched vertebrate groups in the world. This creates the opportunity to use birds as indicators for biodiversity and to study biodiversity trends over time, including the effects of habitat loss and fragmentation (Gregory et al. 2003; Birdlife International, 2013). One of the regions in the world that are currently under pressure are the tropics, such as the Amazon region, where deforestation, and other human-induced disturbance are causing tremendous habitat loss and fragmentation (Skole & Tucker, 1993; Carvalho & Mustin, 2017). Macaws are one group of bird species in the tropics of Central- and South America that are highly associated with intact landscapes. Many species of macaws prefer old and pristine forests with ample nesting availability, indicating that they are possible biological indicators for the condition of forests (Berkunsky et al., 2016). It is an iconic and widely known group of birds which can be used as flagship species (Guedes, 2004; Guittar et al., 2009). One of those flagship species is the endemic and critically endangered Blue-throated Macaw (*Ara glaucogularis*).

To conserve endemic flagship species, it is necessary to understand their ecology. Consequently, it is important to study what habitat conditions determine their occurrence and abundance. In this study, four concepts are described which potentially play a role in the occurrence and abundance of a species. These are 1) the landscape mosaic in which they occur, 2) landscape disturbance, 3) resource availability, and 4) resource competition. The first aspect, the landscape mosaic, is about the spatial distribution of habitat which can influence the occurrence of a species (Bender et al., 1998; Prugh et al., 2008). The island biogeography theory plays a role in the landscape mosaic as the theory proposes that larger islands have more niches and resources. Moreover, islands closer to the mainland have a higher species richness and abundance through a higher chance of colonization (MacArthur & Wilson, 1967). Secondly, landscape disturbance can affect species occurrence through regulating resource availability. Disturbance such as overgrazing by cattle or human induced fire could influence habitat fragmentation and degradation (Yamashita & Machado de Barros, 1997). Regular human induced fires are known to have large-scale effects on forest fragments (Laurance, 2000; Cochrane & Laurance, 2002). Thirdly, resource availability, plays an important role in determining the occurrence of a species. Habitat fragmentation can influence the availability of resources, such as food or nesting sites, and consequently can be regulating species occurrence (Saunders et al., 1991; Andren, 1994). Lastly, indirect landscape effects, such as resource competition with other species can be an explaining variable affecting occurrence and abundance of a species (Dunning et al., 1992). In this study the Blue-throated Macaw is used as a case study to determine what habitat conditions determine this species occurrence and abundance.

History of the Blue-throated Macaw

An example of a bird species that inhabits fragmented forest areas which is threatened by habitat loss is the Blue-throated Macaw. The Blue-throated Macaw is endemic to the Beni savanna ecoregion in northern Bolivia. It is a critically endangered bird species with an estimated population size of only 250-300 individuals (Birdlife International, 2016). Illegal parrot trapping has resulted in a 70% population decline of the Blue-throated Macaw in the last 50 years (Herrera & Hennessey, 2007). In 1979, the establishment of the CITES treaty resulted in a ban on the illegal trade of wild fauna and flora, nevertheless, the parrot trade continued (Herrera & Hennessey, 2007). Probably 1,200 Blue-throated Macaws have entered the commercial trade during the 1980s (Yamashita & Machado de Barros, 1997). During these years, it remained a mystery where the species was occurring and it was only rediscovered in the wild in 1992 in the Beni savanna (Jordan & Munn, 1993). Currently, the Blue-throated Macaw is less threatened by illegal trapping for the pet trade, though habitat loss and degradation are new and additional threats to the species. Results from a population viability analysis conducted by Bouzat & Strem (2012) indicated that the species is highly sensitive to even small changes in habitat loss, but the population is assumed to be stable (Berkunsky et al., 2015). Until recently, only two populations of the critically endangered Blue-throated Macaw were known, though in 2007 an unexpected discovery was made, when a large group of Blue-throated Macaws were found roosting at an unknown location (Waugh, 2007). This discovery led to the establishment of the first nature reserve aiming to protect the Blue-throated Macaw and the Beni savanna habitat. The Barba Azul Nature Reserve (BANR) was founded in 2008 by Asociación Armonía, Bolivia's leading bird conservation NGO. BANR is an important site for a significant amount of the world population of Blue-throated Macaws and it is therefore important to understand how the macaws use the reserve and what environmental and ecological factors drive their presence.

Ecology of the Blue-throated Macaw

The Blue-throated Macaw is home to the Beni savanna, or the so-called Llanos de Moxos, located in the northern part of Bolivia. This ecoregion is identified as a plant diversity and endemic centre, by the World Wildlife Fund (WWF, Ecoregions, 2017). The entire region is a stronghold for lowland parrot species and research on these parrots is a priority for conservation (Herzog et al., 2005, Larrea Alcázar et al., 2011). The main habitat of the Blue-throated Macaw is a landscape of riverine gallery forests and fragmented forest islands surrounded by savanna grassland. In the BANR, the gallery forests are mostly used as foraging sites and the macaws use the forest islands as roosting sites (Kingbury, 2010; Glasgow University Expedition Report, 2014). The forest islands in the Beni are believed to be both of anthropogenic and natural origin, and the presence of these anthropogenic forest islands indicate that there have been anthropogenic influences for many centuries (Mayle et al., 2007; Lombardo & Prümers, 2010). The main tree species occurring on these islands and gallery forest is the *Attalea phalerata* palm (Yamashita & Machado de Barros, 1997). *A. phalerata* is the main food, nesting, and roosting resource for the Blue-throated Macaw (Hesse & Duffeld, 2000). Apart from *A. phalerata*, the Blue-throated Macaw also utilises other trees for feeding, see Appendix I (derived from Yamashita & Machado de Barros, 1997). For nesting sites, the Blue-throated Macaw needs trees with a stem diameter at breast height (DBH, at 1,3 m height) of at least 60 cm, and a cavity of at least 30 cm diameter (Yamashita & Machado de Barros, 1997; Berkunsky et al., 2014). Blue-throated Macaws usually lay 1-3 eggs and incubation takes on average 26 days (Berkunsky et al., 2014). The hatched young usually fledge in 13-14 weeks, and afterwards parental care will continue for an extended period of time, possibly into the next breeding season. This could mean that if the breeding birds have

a successful breeding attempt, they will not breed the following year (Kyle, 2007; Berkunsky et al., 2014).

The Blue-throated Macaw shares its distribution with two other macaw species, the Red-and-Green Macaw (*Ara chloroptera*) and the Blue-and-Yellow Macaw (*Ara ararauna*). As these species are far more common and have a larger body size, it is likely that they can outcompete the Blue-throated Macaw in both food and nesting resources (Yamashita & Machado de Barros, 1997; Hesse & Duffeld, 2000). This has been the case in one of the Blue-throated Macaw populations where Blue-and-Yellow Macaws occupied nest boxes destined for Blue-throated Macaws (Kyle, 2007).

In the BANR, one of the main areas for the Blue-throated Macaw, the Blue-and-Yellow Macaw is the other large macaw species that occurs there, therefore this species was also included in this study. The Blue-and-Yellow Macaw is found in lowland forests, savannas, and gallery forests throughout South America, from eastern Panama to Bolivia, and south-eastern Brazil (Forshaw, 1989). This species has a strong preference for the palm *Mauritia flexuosa*, which is its most important nesting tree (Brightsmith & Bravo, 2006). It can be considered one of the most generalist species of macaw as it occurs in a variety of habitats and feeds on a variety of resources (Ragusa-Netto, 2004). This means they are flexible in their resource preferences, nevertheless, this species is suffering from habitat loss and fragmentation and as it is most common in remote and protected places (Forshaw, 1989).

Aim and hypotheses

The aim of this study is to get a broader understanding of the ecology of the Blue-throated Macaw by identifying what habitat conditions determine Blue-throated Macaw occurrence and abundance. In this study the focus is put on the abundance of the macaws, and not occurrence (i.e. presence/absence). In previous studies on the Blue-throated Macaw, surveys were conducted on a large scale, using survey hexagons of 232 km², totalling 6,750 km² (Berkunsky et al., 2016). It is suggested that studies of habitat use at smaller scales should be conducted to examine suggested associations between palms and macaws (Berkunsky et al., 2016).

Research questions:

How does the abundance of the Blue-throated Macaw depend on the:

1. Landscape mosaic in which they occur?
2. Landscape disturbance: anthropogenic disturbance by fire & cattle?
3. Resource availability i.e. patch quality?
4. Resource competition for food with the Blue-and-Yellow Macaw (*A. ararauna*)?

Hypotheses

1. Landscape mosaic. At the landscape level, there can be several spatial aspects that play a role in a species occurrence. Island biogeography theory proposes that larger islands have more niches and resources, and islands closer to the mainland have a higher species richness and abundance through a higher chance of colonization (MacArthur & Wilson, 1967). In this case the gallery forests function as a mainland in comparison with the smaller forest islands. It is expected that there is a higher density of palm resources in the gallery forests than at the forest islands, as gallery forests are larger and might suffer less from edge effects (Williams-Linera, 1990). Also, I expect a higher tree species richness in the gallery forests than in the forest islands. Next, habitat fragmentation can reduce food resource availability, through decreasing size and increasing isolation of habitat. This mechanism of habitat

fragmentation can regulate species occurrence and abundance (Saunders et al., 1991). Consequently, it is expected that there is a higher abundance of macaws in the gallery forests, because the gallery forests contain a higher resource availability and patch quality because the gallery forest are less fragmented forest patches than the forest islands.

2. Landscape disturbance. Disturbance such as fire and cattle can affect species occurrence through regulating resource availability. The main human activities in the Beni savanna are cattle ranching and intensive burning of savanna for producing grazing land with fresh fodder of high nutritive quality (Hesse & Duffeld, 2000; Berkunsky et al., 2016). Grazing pressure of cattle is high in this area and has a negative effect on the regeneration of trees (Yamashita & Machado de Barros, 1997). Human induced fires occur on a regular basis, are known to have large-scale effects on forest fragments (Laurance 2000; Cochrane and Laurance, 2002). Degradation of palm health, and browsing of seedlings could result in a decline in palm abundance which decreases resource availability for the macaws. It is expected that palm resources are negatively influenced by disturbance variables such as fire and overgrazing by cattle (Killeen, 1991; Yamashita & Machado de Barros, 1997; Killeen et al., 2003). It is expected that the smaller forest islands are more affected by fire disturbance and cattle grazing than the gallery forests, since they have a larger possibility of edge effects.

3. Resource availability. The main food source for the Blue-throated Macaw is expected to be the fruits of *A. phalerata* (Hesse & Duffeld, 2000; Yamashita & Machado de Barros, 1997). It is hypothesized that Blue-throated Macaw abundance is positively correlated to *A. phalerata* resources, such as adult palm density and amount of infructescences. It also expected that Blue-and-Yellow Macaw follows a similar pattern, as it also feeds on *A. phalerata*.

4. Resource competition. Interspecific competition with other species, especially with the larger Blue-and-Yellow Macaw could influence the abundance. Blue-and-Yellow Macaws occur in Barba Azul Nature Reserve, but are not breeding there. It is expected that Blue-throated macaw and the sympatric Blue-and-yellow macaw are competing for resources at feeding sites, but also are competing for roosting sites. I hypothesize that this could lead to a lower abundance of the Blue-throated Macaw.

In figure 1 the conceptual model is shown with the each of the hypothesized concepts that could influence the abundance of macaws.

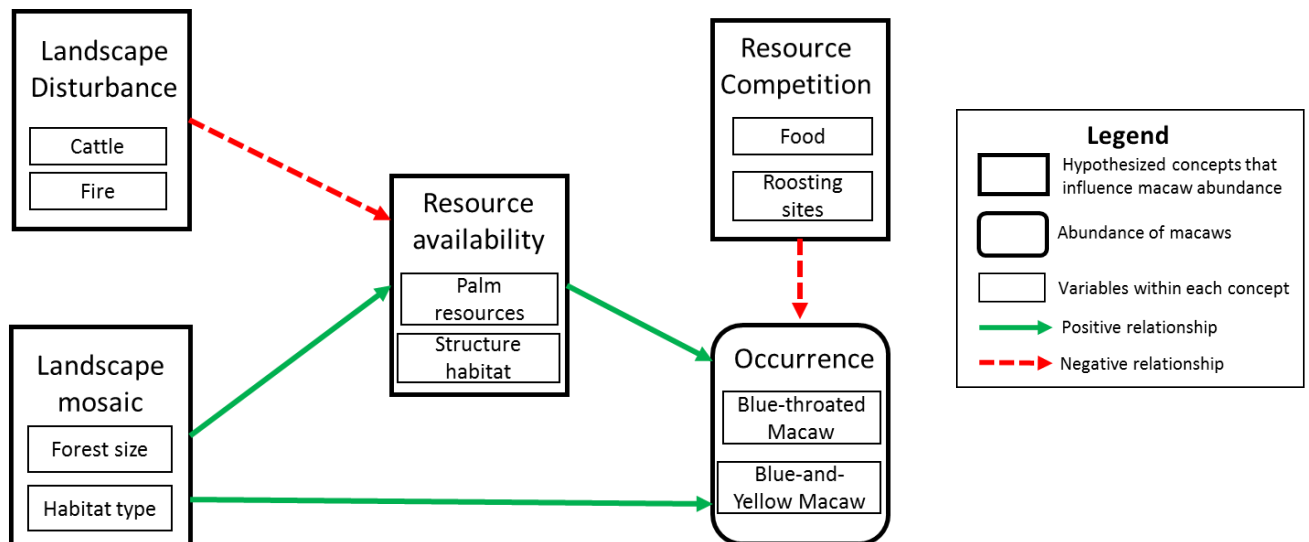


Figure 1 Conceptual model of the hypothesized effects of landscape mosaic, landscape disturbance, resource availability and resource competition on macaw abundance. A green arrow indicates a positive expected relationship, and a red arrow indicates a negative expected relationship

Methods

Study area

Fieldwork for this study was conducted in the remote Barba Azul Nature Reserve, 13°45'44.50"S 66° 5'53.69"W, located in the Beni department of northern Bolivia. The Beni savanna is a unique ecoregion covering 160,000 km², classified as a tropical savanna with an annual precipitation of 1,300-2,000 mm (Hanagarth & Beck, 1996). In the wet season (October-May) the savanna turns into a largely inundated savanna, allowing only very little human urbanisation and land use (Hesse & Duffeld, 2000). Cattle farming is the main type of land use in the Beni savanna. Even though this happens extensively, it can have a significant negative impact in the forest islands, as regeneration of new trees, and especially *A. phalerata*, is hampered by overgrazing and burning of pastures (Yamashita & Machado de Barros, 1997). Currently, the Barba Azul Nature Reserve contains 11,000 hectares of tropical savanna, gallery forest, 25 forest islands, river habitat and some cerrado remnants. The Barba Azul Nature Reserve is an important area for a significant amount of the worldwide Blue-throated Macaw population as over 100 individuals have been recorded there. The species is not breeding in the reserve, despite the placement of suitable nest boxes (BANR Annual Report, 2015). The Blue-throated Macaw only occurs in the reserve in the dry season (May-October), together with the Blue-and-Yellow Macaw.

Data collection

Data collection took place in the Barba Azul Nature Reserve from the 3rd of August until the 3rd of October 2016. The first six weeks were spent conducting plots in the forests, and the remaining three weeks were spent to inventory the macaws. *A. phalerata* provides food, nesting and roosting for the Blue-throated Macaw. In a companion study the occurrence, ecology and dynamics of *A. phalerata*, was studied in detail (Hordijk, 2017).

Study design. To evaluate the resource availability for the macaws in different habitats, plots were established in gallery forests and forest islands. Forest fragments (size ranging from 8-60 ha) situated along the main river, or an old river arm were considered gallery forests. The small forest patches (size ranging from 0.02-0.8 ha) in the savanna were considered forest islands. For the small forest patches, the diameter of the islands was measured in the field, to calculate the size of the forest islands. Plots of 20x10 metres were established in centres and edges of the forest to collect forest composition data. In total, 91 plots were established in these two habitats. On all 25 forest islands plots were positioned, which resulted in 24 forest islands edge plots, 16 forest islands centre plots, and one forest island was surveyed as a whole because of its small size. In the gallery forests 25 locations were chosen using a random stratified design, resulting in 25 centre and 25 edge plots. Plots were always positioned in the same direction, with the long side perpendicular to the north. As *A. phalerata* can reach a height of up to 10 metres (Moraes et al., 1996), the edge of a patch was considered up to 10 metres inside the gallery forest or forest island. This meant that on small islands (<40 metres diameter) only edge plots could be conducted. Locations of edge plots were always randomized (facing north or south) in both gallery forests and forest islands to avoid bias in edge selection.

Plot measurements. In each plot, every *A. phalerata* was tagged and the following data was gathered on every palm to measure resource availability: number of -old male flowers, -old female flowers and -infructescences. The condition of the palms was also noted down (four classes: dead, bad, medium,

good). Additionally, to measure resource availability and use of *A. phalerata* by macaws, a fruit plot of 1m² was randomly laid out below each palm to count the total amount of palm fruits on the ground, and the total amount of eaten palm fruits by macaws. To quantify fire disturbance, for each palm fire scar height was measured using a Nikon Forestry 550 clinometer, and percentage of scarred stem was estimated. To quantify cattle disturbance, the number of dung piles in each plot was counted. Furthermore, trees of all other tree species were identified and measured for their dbh.

Macaw inventory. The target species of macaws, Blue-throated Macaw (*A. glaucogularis*), and Blue-and-Yellow Macaw (*A. ararauna*) were inventoried from the 6th of September until the 2nd of October 2016. For the macaw surveys, the gallery forests were divided into eight different forests. These eight gallery forests are naturally separated by savanna grassland or a river and are considered independent. To survey the number of macaws accurately, the macaws were surveyed per gallery forest and forest island as a whole, and not per plot. To take possible variation in macaw behaviour between morning and afternoons into account, each forest was visited four times; twice in the morning (between 6:30-10:00), and twice in the afternoon (between 15:30-18:00). Because of the shape of the gallery forests, it was chosen to conduct point counts along the edges of the gallery forests. Every 200 metres point counts were conducted for five minutes. On average 13 point counts were conducted per gallery forest, with a minimum of six and maximum of 20 point counts. During these five minutes all Blue-throated Macaws and Blue-and-Yellow Macaws were counted. For the data analysis, only birds present in the forest were used, so birds that were flying over the patch, or occurred outside the patch, were not included. Macaw observations from each point count were added up per gallery forests which resulted in a total number of macaws per visit. From the four visits per gallery forest, the visit with the highest observed number of macaws could be used for the analysis, since the amount of points counts was not correlated to the maximum number of macaws (see section data analysis). Due to logistics, limitation of time, and size of forest islands, another inventory method was used for the forest islands. Hence, in the forest islands abundance of Blue-throated Macaw and Blue-and-Yellow Macaws on the island was noted down for each visit of the forest islands when fieldwork for the plots was conducted. Most forest islands (23 out of 25) were visited once, and two forest islands were visited twice. On average four hours were spent per forest island, during which occurrence and abundance of macaws was noted down. To see if there was any evidence of resource competition, when macaws were observed feeding the tree species that they were feeding on was noted down. Additionally, for five consecutive nights, roost counts were conducted (from 17:45-18:40) in the northern part of the reserve, at one of the main roosting sites of the Blue-throated Macaw.

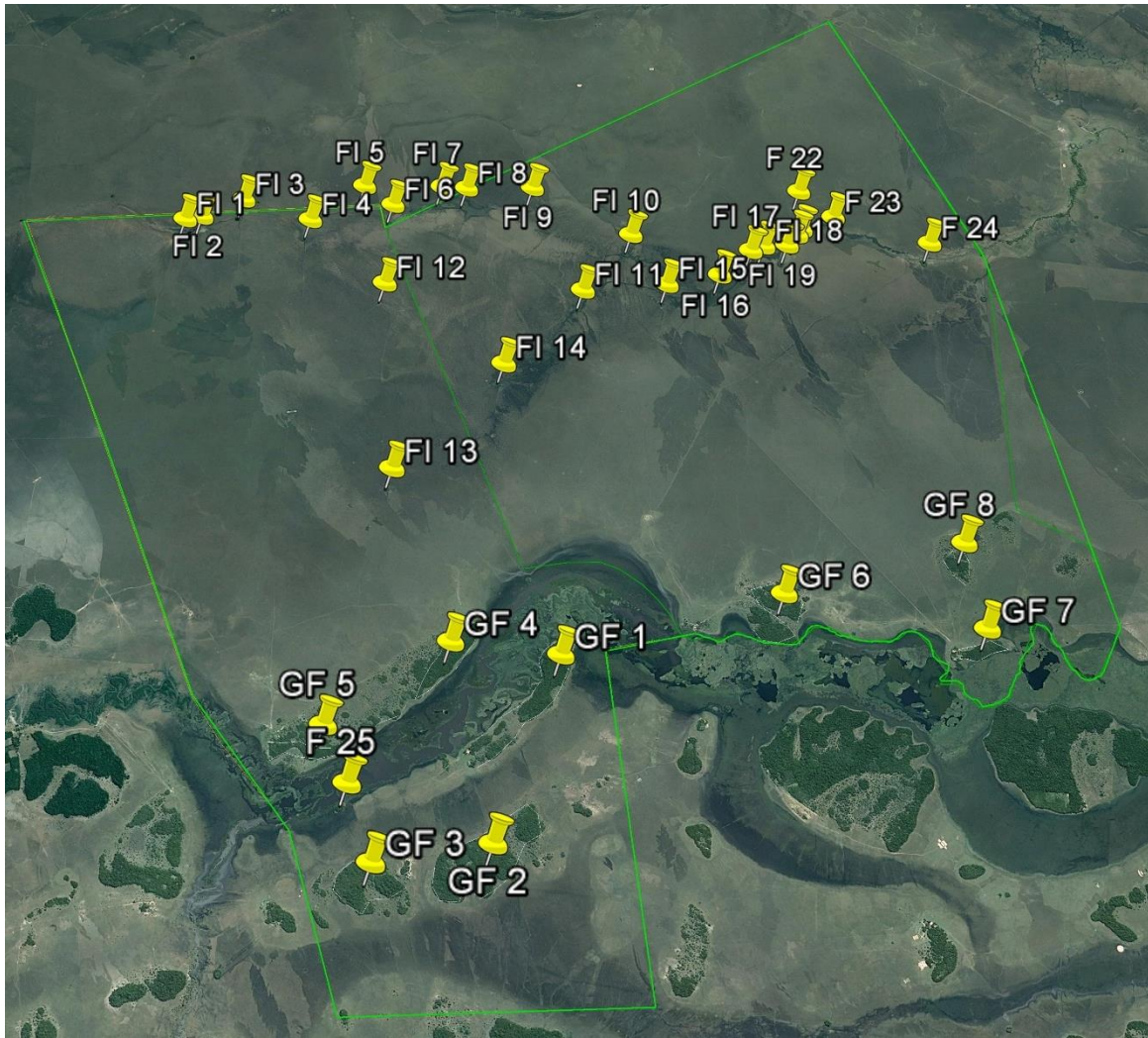


Figure 2 Study area: the Barba Azul Nature Reserve. This satellite photo (Google Earth) shows an overview of the eight gallery forest patches (GF) and the 25 forest islands (FI). The green line indicates the border of the BANR.

Data analysis

Landscape mosaic. To evaluate the differences between the gallery forests and forests islands, the variables related to palm resources were averaged at the plot level (see Appendix II for all variables). Next, for each patch (i.e., a forest island or gallery forest) the values for the centre and edge plots were averaged, to obtain a single estimate per patch. In the macaw inventory, macaws were surveyed per forest patch and no difference was made between centre and edge. Thus, because of the difference in study design between palms and macaws, a single estimated was obtained for centre and edge plots. To investigate how the eight drivers of macaw abundance, density *A. phalerata*, % fruiting palms, relative abundance *A. phalerata*, number of old female flowers, number of old male flowers, number of infructescences, number of palm fruits on the ground, and tree species richness were associated, a Principal Component Analysis was used, using Canoco5 (Braak & Šmilauer, 2012) (Appendix II, figure 2.2). In addition to the PCA, a correlation matrix was made, using a Spearman's Rank order correlation, to account for potential non-linear relationships (Appendix II, table 2.2). Based on significant and high correlations of variables, the best variables were selected to test the determining variables for macaw abundance. Density of *A. phalerata* was strongly correlated with relative abundance of *A. phalerata* ($r_s = .86$, $p < .001$, $N=50$) and number of infructescences ($r_s = .61$,

$p < .001$, $N=50$). The number of infructescences was correlated with number of old female flowers ($r_s = .52$, $p < .001$, $N=50$), and numbers of old male flowers ($r_s = .42$, $p < .001$, $N=50$) was also correlated with the amount of infructescences. Tree species composition was calculated using species richness and the Shannon-Wiener index for diversity, which takes the relative abundance of species into account. Species richness and SW were highly correlated ($r_s = .928$) so species richness was selected as the variable used for further analysis, because tree species richness was considered more important for macaw abundance than the relative abundance of tree species.

Differences in palm resources and forest characteristics between gallery forests ($N=25$) and forest islands ($N=25$) were evaluated using either a t-test or a non-parametric Mann-Whitney U test. All variables were tested for normality using Shapiro-Wilk test, and for t-tests homogeneity of variances was tested using Levene's Test. Based on these criteria either a parametric (t-test) or a non-parametric test (Mann-Whitney U test) was conducted. To evaluate the relation between forest size and palm densities, forest area was calculated. Area of forest islands was calculated using the diameters measured in the field, assuming a circular shape. Size of gallery forests were calculated using Google Earth Pro (Google Inc., 2015). To calculate total palm abundance per forest patch, palm abundance was calculated per forest island centre and edge. This was done by assuming each forest island had a circular shape. For the gallery forest the size of the forest edge was calculated using a buffer function in ArcGIS. For both centre and edge plots the palm density per plot was extrapolated to forest centre and edge size. To get a better fit for the linear regression model, forest size and palm abundance per forest were Ln-transformed. Residuals from the regression followed a normal distribution so a linear model was used.

Landscape disturbance. To take edge effects of landscape disturbance into account, a distinction was made between centre and edge plots. Palm density was therefore calculated separately for centre and edge plots. To compare differences between forest islands ($N=25$) vs. gallery forest ($N=25$) a non-parametric Mann-Whitney U test was used. The same test was repeated for comparing the patch centre (gallery forest $N=25$, forest islands $N=16$) with the patch edge (gallery forest $N=25$, forest islands $N=25$). At the plot level ($N=91$ plots), a generalized linear model (Poisson) was used to test the effect of the average height of fire scars, percentage scarred stems, and amount of dung piles, on palm density. At the individual palm level ($N=498$), a path analysis was used with SPSS Amos 23.0 (IBM Corp., 2015) to analyse the effects of fire disturbance on palm health, and subsequently on palm resources. Hence, in this analysis it was assumed that each palm in a plot is an independent observation. For the path analysis, the effects of variables fire height and percentage of scarred stem were tested against palm health (condition). The next step in the model was to analyse the effect of palm condition on the amount of old female flowers, and consequently the effect of the number of flowers on the amount of fruits on the ground. Old female flowers were used instead of infructescences, since there was more data available from the female flowers.

Effects of resource availability on macaw abundance. For the analysis, the maximum number of observed macaws per forest patch was used. To evaluate if the amount of point counts were correlated with the maximum numbers of macaws per forest patch, a Spearman's correlation test was conducted. As they were not significantly correlated, the maximum number of macaws could be used as proxy (Blue-throated Macaw, $r_s = -1.4$, $p = .747$, $N=8$; Blue-and-Yellow Macaw, $r_s = -.29$, $p = .588$, $N=8$). Maximum numbers were Ln-transformed to have a better fit for the linear regression model that was used. The analysis was conducted for gallery forest ($N=8$) and forest islands ($N=25$) combined,

but also separately for gallery forests. For the gallery forests, the predictors were averaged per forests because macaw abundance was estimated per forest patch. A PCA was done to assess which variables were correlated with each other, and to identify which variables could be predictors of macaw abundance (see Appendix III, figure 3.1). For both macaws, a multiple linear regression model was used to determine the significant predictors of macaw abundance in forest patches (N=33). For this, the variables forest area, *A. phalerata* density, number of palm fruits and tree species richness were used. Forward selection of variables was used to determine the best predictor for the model. Residuals from the regression followed a normal distribution, therefore a linear regression model could be used. A Weighted Least Squares (WLS) linear regression was used to correct for heteroscedasticity, but as it did not improve the model the initial model was used.

Resource competition. To evaluate whether resource competition occurs, the abundance of the Blue-throated Macaw was correlated with the abundance of the Blue-and-Yellow Macaw, using a Spearman's Rank order correlation. To analyse the differences in total number of each species of macaw per night at the roosting site a Mann-Whitney U test was conducted. Furthermore, observational data were collected that could not be analysed statistically, but that provide a better insight in Blue throated macaw ecology and behaviour.

All statistical analyses were performed with IBM SPSS Statistics 24.0 (IBM Corp., 2016).

Results: Resources

Landscape mosaic

Forest level. The total abundance of *A. phalerata* per forest (gallery forest or forest island) was significantly and positively related to forest size (linear regression, $F_{1,31} = 198.3$, $p < .001$, adjusted $R^2 = .86$). Larger forest patches contain therefore a larger total amount of palm trees, with gallery forests being larger and containing more palm trees than the forest islands (Appendix II, Figure 2.1). More palm trees mean more palm resources, as the density of palm trees per plot was positively correlated with number of infructescences per plot (Spearman's $r_s = .61$, $p < .001$, Appendix II, table 2.2).

Plot level. Forest structure and palm abundance were compared between gallery forests and forest islands (Table 1). The average density (fruit plot per $1m^2$ / per palm) of palm fruits found on the ground was on average 2.8 times higher in the gallery forest than in the forest islands (T-test, $t_{48} = 3.8$, $p < .001$), and the average number of eaten palm fruits on the ground, which was 6.5 times higher in the gallery forest (Mann Whitney U, $Z = -5.0$, $p < .001$). Regarding forest characteristics, tree species richness was 1.6 times higher in the gallery forest than in the forest islands (T-test, $t_{48} = 4.4$, $p < .001$).

Table 1 Differences of all palm resources and habitat characteristics between gallery forests (N=25) and forest islands (N=25) per plot (200 m²). For t-test of equal variances $df=48$, t-test for unequal variance $df = 38.6$.

	Variable	Mean (+ SE)		Test	Test statistic	P-value
		GF (N=25)	FI (N=25)			
Palm Resources	Density <i>A. phalerata</i>	5.36 ± 3.35	5.46 ± 4.43	T-test	$t = 0.39$	$p = .702$
	% Fruiting <i>A. phalerata</i>	0.16 ± 0.17	0.09 ± 0.15	Mann Whitney U	$U = 236, Z = -1.53$	$p = .125$
	Average # infructescences	0.53 ± 0.45	0.48 ± 0.55	Mann Whitney U	$U = 283, Z = -0.60$	$p = .550$
	Av. # old male flowers	3.08 ± 1.26	3.33 ± 2.17	T-test unequal variances	$t = -0.49$	$p = .629$
	Av. # old female flowers	2.36 ± 1.02	2.00 ± 1.44	T-test	$t = 1.03$	$p = .308$
	Av. # palm fruits	16.31 ± 11.28	5.86 ± 4.97	T-test	$t = 3.80$	$p < .001$
	Av. # eaten palm fruits	5.81 ± 4.64	0.89 ± 1.41	Mann Whitney U	$U = 57, Z = -5.04$	$p < .001$
Forest characteristics	Relative abundance <i>A. phalerata</i>	0.36 ± 0.20	0.37 ± 0.31	Mann Whitney U	$U = 301.5, Z = -0.21$	$p = .831$
	Species Richness	6.06 ± 1.73	3.82 ± 1.90	T-test	$t = 4.36$	$p < .001$
	Shannon-Wiener index	1.34 ± 0.38	0.91 ± 0.46	T-test	$t = 3.54$	$p = .001$

Landscape disturbance

Comparison habitats. Regarding landscape disturbance, gallery forest and forest island only differed significantly in the average amount of dung piles found in the plots (Mann Whitney U, $U = 170$, $Z = -6.9$, $p < .001$), which was on average 7.8 times higher in the forest islands. Only for the forest islands,

forest centre and edge differed significantly, as density of palm trees was 2.4 times higher in the edge (Mann Whitney U, $U = 106$, $Z = -2.4$, $p = .017$). The habitat types did not differ significantly in fire scar height and the percentage of scarred stems.

Effects of landscape disturbance on palms. At the plot level the density of palm trees showed a positive relationship with the percentage of scarred stem (Poisson regression, $B = .743$, Wald Chi-Square = 34.065, $p < .001$). But no relationship with the amount of dung piles (as an indicator of grazing disturbance). At the individual palm level, the path analysis (figure 3) showed that fire height had a significant negative effect on palm condition ($B = -.237$, $p < .001$). The palm condition had, in turn, a significant positive effect on the amount of old female flowers ($B = .249$, $p < .001$), and the amount of old female flowers showed a strong positive relationship with the amount of palm fruits on the ground ($B = .449$, $p < .001$). This model explains 20% of the amount of palm fruits on the ground.

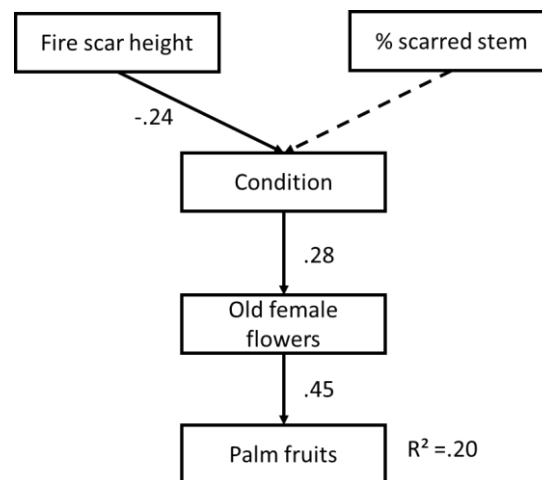


Figure 3 The results from the path analysis which shows the effect of fire disturbance on individual palm level ($N=498$), solid lines indicate significant relationship, dashed line indicates no significant relationship

Results: Macaws

Macaw inventory. During the inventory period, 89 Blue-throated Macaws were recorded in the gallery forests. They were recorded in three of the eight gallery forests that were sampled. In the forest islands, a total of 12 Blue-throated Macaws were recorded on seven of the 25 forest islands. 285 Blue-and-Yellow Macaws were recorded in all the eight gallery forests. In the forest islands six Blue-and-Yellow Macaws were recorded on three of the 25 forest islands. In Appendix IV, the maximum numbers for each species per forest patch can be found.

Habitat comparison. Maximum numbers of Blue-throated Macaw did not differ between gallery forests and forest islands, even though abundance was roughly nine times higher (Mann-Whitney U, $U = 80$, $Z = -1.0$, $p = .420$). For Blue-and-Yellow Macaw, abundance differed significantly between gallery forests and forest islands and it was 44 times more abundant in the gallery forests (Mann-Whitney U, $U = .5$, $Z = -4.9$, $p < .001$).

Predictors of macaw abundance

Blue-throated Macaw. A multiple linear regression model was developed to test what environmental variables would predict macaw abundance in both the gallery forests and forest islands. Predictors that were put in the model were: island size, density *A. phalerata*, average number of palm fruits on

the ground, and species richness. A forward linear regression shows that macaw abundance increases with the average number of palm fruits on the ground (Figure 4a, ($F_{1,31} = 22.1$, $p < .001$, adjusted $R^2 = .40$). A similar analysis was also conducted for the gallery forests alone, and again Blue-throated Macaw abundance increased with the average number of palm fruits on the ground ($F_{1,6} = 10.9$, $p = .016$, adjusted $R^2 = .59$)

Blue-and-Yellow Macaw. For the Blue-and-Yellow Macaw the same multiple regression model was used, using the same explanatory variables. In this model ($F_{1,31} = 69.5$, $p < .001$, adjusted $R^2 = .81$), macaw abundance increased significantly with island size ($B = .367$, $t_{31} = 10.6$, $p < .001$) and tree species richness ($B = .092$, $t_{31} = 2.2$, $p = .036$) (Figure 4b). No explanatory variables were found for the gallery forests alone.

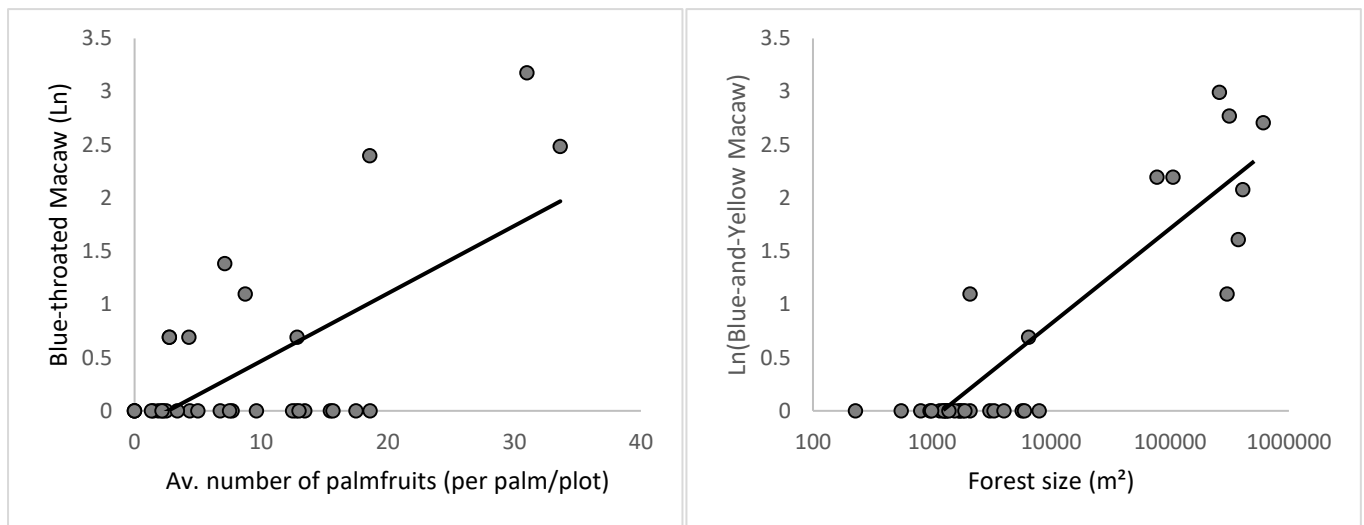


Figure 4 The left graph (4a) shows the relation between Blue-throated Macaw occurrence (Ln-transformed) and the average number of palm fruits (per palm/per plot). Graph 4b shows the relation between Blue-and-Yellow Macaw occurrence (Ln-transformed) and forest size (m²) on a logarithmic scale for illustration purposes.

Resource competition

Feeding ecology. Across the eight gallery forests, the numbers of observed Blue-throated- and Blue-and-Yellow Macaws were negatively correlated, but not significantly (Spearman's correlation, $r_s = -.33$, $p = .429$, $N=8$). Blue-and-Yellow Macaws seemed to be more abundant in forests where Blue-throated Macaws were absent. The two Macaws mainly foraged on different food sources (Table 1). The only food source that they shared was *Attalea phalerata*, the Motacú palm.

Table 1 This table shows the observed feeding preferences of the two species of macaw in the reserve.

Tree species	Blue-throated Macaw	Blue-and-Yellow Macaw
<i>Attalea phalerata</i>	20 (61%)	10 (29%)
<i>Tabebuia heptaphylla</i>	2 (6%)	
<i>Vochysia divergens</i>	8 (24%)	
<i>Acrocomia aculeata</i>	3 (9%)	

<i>Mangifera indica</i>		6 (18%)
<i>Vatairea macrocarpa</i>		8 (23%)
<i>Garcinia humilis</i>		6 (18%)
<i>Hymenaea courbaril</i>		2 (6%)
<i>Sp. unknown</i>		2 (6%)
Total of observations	33	34

Roosting patterns. For five consecutive nights Blue-throated- and Blue-and-Yellow Macaws were counted at their main roosting site, a forest island in the northern part of the reserve (Fig. 5). Blue-throated Macaw abundance was 2.5 times higher than Blue-and-Yellow Macaw (Mann-Whitney U, $U = 2$, $Z = -2.193$, $p = .032$). The last evening a change in numbers was observed, the numbers of Blue-and-Yellow Macaws were much higher than the previous evenings. On 14/09/2016 a record number of 118 Blue-throated Macaws was observed at the roosting site.

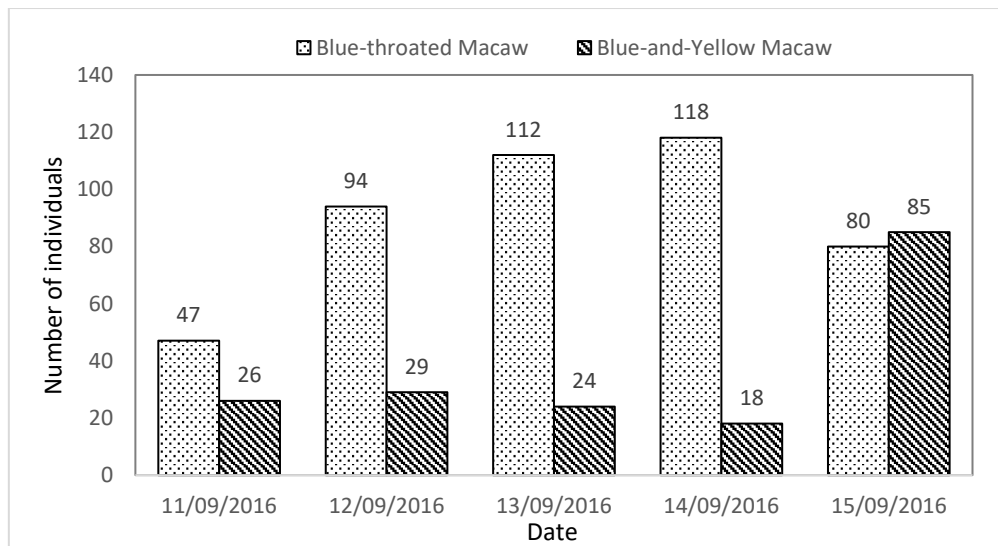


Figure 5 This graph shows the number of Blue-throated- and Blue-and-Yellow Macaws that came to roost at their main roosting site, forest island number 6.

Discussion

This aim of this study was to identify the most important habitat conditions that determine the abundance of the Blue-throated Macaw and its potential competitor, the Blue-and-Yellow Macaw. The main research question was: how does the abundance of the Blue-throated Macaw depend on 1) the landscape mosaic, 2) landscape disturbance, 3) resource availability, and 4) resource competition. I have presented a conceptual framework how these should affect macaw abundance (Fig. 1). Results indicate that there is a clear difference between the two main habitat types -gallery forests and forest islands- in which both macaw species occur. The gallery forests have a larger forest size, a higher fruit availability of *A. phalerata*, and a higher tree species richness. Landscape disturbance in terms of fire has a negative effect on the condition of palms, which, in turn, negatively affects fruit production. The Blue-throated Macaw abundance shows a positive relation with *A. phalerata* fruit availability. The Blue-and-Yellow Macaw abundance shows a positive relationship with larger patch sizes and a higher species richness of trees. Observation data suggests that Blue-throated Macaw is a more specialist feeder, which mainly focuses on *A. phalerata* whereas the Blue-and-Yellow Macaw uses a higher variety of food sources. Resource competition in terms of food and roosting resources does not appear to play a large role in determining Blue-throated Macaw abundance. In this section, I will discuss the findings of each concept and its hypotheses in more detail.

Landscape mosaic: The gallery forests contain more food resources than forest islands. The first concept that is discussed here is the landscape mosaic in which the macaws occur. I expected that the gallery forest had a higher density of palm resources and a higher species richness than at the forest islands, as the gallery forests are larger and might suffer less from edge effects (Fig.1) (cf. MacArthur & Wilson, 1967; Williams-Linera, 1990). From all the palm variables, the only variables that were significantly different between habitats were the amount of (eaten) palm fruits found on the ground (Table 1). I had expected that variables, such as palm density, or amount of infructescences, would have differed between the two habitats as well because I expected that edge effects would play a larger role in the forest islands. However, *A. phalerata* is a strong and fire-resistant species (McPherson & Williams 1998; Souza et al., 2000), which could explain why it is not immediately affected by disturbance in the forest islands. The amount of infructescences (and old male and female flowers) also did not differ between the habitats, but it was noted that on some of the forest islands infructescences with fresh "hollow" fruits were present. They appeared rotten and/or eaten from the inside, possibly the result of bruchid beetles which are a common source of palm fruit infestation (Salm, 2006). The amount of palm fruits on the ground was significantly higher in the gallery forests than the forest islands, conform my expectations. In conclusion, fruit production is higher in the gallery forests, but this is not reflected in the amount of infructescences, old female flowers, or old male flowers.

In addition to differences of palm resources at the plot level, I looked at the total abundance of palm trees at the forest level and compared those among gallery forests and forests islands. As expected, I found that an increase in forest size results in a higher total abundance of palm trees. I also found a higher species richness of trees in the gallery forests. Both findings support the Island-theory which proposes that larger patches have a higher species richness and a higher abundance of resources (MacArthur & Wilson, 1967). Consequently, I expected that a higher resource availability positively

affects the abundance of macaws, but I will come back to that in the third part of the discussion, about the predictors of macaw abundance.

Landscape disturbance: Fire has an indirect negative effect on palm resources. I expected that palm density and its resources are negatively influenced by disturbance variables such as fire and overgrazing by cattle (Fig. 1)(Killeen, 1991; Yamashita & Machado de Barros, 1997; Killeen et al., 2003). I expected that the smaller forest islands are more affected by fire disturbance and cattle grazing than the gallery forests, since smaller islands have a larger possibility of edge effects (Williams-Linera, 1990). I found that fire height and percentage of scarred stem did not differ significantly between gallery forests and forest islands. Probably because fires occur in both the gallery forests and forest islands (BANR Fire Report, 2015). I expected that fire disturbance would have a negative effect on palm abundance. On plot level, the percentage of scarred stem was positively correlated with the density of palm trees. This is contrary to the expectations because I expected that a higher fire intensity would lead to a lower density of palm trees (Yamashita & Machado de Barros, 1997). A possible explanation of this could be that a higher density of palm trees is found in the edge of the forest islands and in the edge there could be a higher effect of fire on the palm trees. Also, because the effect on density was tested on plot level, the percentage of scarred stem was averaged, which could have an undesired effect on the outcome. For the effects of disturbance on individual palm level, a path analysis was used (Fig. 3). This path analysis revealed that fire height showed a significant negative relation with the palm condition. Next to that, palm condition showed a positive relationship with the old female flowers, and the old female flowers showed a positive relationship with the amount of fruits on the ground. This path analysis suggests that fire disturbance has an indirect negative influence on the palm resources, by influencing the palm condition. There is not a strong effect of fire disturbance on palms, but an increased intensity will not be beneficial for the condition of the palms, and hence not beneficial for fruit production (Souza & Martins, 2004; Barlow & Peres, 2006). Regarding disturbance by cattle, the amount of dung piles was significantly higher in the forest islands and this can be explained by the fact that these forest islands are commonly used by for cattle for resting, and as higher grounds to reside during the wet season. The forest islands are of small size and surrounded by grazed savanna, and therefore there is a higher density of cattle than for example in the gallery forests. I did not find any evidence that a higher cattle pressure resulted in a decline in adult palm abundance. The companion study by Hordijk (2017), which focused on *A. phalerata*, showed that the regeneration of *A. phalerata* was negatively affected by cattle. Especially in the forest islands regeneration was hampered by cattle browsing.

From the results, it is not possible to say if fire or cattle has a negative effect on macaw abundance. Though, on the long term a constant fire disturbance will result in a lower abundance of palm trees and a lack of regeneration, especially in smaller forest fragments (Souza & Martins, 2004). The eventual collapse of the palm populations means that the suitable habitat of the Blue-throated Macaw will decrease (Berkunsky et al., 2016).

Predictors of Macaw abundance. For both species of Macaws, I expected that there would be a higher abundance of macaws in the gallery forests, because the gallery forests contain a higher resource availability and patch quality because the gallery forest are less fragmented forest patches than the forest islands.

Blue-throated Macaw abundance is driven by *Attalea phalerata*. For the Blue-throated Macaw there was no significant difference in abundance between the gallery forests and the forest islands, even though the abundance in the gallery forest was higher. The possible reason for this could be because the Blue-throated Macaw is a rare species with a low encounter rate, since it was only encountered in a few of the inventoried forest patches. Another possible explanation could be that the Blue-throated Macaw is not that strongly associated with large gallery forests. The smaller forest islands are dominated by *A. phalerata*, and thus offer as a possibility for foraging areas. Nevertheless, there is still a tendency towards higher numbers in the gallery forests, where there is a higher total abundance (but also fruit availability) of *A. phalerata* per forest, which makes it most efficiently to forage in an area with the highest food availability. I hypothesized that Blue-throated Macaw abundance is positively correlated to *A. phalerata* palm resources. These palm resources were measured in the plots, such as palm density, amount of infructescences, and amount of palm fruits on the ground. I found that Blue-throated Macaw abundance was positively related to the amount of palm fruits on the ground (Fig. 4a; $p < .001$, $R^2 = .59$). This was the case in both the gallery forests and forest islands combined, and in the gallery forests alone. The amount of palm fruits on the ground shows a strong correlation with the number of infructescences and old female flowers (Appendix II, table 2.2). I had expected to find the same results for palm density, but palm density is not correlated to the amount of palm fruits on the ground, indicating that palm density is not a good predictor of palm resource availability for macaw abundance. The amount of fruits on the ground seem to be a good indicator, but the amount of fruits on the ground can be influenced by other species. There are quite a few other animal species that feed on the fruits of *A. phalerata*, such as agouti, peccary, howler monkey, and even cows (pers. obs.; Galetti & Guimarães Jr, 2004).

From these results, we can deduce that the Blue-throated Macaw shows a strong association with *A. phalerata*, as was expected from the available literature (Yamashita & Machado de Barros, 1997; Hesse & Duffeld, 2000). Specialist species occur in areas that have a stable environment, whereas generalist species tend to occur in unstable and more degraded environments (Devictor et al., 2008). The decline of specialist species worldwide is likely to be related to human-induced landscape degradation (Kotze & O'hara, 2003; Devictor et al. 2007^{ab}; Devictor et al., 2008). The Blue-throated Macaw is endemic to the Beni savanna, and it could be that the Beni savanna used to be a stable environment for this species. However, increased (and intensified) disturbances such as fire and cattle are now starting to have negative effects on the habitat of the Blue-throated Macaw, possibly explaining this species decline (de Carvalho & Mustin, 2017).

Blue-and-Yellow Macaw abundance is related to species richness and forest size. For the Blue-and-Yellow Macaw the abundance was significantly higher in the gallery forests than in the forest islands. This is a much stronger contrast in comparison with the Blue-throated Macaw. This difference suggests that the Blue-and-Yellow Macaw is more likely to occur in larger forest patches, where there is a larger availability of resources. I expected a similar pattern for Blue-and-Yellow Macaw, since this species is also known to feed on *A. phalerata*, and literature suggests that the two species are competing for resources (Yamashita & Machado de Barros, 1997; Hesse & Duffeld, 2000). I did not find a significant relationship between Blue-and-Yellow Macaw and the palm resources. In contrast, the results indicate that Blue-and-Yellow Macaw showed a positive relation with tree species richness, which is also reflected in its diet (Table 2); this will be discussed in the next part of the discussion. Additionally, this species showed a positive relation with forest size, which explains the difference in abundance between the gallery forests and forest islands (Fig. 4b; $p < .001$, $R^2 = .81$). The island-theory seems to

apply, since Blue-and-Yellow Macaw abundance shows a positive relation with a larger area which contains more resources (MacArthur & Wilson, 1967). These results are also supported by other studies that studied the effect of the island-theory in relation to bird species abundance (and richness). Studies in a range of different areas, such as urban areas, urban woodlands, and temperate forests showed that the amount of bird species and their abundance was primarily explained by forest size (Askins et al., 1987; Tilghman, 1987; Fernandez-Juricic & Jokimäki, 2001). Interestingly, Berkunsky et al. (2015) found a negative relation between Blue-and-Yellow Macaw occurrence and forest size. I did not find any significant predictors of Blue-and-Yellow Macaw in just the gallery forests. The reason for this could be because I found Blue-and-Yellow Macaws in all eight gallery forests, and the number of Blue-and-Yellow Macaws did not differ largely among forests. Moreover, the gallery forests appear quite homogenous in resources, which could be another explanation for this lack of a pattern.

Resource competition: little evidence for competition for food and roosting sites. I expected that Blue-throated Macaw and the Blue-and-yellow macaw are competing for resources at feeding and roosting sites, which should lead to a lower abundance of the Blue-throated Macaw.

I observed Blue-throated Macaws consuming four different resources in 33 feeding observations. These were *Attalea phalerata* (61%), *Vochysia divergens* (24%), *Acrocomia aculeata* (9%), and *Tabebuia heptaphylla* (6%) (Table 1). Blue-throated Macaws have been reported feeding on *A. phalerata*, *A. aculeata*, and *V. divergens* (e.g. Yamashita & Machado de Barros, 1997), but I could not find any literature that reported Blue-throated Macaw feeding on *T. heptaphylla*. This observation data supports the previous findings that the Blue-throated Macaw is indeed a *A. phalerata* specialist. Blue-and-Yellow Macaws were observed feeding on 6 different resources in 34 feeding observations. These were *Attalea phalerata* (29%), *Vatairea macrocarpa* (23%), *Garcinia humilis* (18%), *Mangifera indica* (18%), *Hymenaea courbaril* (6%), and on two occasions (6%) the feeding resource could not be identified. The Blue-and-Yellow Macaw is known to feed on *A. phalerata*, *V. macrocarpa*, *M. indica*, and *H. courbaril* (Yamashita & Machado de Barros, 1997; Ragusa-Netto, 2006), but I could not find previous evidence in the literature on *G. humilis*. The study of Ragusa-Netto (2006) showed that Blue-and-Yellow Macaw occurrence largely coincided with the fruiting peak of *V. macrocarpa* during the month September in a cerrado remnant in Brazil. My observations support the same finding as several groups of Blue-and-Yellow Macaws were seen feeding on the seeds of this tree in the reserve. The only food source that was consumed by both species of macaw was *A. phalerata*, but Blue-throated Macaw was observed feeding twice as much on *A. phalerata* as Blue-and-Yellow Macaw. These observations suggest that Blue-and-Yellow Macaw seems more a generalist than Blue-throated Macaw in the reserve. This is also supported by the other data as Blue-and-Yellow Macaws were much more abundant in the larger gallery forests, and the data from the plots suggest a higher species richness in the gallery forests. Its wide distribution throughout South-America and occurrence in a large variety of habitats could be an explanation of this generalist behaviour (Devictor et al., 2008). Also, across the eight gallery forests, I did not find a significant correlation between the number of Blue-throated Macaws and Blue-and-Yellow Macaws in the gallery forests, ($r_s = -.33$, $p = .429$), which could be because the Blue-and-Yellow Macaw is a flexible and generalist species occurring in all the gallery forests. These findings raise the question if there is any form of resource competition regarding food resources in the area. It appears not to be a leading factor that could determine Blue-throated Macaw abundance. All these observations were done in the dry season and thus only shed light on the feeding resources in this period. Seasonality can play a role in the abundance of fruits of different tree species, and could also influence the choice of resources in other periods of the year. Roosting

sites were surveyed to see if there was any presence of resource competition. Five nights in a row I conducted roost counts at their main roosting site. Here I observed that Blue-throated Macaw was significantly higher than Blue-and-Yellow Macaws. Only on the last night Blue-throated Macaw and Blue-and-Yellow Macaw abundance was similar. On the 14th of September 2017, I counted a record-breaking 118 Blue-throated Macaws at the roost. This is the highest count ever of this species (half of the known population size) and this high count shows that the populations appears to be doing well. Even though I only performed roost counts five nights in a row, the data does not suggest resource competition which indicates that Blue-throated Macaws are negatively influenced by the Blue-and-Yellow Macaws. Nevertheless, I did not collect sufficient data to draw strong conclusions.

Management implications. Disturbance elements such as fire and cattle have a negative effect on the habitat of the Blue-throated Macaw. The effect of cattle has been studied in more detail in the study of Hordijk (2016), which shows that cattle have a detrimental effect on the regeneration of *A. phalerata*. To conserve the habitat, it is necessary to create firebreaks in the savanna to avoid fires from entering the gallery forests and forest island (Ramos-Neto & Pivello, 2000; and references therein). To prevent cattle from entering the forests, fences should be established around the designated forest islands. Moreover, the forest island which is the main roosting site of the macaws lies just outside the reserve. By extending the reserve boundaries, this important forest island can be protected.

Strengths and limitations of the study. There has only been limited amount of scientific research on the ecology of the Blue-throated Macaw. A strength of the study is that it confirms the habitat preferences of the Blue-throated Macaw and provides additional information on the ecology of this critically endangered bird species. Limitations of this study could be that the data collection on the abundance of the Blue-throated Macaw was limited. It only occurred in a few locations and this resulted in more zero-observations which made the analysis less powerful. However, this is often the case when a rare bird is studied. I expected that I would be able to identify macaw presence using eaten fruits on the ground as previous studies suggested that this was possible (Yamashita & Machado De Barros; Kingsbury, 2010), but this proved to be difficult in the field. I wanted to identify the eaten palm fruits, so that I could see where both species of macaws were present. In the field it proved to be difficult to see what kind of species had eaten the food, especially if the fruit was old. This would have improved the analysis because then I would have collected more data from the macaws on plot level, instead of collecting data on the macaws on forest level. This resulted in a lower sample size and less power for the statistical analysis.

Future research. In this study both the gallery forests and forest islands were studied, but it is also interesting to study the gallery forests in more detail. The Blue-throated Macaws have a strong preference for certain parts of the gallery forests, which could be explained by the fruit availability of *A. phalerata*, as the results indicate. However, to determine other potential factors of importance, it could be interesting to study and identify differences between gallery forests in more detail. Additionally, different methods could be used for this. For example, the study by Evans et al. (2005) performed point counts in forests (whereas I did point counts in the edges), and at each point count certain habitat variables were measured. This could be a good way to identify in what specific parts of the forests macaws (or other parrot species) are present. Future research could also focus on identifying the habitat conditions of nesting sites of Blue-throated Macaws. There are no macaws breeding in the reserve, but their known breeding grounds could be analysed. Seasonality is another

factor that could be considered in these kind of studies (Galetti, 1997; Renton, 2002; Ragusa-Netto, 2006). This study was performed in the dry season (August-October), but it could be interesting to see if there are shifts in habitat use and/or food preferences throughout the year. It is known that in the BANR the macaws move away in the wet season, and it would be interesting to see what influences these changes.

Conclusion

This study contributes to the knowledge gap of the ecology of the Blue-throated Macaw by examining its habitat characteristics and suggested association with *A. phalerata* on a small-scale level. Results indicate that there is a clear difference between the two main habitat types -gallery forests and forest islands- in which both the Blue-throated Macaw and Blue-and-Yellow Macaw occur. The gallery forests have a larger forest size, a higher fruit availability of *A. phalerata*, and a higher tree species richness. Landscape disturbance in terms of fire has a negative effect on the condition of palms, which, in turn, negatively affects fruit production. The Blue-throated Macaw abundance shows a positive relation with *A. phalerata* fruit availability. The Blue-and-Yellow Macaw abundance shows a positive relationship with larger patch sizes and a higher species richness of trees. Observation data suggests that Blue-throated Macaw is a more specialist feeder, which mainly focuses on *A. phalerata* whereas the Blue-and-Yellow Macaw uses a higher variety of food sources. Resource competition in terms of food and roosting resources does not appear to play a large role in determining Blue-throated Macaw abundance. This study provides a comprehensive overview of the ecology of the Blue-throated Macaw as I show how its habitat is influenced by the landscape mosaic and disturbance, and I shed light on the confirmed association with *A. phalerata* and on resource competition with the Blue-and-Yellow Macaw.

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Appendices

Appendix I

Table 1.1 Food items observed eaten by Blue-throated Macaw (adapted from Yamashita & Machado de Barros, 1997)

Latin name	Local name	Part consumed	Observed habitat	
			Palm island	Gallery forest woodland
<i>Attalea phalerata</i>	motacu	mesocarp	X	X
<i>Acrocomia aculeata</i>	totali	mesocarp	X	X
<i>Syagrus botryophora</i>	sumuque	inflorescence	X	
<i>Astrocaryum vulgare</i>	chontilla	inflorescence	X	
<i>Hura crepitans</i>	ochohs	unripe seeds, leaf stem	X	
<i>Cochlospermum hybiscoides</i>	tutumillo	flower petals	X	
<i>Sapindus saponaria</i>	isotoubo	unripe seeds	X	
<i>Genipa americana</i>	bi	leaf stem	X	

Appendix II Landscape mosaic

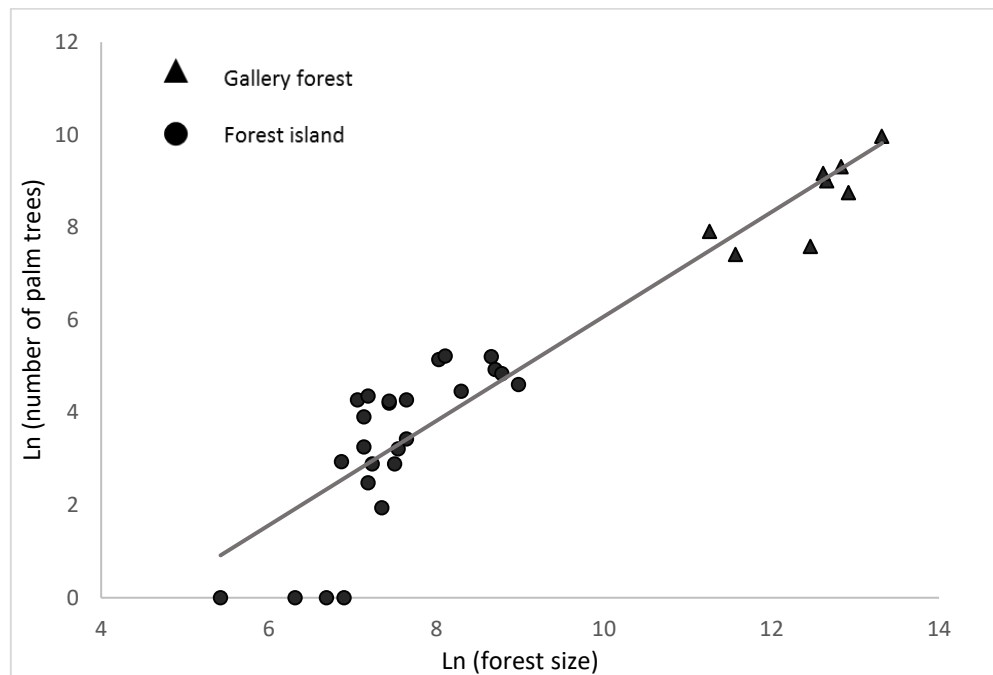


Figure 2.1 Abundance of palms vs forest size

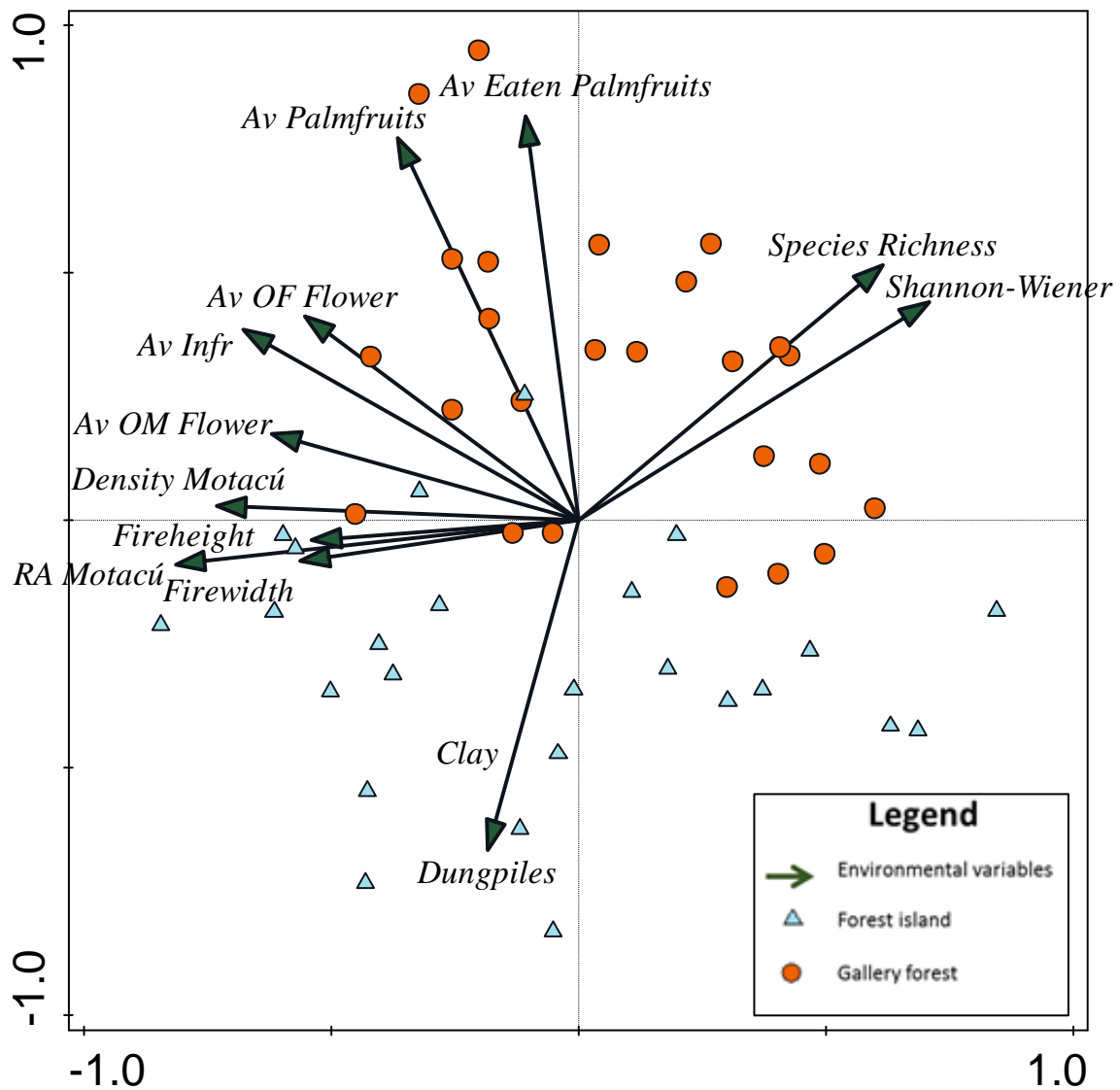


Figure 2.2 PCA biplot of all variables with plots gallery forest (n=25) and forest islands (n=25)

Table 2.1 Output of Unconstrained PCA. Total variation is 1988.000

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5386	0.2561	0.1290	0.0504
Explained variation (cumulative)	53.86	79.46	92.37	97.40

Table 2.2 Correlation matrix (Spearman's rank order correlation) of all environmental variables. Correlation coefficients in bold indicate a correlation >.500 and asterisks behind correlation coefficients indicate significance (* = $p < .05$, ** = $p < .001$)

	Density Motacú	RA Motacú	Old female flower	Old male flower	Infructes cences	% fruiting palms	Palm fruits ground	Eaten Palm fruits ground	Fire height Motacú	Fire width Motacú	Dung piles	Species Richness	Shanno n Wiener
Density Motacú	1.000												
RA Motacú	.860**	1.000											
Old female flower	.286*	0.253	1.000										
Old male flower	.292*	.280*	.689**	1.000									
Infructescences	.614**	.498**	.521**	.415**	1.000								
% fruiting palms	.383**	.322*	.628**	.396**	.885**	1.000							
Palm fruits ground	.384**	.348*	.581**	.312*	.553**	.587**	1.000						
Eaten Palm fruits ground	0.197	0.147	.389**	0.070	.351*	.421**	.727**	1.000					
Fire height Motacú	.384**	.406**	0.189	.384**	0.264	0.194	.330*	0.069	1.000				
Fire width Motacú	.294*	.407**	0.123	0.255	0.174	0.075	0.099	-0.007	.401**	1.000			
Dung piles	-0.040	-0.005	0.026	0.124	-0.218	-0.251	-.488**	-.553**	0.129	0.108	1.000		
Species Richness	-0.242	-.471**	-0.085	-0.186	-0.187	-0.077	0.088	.325*	-.295*	-0.208	-.461**	1.000	
Shannon Wiener	-.377**	-.588**	-0.185	-0.257	-.280*	-0.134	-0.061	0.214	-.322*	-0.261	-.363**	.928**	1.000

Appendix III Predictors of Macaw abundance

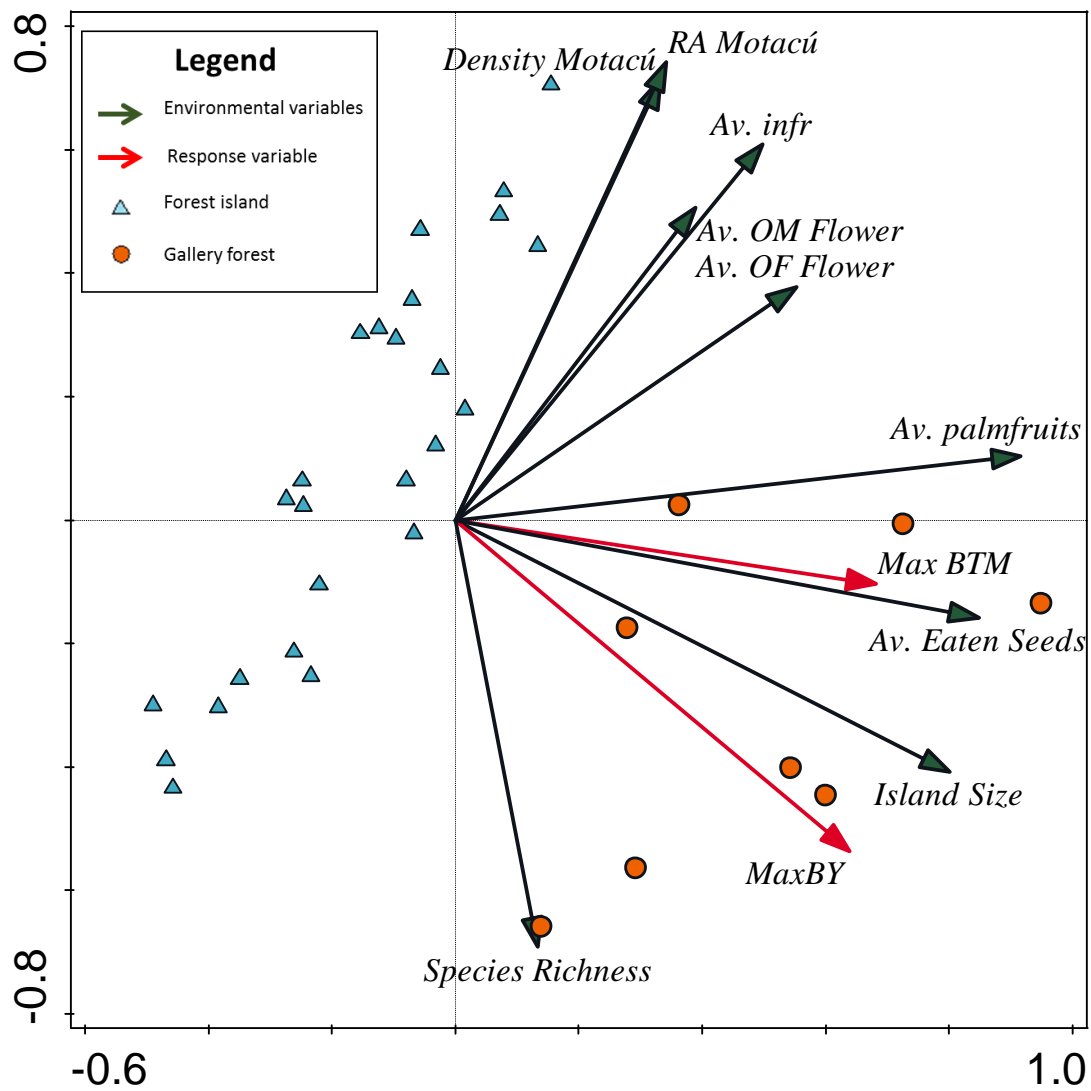


Figure 3.1 PCA biplot of environmental variables and response variables (Blue-throated- and Blue-and-Yellow Macaw).

Table 3.1 Output Unconstrained PCA, total variation is 396.00000

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.3713	0.2553	0.1208	0.0932
Explained variation (cumulative)	37.13	62.67	74.75	84.07

Appendix IV Macaw inventory and information on the forests

Table 4.1 Maximum numbers of Blue-throated Macaws and Blue-and-Yellow Macaws, forest size, and total palm abundance for both the gallery forests and forest islands. GF = gallery forest and FI = forest island

Habitat	Nr.	Blue-throated Macaw	Blue-and-Yellow Macaw	Forest size (m ²)	Total nr. of palms
GF	1	0	8	408562	6271
GF	2	0	15	609080	21186
GF	3	0	20	259600	1967
GF	4	11	16	315225	8095
GF	5	12	3	302150	9497
GF	6	0	5	374000	11020
GF	7	24	9	105900	1660
GF	8	0	9	78000	2730
FI	1	0	0	5741	183
FI	2	0	0	1164	72
FI	3	2	0	3068	172
FI	4	3	0	1257	50
FI	5	0	0	1698	67
FI	6	1	0	3318	185
FI	7	0	0	1320	78
FI	8	2	0	2083	31
FI	9	0	0	1320	12
FI	10	2	0	1257	26
FI	11	0	0	1698	70
FI	12	0	0	804	0
FI	13	0	3	2083	72
FI	14	0	0	4015	87
FI	15	0	0	227	1
FI	16	0	0	1810	18
FI	17	0	0	962	19
FI	18	0	0	1555	7
FI	19	0	0	7933	100
FI	20	0	0	1385	18
FI	21	0	0	552	0
FI	22	0	0	990	0
FI	23	0	0	1886	25
FI	24	2	1	6000	139
FI	25	4	2	6504	127