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Mapping the drivers of parasitic weed abundance at a national scale- a new approach applied to Striga asiatica

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Title: Mapping the drivers of parasitic weed abundance at a national scale: a new approach applied to *Striga asiatica*

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Running head: *Mapping the drivers of Striga abundance at a national scale*

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Summary

The parasitic weed genus *Striga* causes huge losses to crop production in sub-Saharan Africa, estimated as being in excess of $7 billion per year. There is a paucity of reliable distribution data for *Striga*, however such data are urgently needed to understand current drivers, better target control efforts, as well as to predict future risks. To address this we developed a methodology to enable rapid, large-scale monitoring of *Striga* populations. We used this approach to uncover the factors that currently drive the abundance and distribution of *Striga asiatica* in Madagascar. Two long-distance transects were established across the middle-west region of Madagascar in which *Striga asiatica* abundance in fields adjacent to the road was estimated. Management, crop structure and soil data were also collected. Analysis of the data suggests that crop variety, companion crop and previous crop were correlated with *Striga* density. A positive relationship between within field *Striga* density and the density of the nearest neighbouring fields indicates that spatial configuration and connectivity of suitable habitats is also important in determining *Striga* spread. Our results demonstrate that we are able to capture distribution and management data for *Striga* density at a landscape scale and use this to understand the ecological and agronomic drivers of abundance. The importance of crop varieties and cropping patterns is significant, as these are key socio-economic elements of Malagasy cropping practices. Therefore, they have the potential to be promoted as readily available control options, rather than novel technologies requiring introduction.

Keywords: weed survey, weed management, *parasitic weeds, Striga asiatica, NERICA rice varieties, legumes, Madagascar*

Introduction

Among the most economically damaging agricultural weeds are parasitic plants belonging to the family Orobanchaceae (Joel et al. 2007). The most agriculturally damaging weed genera in this family are *Striga, Rhamphicarpa* and *Alectra* species in sub Saharan Africa (SSA) and *Orobanche* and *Phelipanche* species in the Mediterranean region, eastern Europe and north Africa. (Mohamed et al. 2006, Spallek et al. 2013, Parker 2013).

Of the suite of economically significant parasitic weeds, the genus *Striga* is among the most problematic (Mohamed et al 2006, Parker 2009). The genus comprises over 30 recognised species with the greatest damage cause by *Striga hermonthica* (Del.) Benth and *S. asiatica* (L) Kuntze (Mohamed et al. 2001). This is due to the often-catastrophic losses caused by these two species to a wide range of staple cereal crops grown by subsistence farmers in SSA (Runo and Kuria 2018).

The *Striga* problem is recognised as a major factor limiting crop production in SSA (Ejeta et al. 2007), and is directly related to global issues of food security and poverty alleviation. It is widely accepted that the extent and intensity of infestation by *Striga* is increasing (Joel et al. 2007, Ejeta 2007, Parker 2009, Gebreslasie et al. 2018). This is largely due to the lack of access to agricultural inputs (Sauerborn et al. 2003), population pressure reducing fallow periods, and a reduction in traditional intercropping methods (Joel et al. 2013).

Striga has resulted in reported yield losses of between 35 - 80% in rice (Rodenburg et al. 2016), 50 - 100% for sorghum (Abunyewa and Padi, 2003) and losses of maize of between 21 - 74% (De Groote et al. 2007). Estimates of economic losses from *Striga* range from between \$111 and \$300 million per year for rice (Rodenburg et al. 2016), \$383 for maize (Woomer and Savala 2007) and between \$1 billion (Labrada, 2008) and \$7 billion in SSA as a whole

(Ejeta 2007). There is great variation in estimates of the geographic extent of *Striga*. Lagoke et al. (1991) estimated around 40 million ha of cereal crops affected in West Africa, while Sauerborn (1991) estimated that 21 million ha in Africa was infested. A contemporary estimate is 20 million ha across SSA (Baiyegunhi et al. 2019), while Ejeta (2007) suggests between 50 – 100 million ha annually. The uncertainty represented by this variance in estimated extent reveals that robust methods for estimating the spatial extent of infestations are lacking.

Resistance of host crops has long been identified as a key management tool for control for *Striga* (Scholes and Press 2008; Hearne 2009), with a research on resistance in rice cultivars, specifically the NERICA group of varieties. NERICA is an acronym of 'NEw RIe for AfriCA', which comprises a group of conventionally crossed rice varieties using *Oryza sativa* (L) and *Oryza glaberrima* (Steud.), developed for sub-Saharan agriculture. A series of NERICA varieties have been developed for rain-fed, upland rice regions, with another series for lowland areas (Somado et al 2008). Widely variation in the resistance of NERICA varieties to *S. asiatica* has been demonstrated from laboratory experiments by Cissoko et al (2011) and in field trials by Rodenburg et al (2015; 2017).

Recent work undertaken by Randrianjafizanaka et al (2018) in Madagascar indicates the potential importance of cropping practices and rice variety in the management of *S. asiatica*; incorporating cropping with NERICA rice varieties. NERICA-9 and NERICA-4 reduced *S. asiatica* infection levels by 57% and 91% respectively, compared with levels of infection on non-NERICA variety B22. In addition, *S. asiatica* densities were reduced by 20 and 60% in maize grown after planting NERICA-9 and NERICA-4 respectively, compared to B22. In the same study, intercropping with legumes (*Vigna unguiculata, Mucuna pruriens, Vigna umbellata and Stylosanthes guianensis*) resulted in significant reductions in *S. asiatica* infection levels and delays in emergence. Intercropping of legumes and cereals has been shown to significantly reduce *Striga* infestation in a number of other studies (e.g. Oswald et al 2002, Rodenburg & Johnson 2009). It is hypothesised that leguminous crops reduce levels of *Striga* germination via nitrogen fixation, causing germination or *Striga* without host root attachment, or that they alter soil surface conditions to interfere in germination (Khan et al 2002). Conversely continuous monocropping without rotation has been shown to increase levels of infestation and build ups of *Striga* seed within the soil seed bank (Ejeta 2007).

In vitro experiments have demonstrated the role of macronutrients on *S. asiatica* infestation via the mechanism of host strigolactone root exudation. Strigolactones are signalling compounds which stimulate the germination of *Strig*a (Xie et al. 2010, Jamil et al 2011). Nitrogen deficiency has been shown to increase strigolactone production by sorghum and hence increase *S. asiatica* and *S. hermonthica* germination (Raju et al. 1990, Yoneyama et al 2007). Significant reductions in *S. asiatica* infestation have been observed with increased N application (Farina et al. 1985). Yaduraju et al. (1979) concluded that sorghum growth was negatively affected by *S. asiatica* in the absence of N application, an effect which decreased with increased levels of application. The results of field trials testing the role of N in *Striga* have proved less conclusive. Several studies found application of N to field plots did not affect levels of *S. hermonthica* infestation (Smaling et al. 1991, Kamara et al 2007), whereas others noted significant reductions (Soon-Kwon et al 1997, Kamara 2009). Temporal variations of *Striga* infestation rates in response to N application have also been observed, with greatly differing results to the same levels of application between years (Mumera & Below 1993).

Successful management of any weed relies on strong predictive systems, underpinned by accurate distribution data, together with a sound understanding of the ecological niche of the target species (Mohamed et al. 2006). The variance and reliability of estimates of the geographic extent of *Striga* is a knowledge gap requiring urgent attention (Parker 2009). The paucity of accurate distribution data also prevents accurate estimates of economic losses (Rodenburg 2016, De Groote 2007), which serves to justify increased investment to address the problem.

Madagascar has been identified as a priority country for parasitic weed research (Rodenburg et al. 2016). This is because of the scale of *Striga* infestation and the lack of current distribution and agroecological data available to address the problem. Fig.1 provides representations of the topography, climate and soil types of Madagascar. Very few studies of *Striga* have been undertaken in Madagascar (Eliot et al. 1993, Geiger et al. 1996, Randriamampianana, Unpub.). Herbaria records are also scant, with just one new record submitted since 2014 (see Fig. 2).

INSERT FIG 1 HERE

The first introductions of *S. asiatica* to Madagascar occurred over a century ago (Fig.2.), resulting in the spread and establishment of separate populations which exist today. Following a rapid increase in cereal production during the early 1980s *S. asiatica* has spread rapidly across the mid-west of Madagascar. As of 1995 the rate of infested fields within the zone of infection was estimated at around 49% (Randriamampianana (date), pers. comm.). Within infested areas, losses can vary from between 20 -100% (Joyeux 2014) and 30 - 90% (Geiger et al. 1996). In many instances, losses resulting from *Striga* infestation have caused farmers to abandon fields or, in some instances, entire settlements (Geiger et al. 1996, Andrianaivo et al. 1998).

INSERT FIG 2 HERE

The majority of weed population studies have been conducted on single sites using small (≤ $1m^2$) quadrats (Rew and Cousens 2001, Freckleton and Stephens 2009, Queenborough et al. 2011). This approach is inherently labour-intensive and results in coverage of very small spatial extents (Rew and Cousens, 2001). This small scale limits the ability of data to inform predictions of the effects of large-scale environmental change or management on weed population dynamics (Freckleton and Stephens 2009, Treddennick et al. 2017). The use of small quadrats will also almost certainly result in weed patches being missed, creating complications for subsequent statistical analysis (Rew and Cousens, 2001). Large-scale coarse-resolution datasets can be used effectively for distribution modelling on macro scales; for example, using presence data from herbaria or historical records (e.g Kriticos et al. 2003, Mohamed et al. 2006). However, analyses based on presence data alone will not provide information on weed population dynamics in response to changing abiotic or land management factors.

To address the lack of appropriately scaled data, collection methods to enable such analyses; density-structured techniques have been developed (Queenborough et al. 2011, Freckleton et al. 2011a). These methods enable the relatively rapid collection of comprehensive data on weed densities with a small team and limited resources. This approach enables the production of regional and national-scale mapping of distributions and abundances, including relating population abundances to environmental drivers (Mieszkowska et al 2013) and management (Freckleton et al 2018). .

Here we analyse the factors driving the abundance and distribution of *Striga* at a large scale. We used ecological surveys to obtain landscape-scale distribution data alongside detailed agroecological information for *S. asiatica*. The objectives were to (i) develop a rapid and repeatable methodology that would permit the mapping of this weed at a national scale; (ii) test the role of management (crop and cropping history) in driving increases in abundance; (iii) analyse the impact of variation in soil nutrients in explaining differences in the distribution of *Striga*.

Methods

Study system

Field surveys were undertaken between February and March 2019 in the mid-west of Madagascar, one of the six major rice growing regions in the country (Fujisaka, 1990). The mid-west covers 23,500 km^2 with an elevation between 700 m and 1000 m above sea level. The climate is semi-humid tropical, with a warm, rainy season from November to April and a cool, dry season from May to October. Mean annual rainfall ranges from 1100mm to 1900 mm with a mean temperature of 22 C.

Large-scale transects

Field sampling involved undertaking two long-distance, driven transects along which *S. asiatica* abundance was estimated in fields adjacent to the road. These comprised a transect of 116 km along the RN34 (T1, n=153) and one of 70 km along the RN1 (T2, n=83). T1 was located within Vakinakaritra province, between the towns of Betafo and Morafeno and T2 was located within Itasy and Bongolava provinces, approximately 3km east of Sakay and the outskirts of Tsiroamandidy (Fig. 3).

INSERT FIG 3 HERE

The location and orientation of transects was based on expert advice and previous work undertaken by agricultural researchers familiar with the historic distribution of *S. asiatica* in the mid-west of Madagascar. Fieldwork was undertaken with local technicians or guides.

Within-field sampling

One field was surveyed on adjacent sides of the road every kilometre. In the absence of fields in the immediate vicinity of a given 1 km section, the next available field was surveyed. Prior to undertaking the survey, pilot work was undertaken in order to ensure consistency of scoring between observers, and measure the detectability of the *Striga* within fields. This work was undertaken within an experimental field station maintained by French agricultural research organisation: CIRAD, located at Ivory (Lat: 46.411254, Long: -19.552421). Systematic density scoring was undertaken by principal field surveyors within three rice fields possessing highly varied levels of *Striga* infestation.

Fields were divided into quadrats, with two observers recording *Striga* density within up to three quadrats per field, each quadrat measuring 10 m wide by 20 m in length. Where a field was greater than 1200m^2 is size, the survey was limited to 3 x 200 m^2 quadrats per observer (Fig. 4). In each instance a field corner was randomly selected as the point to begin survey.

Striga density was estimated within quadrats using a six-point, density structured scale, ranging from absent (0) to very high (5). Based on available information, Crop type, rice variety, companion crop, previous crop, estimated mean crop height, and percentage cover data were collected. In addition, information on fertiliser addition and any other pertinent information on the general area were recorded (where available). Photographs of each field were also taken.

Each quadrat was walked in parallel by the two observers, moving at a steady pace. During the walk, each observer scanned 5 m either side of their path to look for *Striga* (see Fig.4.). At the end of each quadrat the mean density score for that quadrat (along with average crop height and cover and other weed cover) was called and entered on the mobile app. If no *Striga* was found within any quadrats, a thorough walk throughout the entire field was undertaken to verify that *Striga* was truly absent.

INSERT FIG 4 HERE

Where scores varied in excess of one density point between surveyors, a discussion was undertaken as to why the quadrat had been scored as such in order to standardise density estimates between observers.

During the pilot work, it was agreed between surveyors that reliable detection of *S. asiatica* within typically planted, pluvial rice fields was possible at distances up to 5 m on either side of each surveyor. As a 10 x 10m quadrat per surveyor would have negatively affected the speed of repeatability, quadrat dimensions of $200m^2$ (10x20m) were agreed. Definitions of density states were determined, and a table was produced with narrative descriptors of the scale used.

Data were recorded using a GPS-enabled smartphone with the mobile application 'Fulcrum' (Fulcrumapp.com, 2019, version 2.31.1) to allow geo-referencing and rapid data entry. Accurate location of the fields will permit the sites to be subsequently resurveyed.

Soil Samples

The role of available nitrogen in determining *S. asiatica* densities was addressed through collecting and analysing soil samples for NO_3. These samples were collected in pairs from quadrats with contrasting *Striga* densities within the same field. The aim was to collect equal numbers of paired samples for all combinations of *Striga* density. However a paucity of very high *Striga* densities during survey resulted in an unbalanced composition of density pairs (see Appendix 3). The soil samples comprised: 47 pairs representing differing densities and nine single samples from individual fields lacking any *Striga*. Soil samples were obtained from the centre of each chosen quadrat using a 20 mm diameter, hand-held, tubular soil sampler to a depth of approximately 20 cm. Soil samples were subsequently air dried for analysis.

NO_3 analysis was undertaken using a LAQUAtwin NO_3-11 nitrate meter (Horiba Scientific, Japan). Owing to low levels of NO_3 within the soil, it was necessary to dilute the standard solution supplied with the meter. Therefore, calibration was undertaken between 15 and 150 ppm NO_3 to improve sensitivity. One gram of dried soil was mixed with one millilitre of water and ground in a pestle and mortar. The resultant solution was then placed on the sensor of the meter. This procedure was repeated a minimum of two times per soil sample. If agreement between the first two readings was observed (i.e: between +/- 5 ppm NO3 between readings), then the readings were taken, and the mean of the readings was used. If the readings did not concur, then sampling was repeated until stabilisation of readings.

Soil pH was measured on the soil samples using a Hanna Instruments HI99121 pH meter (Hanna Instruments Ltd, UK). For each sample, 20 g of soil were mixed with 50 ml of soil preparation solution for 30 seconds. After 5 minutes the soil pH was measured using the meter.

Statistical Methods

The first set of analyses tested the roles of crop variety, weeding, previous crop, companion crop and field area in determining the density of *Striga*. A second set examined the potential effect of edaphic factors (mean annual temperature, mean annual rainfall, altitude pH and NO_3) on *S. asiatica* density. Within-field *Striga* density was also plotted against that of neighbouring fields. A final set of analyses used *Striga* density as the independent variable and mean crop height, crop cover and other weed cover as response variables; to examine potential effects of *Striga* on crops and any covariation with cover for other weeds present.

Diagnostic plots (density plots, QQ plots and histograms) were produced for each model. Statistics were calculated using R 3.5.1 (R Core Team, 2018) and the packages: dplyr (v0.8.0.1; Wickham, François, Henry & Müller, 2019), mgcv (Wood 2011), lme4 (v067.i01, Bates, Maechler, Bolker, & Walker, 2015), lmerTest (Kuznetsova , Brockhoff & Christensen 2017), MASS (Venables & Ripley 2002), DescTools (v 0.99.28, Signorell et mult. al. 2019). and psych (Revelle 2018, v1.8.12). The full reproducible code is available in Appendix 1.

Striga density was log (x+1) transformed owing to the presence of large numbers of zero densities. Polynomial contrasts were applied to categorical variables incorporated into models (crop variety, previous crop, companion crop). Linear models and generalised additive models (GAMs) were used to test significance of independent variables. Linear regression analyses are robust against high degrees of collinearity among independent variables (Freckleton 2011b) and violation of normality assumptions for distribution of residuals (Fitzmaurice, Laird & Ware 2004). GAMs were also chosen due to their flexibility in dealing with non-normal distributions and ability to handle non-linear relationships between response and explanatory variables (Guisan et al 2002).

To test the effects of previous crops, two sets of analyses were undertaken. The first was to examine the effect if the previous crop was a legume or non-legume (dichotomous, yes / no). For this analysis, Shapiro-Wilk tests were undertaken to check for normality of distribution for the two levels of *Striga* density. A Welch Two Sample t-test was subsequently performed on these data. To enable comparison with the study of Randrianjafizanaka et al. (2018) a Welch Two Sample t-test for mean *Striga* density and rice varieties B22 and NERICA-4 was also undertaken. The second analysis examined any effects of specific crop or crop combinations on *Striga* density. Linear models and GAMs for previous crop and *Striga* density with latitude and longitude included as smoothed terms were performed (see Appendix 1). Crop-crop combinations with fewer than two records were omitted from these analyses. An additional model testing for autocorrelation between *Striga* density and latitude / longitude was also performed.

Preliminary model testing for collinearity between edaphic factors indicated strong correlation between altitude and mean temperature (f=1860, df=2, 239, R^2=0.93, p < 2.2e-16, VIF: 16.56). Potential correlation between mean rainfall and altitude and mean temperature was less evident (f=3.40, df=2, 239, R^2= 0.03, p = 0.04, VIF=1.03). However, this interaction was anticipated and is commonplace amongst analyses using edaphic data and was therefore not considered a constraint to the analysis undertaken. Smoothed lines fitted to scatterplots for (pH, NO_3, field area, altitude, mean rainfall, mean temperature) indicated potential non-linear relationships with *Striga* density; providing additional justification for the use of GAMs in the analyses (see Appendix 2).

Results

Management Factors

Analysis of management data suggests that rice variety had a significant effect on *Striga* density (linear model F=1.72, df=20, 102, p=0.04, GAM F=11.14, df=21, 102? p <2e-16p), most notably with NERICA-10 and NERICA-4. NERICA-10 exhibited greater resistance than NERICA-4, which was associated with consistently higher *Striga* densities (see Fig. 5 A). A Welch Two Sample t-test for mean *Striga* density and previous crop legume (yes/no, Fig. 5 B) indicated significant differences of means (t=2.05, df=141.08, p=0.02). The t-test for B22 and NERICA-4 did not indicate significant differences of means (μ: B22=0.85, NERICA-4=1.15, t=2.05, df=141.08, p=0.02) although the mean *Striga* density was lower for B22 than for NERICA-4. The effect of previous crop type or variety on mean *Striga* density (Fig. 5 C) was not significant for a linear model (F=1.08, df =25, 159, p= 0.369) but was significant for the associated GAM (F=15.84, df=21, p<2e-16). Specifically, the effects of previous cropping with bambara groundnut (*Vigna subterranea*) and rice / Bambara groundnut were correlated with significantly lower mean *Striga* density.

There was a positive relationship between within field *Striga* density and the density of the nearest neighbouring fields (F=9.015 df=1, 242, p=0.01 and GAM (F=10.91, df=1, p=0.01). This suggests that spatial factors could be important in determining *Striga* distribution and spread (see Fig. 6). No significant results were obtained from the analyses of mean *Striga* density used as an explanatory variable for mean crop height (F=0.83, df=1, 223, p=0.36) crop cover (F=2.329 df=1, 223, p=0.13) and other weed cover (F=0.08 df=1, 151, p=0.77).

INSERT FIG 5 HERE

INSERT FIG 6 HERE

Edaphic Factors

A linear model and GAM combining edaphic factors to predict *Striga* density (mean rainfall, mean temperature and altitude) did not produce significant results (linear model: f = 1.39, df= 3, 238., p=: 0.25, GAM f =1.297 df= 14.38 p =0.19). A linear mixed model and GAM examining the effects of soil pH and NO3 on *Striga* density did not produce significant results (linear model: pH: t= 0.72, df= 92.58., p=: 0.48, NO_3 : t= -1.12, df= 89.33, p=: 0.27., GAM pH: X^2 = 0.72, df= 1., p=: 0.39, NO_3 : X^2 = 0.48, df= 1., p=: 0.49). Ranges for pH were: 4.16 - 6.43 for T1 (n=68) and 4.51 - 5.81 for T2 (n=35). Ranges for NO_3 were: 15 – 135 ppm for T1 (n=68) and 18 – 130ppm for T2 (n=34: one sample was discarded).

Discussion

This paper describes the first known systematic, landscape-scale agroecological study of the factors driving the occurrence and abundance of *Striga*. Our results, employing a novel methodology reveals key agroecological factors influencing *Striga* density. Our study demonstrates the role of crop variety, companion crop and crop rotation in determining *Striga* density and highlights the importance of densities within adjacent fields; providing evidence of the localised nature of *Striga* dispersal.

Cropping practices

There was a significant role of rice variety on *Striga* density, and this was in line with previous studies which analysed the resistance of (NERICA) rice varieties. During the current study NERICA-10 was found to be more resistant than NERICA-4. This is significant as it is consistent with other studies undertaken in the laboratory by Cissoko et al (2011) and during field trials by Rodenburg et al (2015). Cissoko et al. (2011) found that NERICA-10 was more resistant to both *S. asiatica* and *S. hermonthica* than NERICA-4. This resistance was demonstrated in terms of numbers and mean height of attached *Striga* plants. Similarly, field trials by Rodenburg et al (2015) in Tanzania found the NERICA-10 was significantly more resistant to *S. asiatica* than NERICA-4. This resistance was expressed by maximum emerged *Striga* per m^2. However additional field trials by Rodenburg et al (2017),-also in Tanzania- indicated similar levels of emerged *S. asiatica* between NERICA-10 and NERICA-4.

Randrianjafizanaka et al. (2018) identified significantly lower *Striga* infection levels for NERICA-4 than variety B22. During the current study however, lower mean *Striga* density was recorded for B22 than for NERICA-4, though the means were not statistically different. NERICA-4 was the worst performing of all rice varieties recorded in terms of *Striga* density, which is the inverse of the findings of Randrianjafizanaka et al. (2018). However, NERICA-9, used in the study by Randrianjafizanaka et al., was not recorded, preventing a complete comparison. The results of Randrianjafizanaka et al. are consistent with regards to the significant effect of previous crop and legumes in reducing *Striga* infestation. This effect has also been found in other research (e.g. Rodenburg & Johnson 2009, Kureh et al 2006).

That such variance should exist between observed resistance of rice varieties between these two studies could be due to several reasons. Firstly, high degrees of genetic variability have been identified between separate populations of *S. asiatica* (Mohamed et al 2007) to the extent that even proximate populations can be considered as separate ecotypes (Botanga et al. 2002). Such variation also appears to be positively related to time since introduction to a region or locality (Gethi et al 2005), which influences the degree of *Striga* virulence and levels of host infection (Cissoko et al 2011).

Secondly, the higher level of complexity associated with open systems could also account for observed variation with controlled studies in a geographically discreet locality. Indeed, the effect of the inherently greater complexity of agroecological systems on resistance of rice cultivars to *Striga* is largely unknown (Rodenburg 2015, 2017). Interactions of environmental factors such as soil composition, nutrients, microclimate, slope, aspect, can interact to influence the expression of host resistance. Interactions of these factors with the phenotypic expression of *Striga* ecotypes may also be responsible. Observations of resistance to *Striga*, due to the factors detailed above, therefore vary greatly according location. This may account for differences between the findings of a study concerning single population, when compared with those aggregated over several populations across a large geographic extent.

Dispersal

The correlation between within-field *Striga* density and that of nearest neighbouring fields suggests that there is transfer between adjacent, suitable habitat patches. Studies of the dispersal of *S hermonthica* (Berner et al 1994, van Delft 1997) and *S asiatica* (Sand et al 1990) also suggest localised seed dispersal to adjacent patches of suitable habitat, as opposed to long-distance, random dispersal via wind or water. In support of these observations, *S asiatica* seed weight and size has also been positively correlated with germination rate and virulence (Bewabi et al 1984).

Contamination of seed is responsible for initial introductions between countries or regions (Berner et al 1994, Gethi et al 2005). This assertion is supported by herbarium records for

Madagascar (see Fig.2.), which show the earliest records around the country's principal historical ports. Once initial introduction has occurred, the evidence for localised dispersal of *Striga* suggests that a spatially explicit approach to management would be most appropriate (Minor and Gardiner 2011).

Crop Productivity

The absence of any observed relationship between mean *Striga* density and crop height / cover could be attributable to the fact that emerged (aboveground) weed density often does not represent total attached *Striga* plants. In the case of *Striga*, density of plants can actually be lower in the event of high levels of host attachment (Hearne 2009). This is caused by an increased delay in emergence, as greater numbers of attached *Striga* plants compete for the same host nutrient source. This is different to the effect of most weeds, where visible weed biomass is related to crop performance (Rajcan & Swanton 2001). Some previous studies have demonstrated a direct effect of numbers of emerged *Striga* plants on crop performance (Rodenburg et al 2017, Mumera & Below 1993). However, these studies controlled for soil nutrient levels, so the role of *Striga* infection on plant growth could be isolated. It is however considered that poor soil nutrient levels observed during the current study represented an overriding limiting factor in crop performance, rather than *Striga* density.

Edaphic Factors

That edaphic factors were not significantly correlated with *Striga* density was consistent with previous studies, as *S asiatica* has been found to be unresponsive to temperature (Patterson et al 1990, Rodenburg et al 2011). Mean rainfall variation within the study area was low (min: 114mm, max: 134mm), which is well within the 50–150mm range tolerated by *Striga* species (Mohamed et al 2006). Similarly, the altitudes encompassed by the current study (713–

1301m) were well within the cited range of occurrence for *S asiatica* (0–2400m) (Agnew & Agnew 1994). In order to detect effects of edaphic factors, if indeed they exist in isolation, it would most likely be necessary to cover a geographic range sufficient to collect density data on the edges of the above-cited edaphic ranges. It is most likely that such factors do not solely influence spread or density of *S asiatica*. If such data were collected, these would require combination as factors within a more complex, future modelling framework.

Conclusion

The results of this study provide a number of important, wider implications for the study and management of parasitic weeds. These implications arise from both the methodology employed and the results obtained. The successful implementation of this novel methodology provides a basis to address the paucity of distribution and open system agroecological data for parasitic weeds. These are two significant concerns, which represent major impediments to the successful management of parasitic weeds. That the methodology was successfully adapted from blackgrass – a morphologically and ecologically very different species – demonstrates that it can be further adapted to survey other important parasitic weed species. This simple methodology can be readily communicated to new field surveyors and the rapid, yet accurate nature of data collection is cost-effective. Therefore, surveys can potentially be expanded to regional or national scales as required.

That the roles of rice variety and leguminous crops are shown to be significant determinants of *Striga* density on a landscape scale is highly significant. The identification of NERICA-10 as a highly resistant variety supports several previous studies. That NERICA-4 has significantly lower resistance to *Striga* than NERICA-10 and other varieties and landraces is highly relevant to policy makers, agricultural researchers, extension workers, NGOs, and farmers in Madagascar. NERICA-4 is widely planted within the mid-west of Madagascar, possibly due to it being *Striga* resistant and a high-yield variety. The use of resistant crop varieties is the most widespread seed-based control option available to subsistence farmers with limited capital (Hearne 2009). However, in light of these findings, it is recommended that alternative varieties are promoted which exhibit greater resistance within this agroecological context.

Lower *Striga* densities recorded in association with planting of legumes also supports a number of previous studies. The use of leguminous companion / rotation crops is already widely practised within farming systems in this region. This control option does not require introduction of novel, unfamiliar crops whose uptake may be subject to potential resistance from farmers. The use of legumes within rotational and intercropping systems should therefore also be promoted in situations where limited access to capital precludes the use of herbicides, fertilisers or other technologies.

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Conflict of Interest Statement

The authors declare that there is no conflict of interest.

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Appendix 1: Model details, outputs and R scripts*

<table>
<tr><th>Model</th><th>#</th><th>Code</th><th>Result</th></tr>
<tr><td>Mean crop height v Log striga density +1</td><td>LM1</td><td>ALOM1<-group_by(AD_1, R_M_O)

lm1 <- lm(MCH ~ log(AvDen + 1), data = ALOM1)</td><td>Analysis of Variance Table

Response: MCH
Df Sum Sq Mean Sq F value Pr(>F)
log(AvDen + 1) 1 3767 3766.9 0.8295 0.3634
Residuals 223 1012696 4541.2
>
Coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept) 99.03 7.36 13.454 <2e-16 ***
log(AvDen + 1) 9.87 10.84 0.911 0.363

Residual standard error: 67.39 on 223 degrees of freedom
(19 observations deleted due to missingness)
Multiple R-squared: 0.003706,
Adjusted R-squared: -0.0007618

F-statistic: 0.8295 on 1 and 223 DF, p-value: 0.3634</td></tr>
<tr><td>Mean crop height v Log striga density +1 + S(Lat-Lon)</td><td>GAM1</td><td>gam1 <- gam(MCH ~ log(AvDen + 1) + s(Lat, Lon), data = ALOM1)</td><td>Parametric Terms:
df F p-value
log(AvDen + 1) 1 0.511 0.475

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 8.187 10.745 1.788 0.0586

Parametric coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept) 100.217 7.212 13.896 <2e-16 ***
log(AvDen + 1) 7.663 10.717 0.715 0.475

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 8.187 10.75 1.788 0.0586 .

R-sq.(adj) = 0.0693 Deviance explained = 10.7%
GCV = 4423.6 Scale est. = 4223.3 n = 225</td></tr>
<tr><td>Mean crop cover v Log striga density +1</td><td>LM2</td><td>lm2 <- lm(MCC ~ log(AvDen + 1), data = ALOM1)</td><td>Analysis of Variance Table

Response: MCC
Df Sum Sq Mean Sq F value Pr(>F)
log(AvDen + 1) 1 637 637.16 2.3293 0.1284
Residuals 223 60999 273.54

Call:
lm(formula = MCC ~ log(AvDen + 1), data = ALOM1)

Coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept) 50.769 1.806 28.105 <2e-16 ***
log(AvDen + 1) -4.059 2.660 -1.526 0.128</td></tr>
</table>

*Green= Low Significance / p value, Yellow = Moderate significance/ p value, Red = High significance / p value

<table>
<tr><td></td><td></td><td></td><td>---
Residual standard error: 16.54 on 223 degrees of freedom
  (19 observations deleted due to missingness)
Multiple R-squared: 0.01034, Adjusted R-squared: 0.0059
F-statistic: 2.329 on 1 and 223 DF, p-value: 0.1284</td></tr>
<tr><td>Mean crop cover v Log striga density +1 + S(Lat-Lon)</td><td>GAM2</td><td>gam2 <- gam(MCC ~ log(AvDen + 1) + s(Lat, Lon), data = ALOM1)</td><td>Parametric Terms:
                df   F p-value
log(AvDen + 1) 1 2.819 0.0947

Approximate significance of smooth terms:
             edf Ref.df   F p-value
s(Lat,Lon) 17.27 21.63 1.685 0.0344

Parametric coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)   50.970   1.758 28.997 <2e-16 ***
log(AvDen + 1)   -4.433   2.640 -1.679 0.0947 .

Approximate significance of smooth terms:
             edf Ref.df   F p-value
s(Lat,Lon) 17.27 21.63 1.685 0.0344 *

R-sq.(adj) = 0.123   Deviance explained = 19.5%
GCV = 263.8 Scale est. = 241.21   n = 225
></td></tr>
<tr><td>Mean other weed cover v Log striga density +1</td><td>LM3</td><td>lm3 <- lm(MWC ~ log(AvDen + 1), data = ALOM1)</td><td>Analysis of Variance Table

Response: MWC
                Df Sum Sq Mean Sq F value Pr(>F)
log(AvDen + 1)   1   45   45.05 0.0847 0.7714
Residuals   151 80320 531.92

Call:
lm(formula = MWC ~ log(AvDen + 1), data = ALOM1)

Residuals:
    Min   1Q Median   3Q   Max
-22.425 -20.773 -8.733 14.012 59.227

Coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)   30.773   3.127   9.843 <2e-16 ***
log(AvDen + 1)   1.319   4.531   0.291 0.771

Residual standard error: 23.06 on 151 degrees of freedom
  (91 observations deleted due to missingness)
Multiple R-squared: 0.0005605,
       Adjusted R-squared: -0.006058
F-statistic: 0.08469 on 1 and 151 DF, p-value: 0.7714</td></tr>
<tr><td>Mean crop cover v Log striga density +1 + S(Lat-Lon)</td><td>GAM3</td><td>gam3 <- gam(MWC ~ log(AvDen + 1) + s(Lat, Lon), data = ALOM1)</td><td>Parametric Terms:
                df   F p-value
log(AvDen + 1) 1 0.218   0.641

Approximate significance of smooth terms:
           edf Ref.df   F p-value
s(Lat,Lon)   2   2 4.636 0.0111</td></tr>
</table>

<table>
<tr><td></td><td></td><td></td><td>arametric coefficients:
Estimate Std. Error t value
Pr(>|t|)
(Intercept) 30.353 3.064 9.906
<2e-16 ***
log(AvDen + 1) 2.077 4.448 0.467
0.641

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 2 2 4.636 0.0111 *

R-sq.(adj) = 0.0402 Deviance explained =
5.91%
GCV = 521.1 Scale est. = 507.48 n = 153</td></tr>
<tr><td>Mean crop height, crop cover and other weed cover as combined response v striga density</td><td>LM4</td><td>lm4 <- lm(MCH + MCC + MWC ~ log(AvDen + 1), data = ALOM1)</td><td>Analysis of Variance Table

Response: MCH + MCC + MWC
Df Sum Sq Mean Sq F value
Pr(>F)
log(AvDen + 1) 1 4878 4877.7 0.8778
0.3503
Residuals 151 839024 5556.5
> summary(lm4)

Coefficients:
Estimate Std. Error t value
Pr(>|t|)
(Intercept) 176.34 10.10 17.451
<2e-16 ***
log(AvDen + 1) 13.72 14.64 0.937
0.35

Residual standard error: 74.54 on 151
degrees of freedom
(91 observations deleted due to
missingness)
Multiple R-squared: 0.00578, Adjusted R-
squared: -0.0008043
F-statistic: 0.8778 on 1 and 151 DF, p-
value: 0.3503</td></tr>
<tr><td>Mean crop height, crop cover and other weed cover as combined response v striga density</td><td>GAM4</td><td>gam4<- gam(MCH + MCC + MWC ~ log(AvDen + 1) + s(Lat, Lon), data = ALOM1)</td><td>Parametric Terms:
df F p-value
log(AvDen + 1) 1 0.44 0.508

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 2.001 2.001 4.331 0.0148
> summary(gam4)

Parametric coefficients:
Estimate Std. Error t value
Pr(>|t|)
(Intercept) 178.651 9.922 18.006
<2e-16 ***
log(AvDen + 1) 9.555 14.405 0.663
0.508

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 2.001 2.001 4.331 0.0148 *

R-sq.(adj) = 0.0415 Deviance explained =
6.04%
GCV = 5464.4 Scale est. = 5321.5 n = 153</td></tr>
<tr><td>Mean crop height of RICE ONLY v Log striga density +1</td><td>LM5</td><td>lm5 <- lm(MCH ~ log(AvDen + 1), data = AD_1, subset = which(R_M_O == "Rice")))</td><td>Response: MCH
Df Sum Sq Mean Sq F value
Pr(>F)
log(AvDen + 1) 1 41 40.89 0.1291
0.7201
Residuals 106 33587 316.86
> summary(lm5)

Residuals:</td></tr>
</table>

<table>
<tr>
<td></td>
<td></td>
<td></td>
<td>Min 1Q Median 3Q Max
-40.129 -9.944 -1.415 6.422 60.980

Coefficients:
Estimate Std. Error t value
Pr(>|t|)
(Intercept) 60.129 2.737 21.971
<2e-16 ***
log(AvDen + 1) -1.599 4.452 -0.359
0.72

Residual standard error: 17.8 on 106 degrees of freedom
(15 observations deleted due to missingness)
Multiple R-squared: 0.001216,
Adjusted R-squared: -0.008206
F-statistic: 0.1291 on 1 and 106 DF, p-value: 0.7201</td>
</tr>
<tr>
<td>Mean crop height RICE ONLY v Log striga density +1 + S(Lat-Lon)</td>
<td>GAM5</td>
<td>gam5 <- gam(MCH ~ log(AvDen + 1) + s(Lat, Lon), data = AD_1, subset = which(R_M_O == "Rice"))</td>
<td>Parametric Terms:
df F p-value
log(AvDen + 1) 1 0.091 0.763

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 11.07 14.37 1.36 0.187
> summary(gam5)

Family: gaussian
Link function: identity

Parametric coefficients:
Estimate Std. Error t value
Pr(>|t|)
(Intercept) 59.988 2.615 22.943
<2e-16 ***
log(AvDen + 1) -1.307 4.322 -0.302
0.763

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 11.07 14.37 1.36 0.187

R-sq.(adj) = 0.126 Deviance explained = 22.5%
GCV = 312.43 Scale est. = 274.61 n = 108
></td>
</tr>
<tr>
<td>Previous crop legume v previous crop not legume?</td>
<td>ttest1</td>
<td>AD1<- (AD_1$AvDen+2)#Adds 2 to the zeros to allow log transformation without excessive zeros

ADL<- log(AD1) # Then log transforms data

AD_1$ADL<-ADL

Make two vectors subsetting if previous crop was legume or not

PCLY = AD_1$ADL[AD_1$PCL=="Y"]

PCLN = AD_1$ADL[AD_1$PCL=="N"]

Plot histogram for each subset with nice normal distribution line

plotNormalHistogram(PCLY)

plotNormalHistogram(PCLN)

ttest1 <-t.test(PCLN, PCLY,</td>
<td>Welch Two Sample t-test

data: PCLN and PCLY
t = 2.0485, df = 141.08, p-value = 0.02118
alternative hypothesis: true difference in means is greater than 0
95 percent confidence interval:
0.01590524 Inf
sample estimates:
mean of x mean of y
1.0444077 0.9614534</td>
</tr>
</table>

<table>
<tr><td></td><td></td><td>"greater")</td><td></td></tr>
<tr><td>Welch Two
Sample t-test
Companion
crop legume v
previous crop
not legume?</td><td>ttes
t 2</td><td>CCLY = AD_1$ADL[AD_1$CCL=="Y"]

CCLN = AD_1$ADL[AD_1$CCL=="N"]

ttest1<- t.test(CCLN, CCLY,
"greater")</td><td>Welch Two Sample t-test

data: CCLN and CCLY
t = -0.51946, df = 89.595, p-value = 0.6976
alternative hypothesis: true difference in
means is greater than 0
95 percent confidence interval:
 -0.1715704   Inf
sample estimates:
mean of x mean of y
0.5239577 0.5648124</td></tr>
<tr><td>Shapiro Wilk
Test for
normal
distribution</td><td>SW1,
SW2</td><td>sw1<-shapiro.test(PCLN)

sw2<-shapiro.test(PCLY)</td><td>Shapiro-Wilk normality test

data: PCLN
W = 0.93023, p-value = 9.952e-06

Shapiro-Wilk normality test

data: PCLY
W = 0.88964, p-value = 2.924e-05</td></tr>
<tr><td>Independent
2-group Mann-
Whitney U
Test
As data looks
non normal</td><td>UT1</td><td>wilcox.test(PCLN,PCLY,
"greater")</td><td>Wilcoxon rank sum test with continuity
correction

data: PCLN and PCLY
W = 4605.5, p-value = 0.02053
alternative hypothesis: true location shift
is greater than 0</td></tr>
<tr><td>Welch Two
Sample t-test
NERICA4 and
B22

As The
results of
Randrianjafiza
naka et al.
compared
these two
varieties</td><td>ttes
t 3</td><td>ttest3<- t.test(NERICA4, B22,
"greater")</td><td>Welch Two Sample t-test

data: NERICA4 and B22
t = 1.0121, df = 53.34, p-value = 0.158
alternative hypothesis: true difference in
means is greater than 0
95 percent confidence interval:
 -0.07241114   Inf
sample estimates:
mean of x mean of y
0.6640107 0.5532828</td></tr>
<tr><td>Linear model
Striga
density v
previous crop</td><td>LM6</td><td>options(contrasts =
c("contr.sum","contr.poly"))
lm6 <- lm(log(AvDen + 1) ~
PC, data = AD_1)</td><td>Analysis of Variance Table

Response: log(AvDen + 1)
           Df Sum Sq Mean Sq F value Pr(>F)
PC   25 4.6514 0.18606   1.082 0.369
Residuals 159 27.3413 0.17196
Multiple R-squared: 0.1454, Adjusted R-
squared: 0.01102
F-statistic: 1.082 on 25 and 159 DF, p-
value: 0.369</td></tr>
<tr><td>GAM Striga
density v
previous crop</td><td>GAM6</td><td>gam6 <- gam(log(AvDen + 1)
~ PC -1 + s(Lat, Lon), data
= AD_1)</td><td>Family: gaussian
Link function: identity

Formula:
log(AvDen + 1) ~ PC - 1 + s(Lat, Lon)

Parametric Terms:
   df   F p-value
PC 21 15.84 <2e-16

Approximate significance of smooth terms:
             edf Ref.df   F p-value
s(Lat,Lon) 2.126 2.247 0.708   0.457
> summary(gam6)

Family: gaussian
Link function: identity

Formula:
log(AvDen + 1) ~ PC - 1 + s(Lat, Lon)

Parametric coefficients:

Estimate Std. Error t value Pr(>|t|)
PCArachis hypogaea
0.591496   0.106648   5.546 1.17e-07 ***
PCArachis hypogaea, Manihot esculenta
0.068891   0.417409   0.165 0.869114</td></tr>
</table>

			PCArachis hypogaea, Solanum lycopersicumes - 0.009785 0.420001 -0.023 0.981442 PCCucumis sativus - 0.082705 0.418120 -0.198 0.843447 PCFallow 0.721657 0.112531 6.413 1.50e-09 *** PCGlycine max 0.504852 0.416996 1.211 0.227780 PCIpomoea batatas 0.621659 0.209986 2.960 0.003534 ** PCManihot esculenta 0.640039 0.085632 7.474 4.61e-12 *** PCManihot esculenta, Vigna subterranea 0.828340 0.293686 2.820 0.005395 ** PCOryza sp 0.483489 0.072564 6.663 4.00e-10 *** PCOryza sp, Arachis hypogaea 0.547073 0.420556 1.301 0.195164 PCOryza sp, Manihot esculenta 0.416930 0.414682 1.005 0.316194 PCOryza sp, Vigna subterranea 0.316803 0.293555 1.079 0.282107 PCOryza sp, Zea mays 0.786737 0.420889 1.869 0.063398 . PCPhaseolus vulgaris 0.685005 0.418282 1.638 0.103434 PCVigna subterranea 0.347235 0.070044 4.957 1.79e-06 *** PCVigna subterranea, Arachis hypogaea 1.019209 0.293910 3.468 0.000672 *** PCZea mays 0.595244 0.073236 8.128 1.07e-13 *** PCZea mays, Manihot esculenta 0.524288 0.159370 3.290 0.001231 ** PCZea mays, Vigna subterranea 0.698396 0.414674 1.684 0.094069 . PCZea mays, Voanjo 0.396548 0.417749 0.949 0.343909 --- Approximate significance of smooth terms: edf Ref.df F p-value s(Lat,Lon) 2.126 2.247 0.708 0.457 R-sq.(adj) = 0.016 Deviance explained = 67.4% GCV = 0.19554 Scale est. = 0.1711 n = 185
Linear model Striga density v mean temp, mean rainfall and altitude	LM7	lm7 <- lm(log(AvDen + 1) ~ MeanRF + MeanTA + Alt, data = AD_1) anova(lm7)	Analysis of Variance Table Response: log(AvDen + 1) Df Sum Sq Mean Sq F value Pr(>F) MeanRF 1 0.171 0.17083 0.8905 0.34629 MeanTA 1 0.572 0.57172 2.9803 0.08558 . Alt 1 0.057 0.05727 0.2985 0.58532 Residuals 238 45.656 0.19183 --- Call: lm(formula = log(AvDen + 1) ~ MeanRF + MeanTA + Alt, data = AD_1) Residuals: Min 1Q Median 3Q Max -0.66661 -0.34131 -0.01941 0.24838 1.10644 Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) -1.3746946 3.5007288 -0.393 0.695 MeanRF -0.0088361 0.0080381 -1.099 0.273 MeanTA 0.1166316 0.1222766 0.954 0.341 Alt 0.0005012 0.0009172 0.546 0.585

			Residual standard error: 0.438 on 238 degrees of freedom (2 observations deleted due to missingness) Multiple R-squared: 0.01722, Adjusted R-squared: 0.004829 F-statistic: 1.39 on 3 and 238 DF, p-value: 0.2465
GAM Striga density v mean temp, mean rainfall and altitude	GAM7	gam1 <- gam(log(AvDen + 1) ~ MeanRF + MeanTA + Alt + s(Lat, Lon), data = AD_1) anova(gam1)	Family: gaussian Link function: identity Formula: log(AvDen + 1) ~ MeanRF + MeanTA + Alt + s(Lat, Lon) Parametric Terms: df F p-value MeanRF 1 0.045 0.832 MeanTA 1 0.649 0.421 Alt 1 0.046 0.830 Approximate significance of smooth terms: edf Ref.df F p-value s(Lat,Lon) 10.72 14.38 1.297 0.191
Linear model Striga density v rice variety	LM8	options(contrasts = c("contr.sum","contr.poly")) lm2 <- lm(log(AvDen + 1) ~ CV, data = AD_1, subset = which(R_M_O == "Rice")) anova(lm2) summary(lm2)	lm(formula = log(AvDen + 1) ~ CV, data = AD_1, subset = which(R_M_O == "Rice")) Residuals: Min 1Q Median 3Q Max -0.6753 -0.2743 0.0000 0.2105 1.1398 Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 0.64723 0.07299 8.867 2.59e-14 *** CV1 -0.09334 0.21212 -0.440 0.6608 CV2 0.96221 0.40497 2.376 0.0194 * CV3 -0.12445 0.11350 -1.096 0.2755 CV4 -0.16463 0.14054 -1.171 0.2442 CV5 -0.15229 0.11057 -1.377 0.1714 CV6 -0.64723 0.40497 -1.598 0.1131 CV7 -0.24177 0.40497 -0.597 0.5518 CV8 0.96221 0.40497 2.376 0.0194 * CV9 -0.24177 0.40497 -0.597 0.5518 CV10 -0.17764 0.11198 -1.586 0.1158 CV11 -0.46397 0.19251 -2.410 0.0177 * CV12 -0.05733 0.11696 -0.490 0.6250 CV13 0.55674 0.40497 1.375 0.1722 CV14 0.02808 0.24128 0.116 0.9076 CV15 0.04591 0.40497 0.113 0.9100 CV16 1.01100 0.40497 2.496 0.0141 * CV17 0.10320 0.24128 0.428 0.6698 CV18 -0.13641 0.40497 -0.337 0.7369 CV19 0.12596 0.40497 0.311 0.7564 CV20 -0.64723 0.40497 -1.598 0.1131

<table>
<tr><td></td><td></td><td></td><td>---
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.4188 on 102 degrees of freedom
Multiple R-squared: 0.2522, Adjusted R-squared: 0.1055
F-statistic: 1.72 on 20 and 102 DF, p-value: 0.04175</td></tr>
<tr><td>GAM Striga density v rice variety</td><td>GAM8</td><td>gam2 <- gam(log(AvDen + 1) ~ CV -1 + s(Lat, Lon), data = AD_1, subset = which(R_M_O == "Rice"))
anova(gam2)</td><td>Family: gaussian
Link function: identity

Parametric Terms:
df F p-value
CV 21 11.14 <2e-16

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 2 2 0.934 0.396</td></tr>
<tr><td>Linear model Striga density v density of nearest neighboring field</td><td>LM9</td><td>AD_1$nCat <- as.factor(round(AD_1$N_dens))

nsummary <- AD_1 %>% group_by(nCat) %>%
summarise(avDens = mean(AvDen), se = stderr(AvDen))

lm3 <- lm(log(AvDen + 1) ~ N_dens, data = AD_1)
anova(lm3)</td><td>Analysis of Variance Table

Response: log(AvDen + 1)
Df Sum Sq Mean Sq F value Pr(>F)
N_dens 1 1.679 1.67911 9.0152 0.002958 **
Residuals 242 45.073 0.18625

Call:
lm(formula = log(AvDen + 1) ~ N_dens, data = AD_1)

Residuals:
Min 1Q Median 3Q Max
-0.75064 -0.34077 -0.01308 0.25523 1.10064

Coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.44773 0.04573 9.792 < 2e-16 ***
N_dens 0.11725 0.03905 3.003 0.00296 **

Residual standard error: 0.4316 on 242 degrees of freedom
Multiple R-squared: 0.03592, Adjusted R-squared: 0.03193
F-statistic: 9.015 on 1 and 242 DF, p-value: 0.002958</td></tr>
<tr><td>GAM Striga density v density of nearest neighboring field</td><td>GAM9</td><td>gam3 <- gam(log(AvDen + 1) ~ N_dens + s(Lat, Lon), data = AD_1)
anova(gam3)</td><td>Family: gaussian
Link function: identity

Parametric Terms:
df F p-value
N_dens 1 10.91 0.0011

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 4.608 6.045 1.311 0.253</td></tr>
<tr><td>Linear model Striga density v pH and NO3</td><td>Lm10</td><td>nutrData$FN <- as.factor(nutrData$FN)
model <- lmer(Den ~ pH + NO3 + (1|FN), data = nutrData)
summary(model)</td><td>Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: Den ~ pH + NO3 + (1 | FN)
Data: nutrData

REML criterion at convergence: 389.7

Scaled residuals:
Min 1Q Median 3Q Max
-1.4520 -0.7703 -0.1183 0.7171 1.8717

Random effects:
Groups Name Variance Std.Dev.
FN (Intercept) 0.3169 0.5629
Residual 2.1968 1.4822</td></tr>
</table>

<table>
<tr><td></td><td></td><td></td><td>Number of obs: 102, groups: FN, 55

Fixed effects:
Estimate Std. Error df t
value Pr(>|t|)
(Intercept) 0.944720 1.943948 90.538263
0.486 0.628
pH 0.277479 0.386763 92.589360
0.717 0.475
NO3 -0.007826 0.007011 89.327229
-1.116 0.267

Correlation of Fixed Effects:
(Intr) pH
pH -0.983
NO3 0.094 -0.258</td></tr>
<tr><td>GAM Striga density v pH and NO3</td><td>GAM10</td><td>model2 <- gam(Den + 1 ~ pH + NO3 + s(latitude, longitude) + s(FN, bs = "re"), family = "ocat(R = 6)", data = nutrData)
anova(model2)</td><td>Family: Ordered Categorical(-1,0.08,0.76,1.89,3.53)
Link function: identity

Formula:
Den + 1 ~ pH + NO3 + s(latitude, longitude) + s(FN, bs = "re")

Parametric Terms:
df Chi.sq p-value
pH 1 0.754 0.385
NO3 1 0.479 0.489

Approximate significance of smooth terms:
edf Ref.df Chi.sq
p-value
s(latitude,longitude) 5.290 6.769 7.519
0.337
s(FN) 7.050 54.000 8.568
0.110</td></tr>
<tr><td>Linear model Striga density v companion crop</td><td>Lm11</td><td>options(contrasts = c("contr.sum","contr.poly"))
lm11 <- lm(log(AvDen + 1) ~ CC, data = AD_1)
anova(lm11)
summary(lm11)</td><td>Analysis of Variance Table

Response: log(AvDen + 1)
Df Sum Sq Mean Sq F value Pr(>F)
CC 18 2.0619 0.11455 0.6131 0.8829
Residuals 111 20.7395 0.18684</td></tr>
<tr><td>GAM Striga density v companion crop</td><td></td><td>options(contrasts = c("contr.sum","contr.poly"))
gam11 <- gam(log(AvDen + 1) ~ CC -1 + s(Lat, Lon), data = AD_1)
anova(gam11)
summary(gam11)</td><td>Family: gaussian
Link function: identity

Formula:
log(AvDen + 1) ~ CC - 1 + s(Lat, Lon)

Parametric Terms:
df F p-value
CC 19 11.61 <2e-16

Approximate significance of smooth terms:
edf Ref.df F p-value
s(Lat,Lon) 4.071 5.331 0.88 0.493
> summary(gam11)

Family: gaussian
Link function: identity

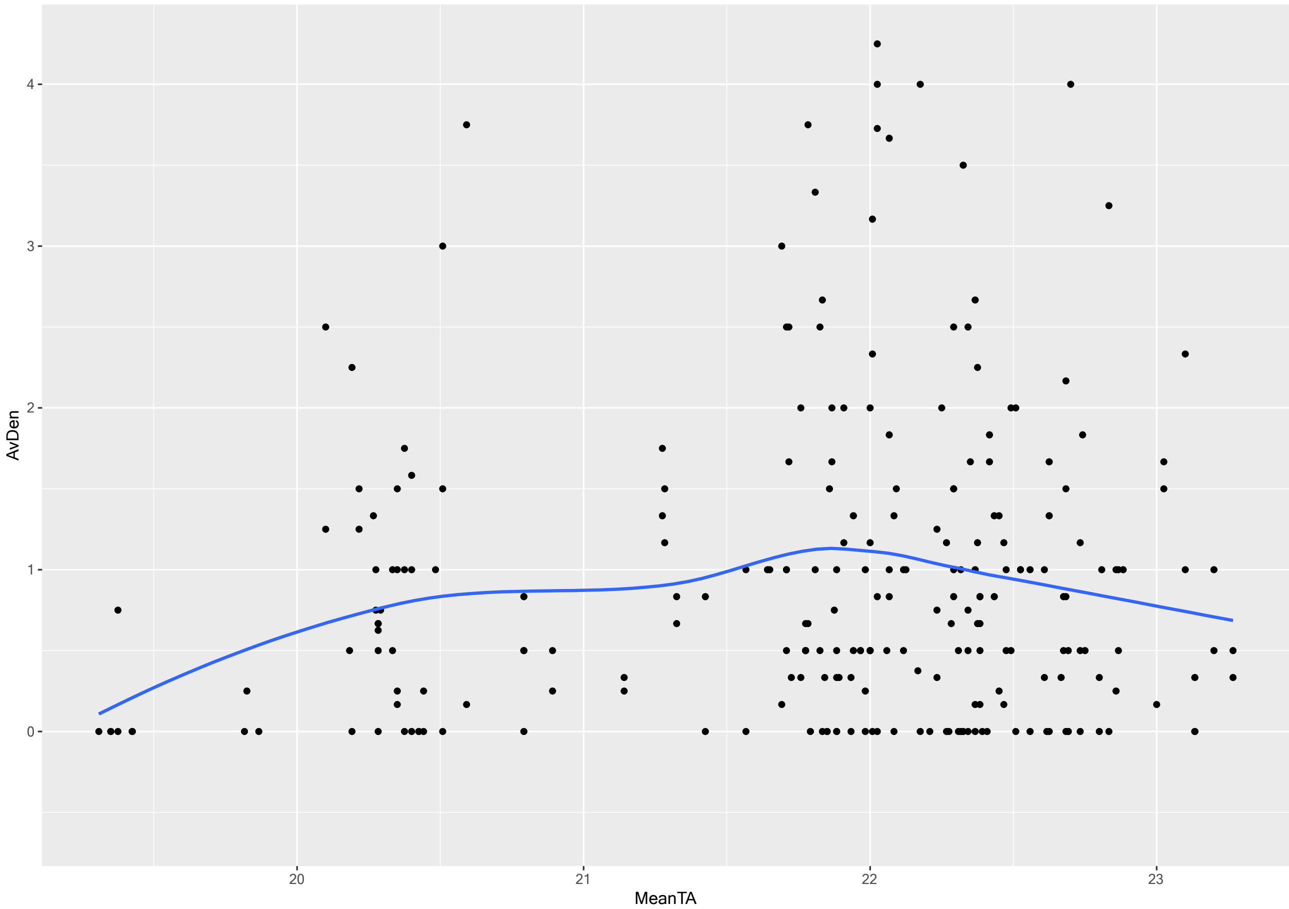
Formula:
log(AvDen + 1) ~ CC - 1 + s(Lat, Lon)

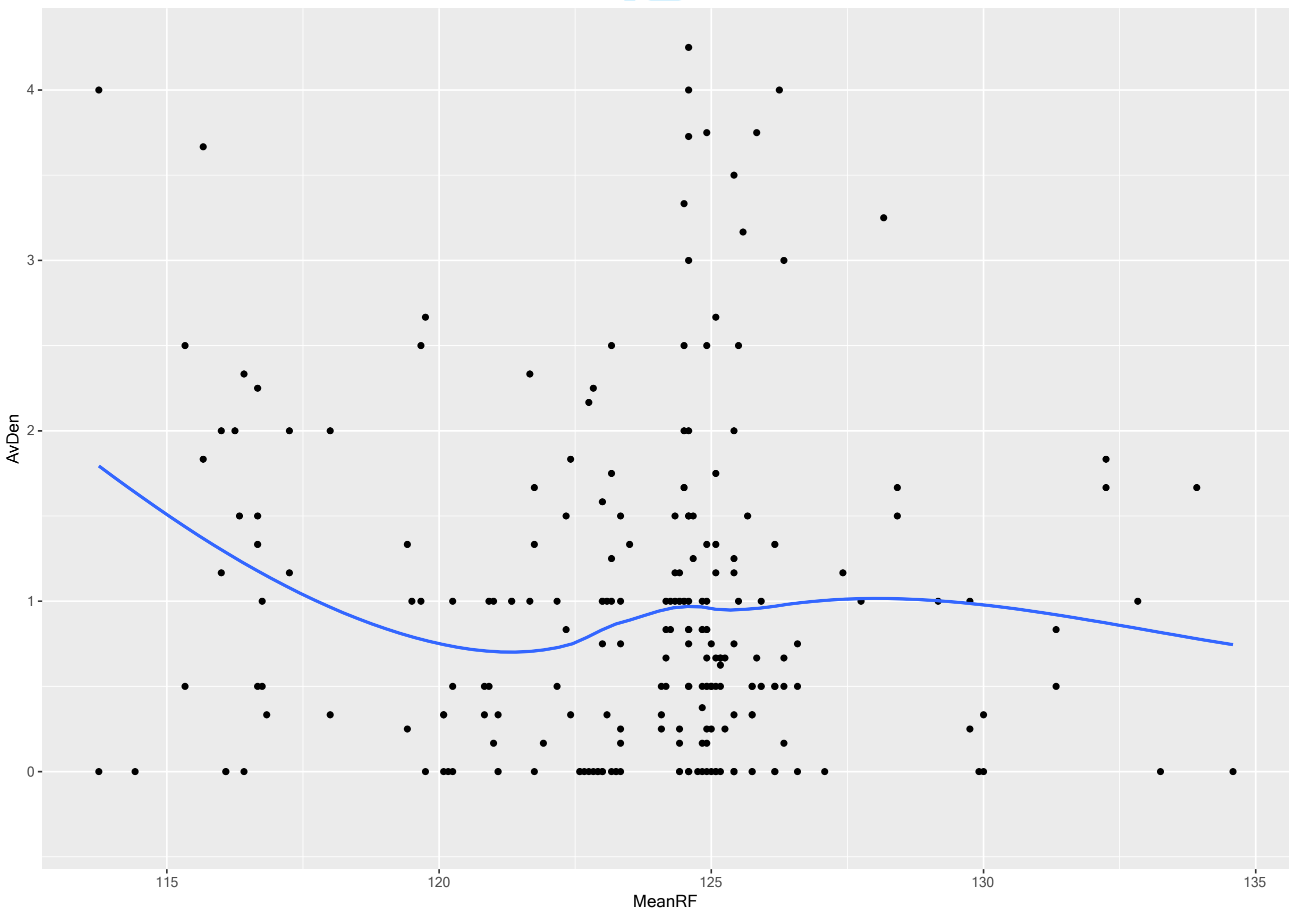
Parametric coefficients:
Estimate Std.
Error t value Pr(>|t|)
CCBalahazo 0.54030
0.11161 4.841 4.37e-06
CCBalahazo, mimosa 0.85393
0.43824 1.949 0.053974
CCBalahazo, soya 0.39466
0.30604 1.290 0.199990
CCBalahazo, voanjobory 1.23788
0.43203 2.865 0.005017
CCBalahazo, voanjolava 0.66420
0.19364 3.430 0.000859
CCMaize 0.51256
0.05292 9.686 2.64e-16</td></tr>
</table>

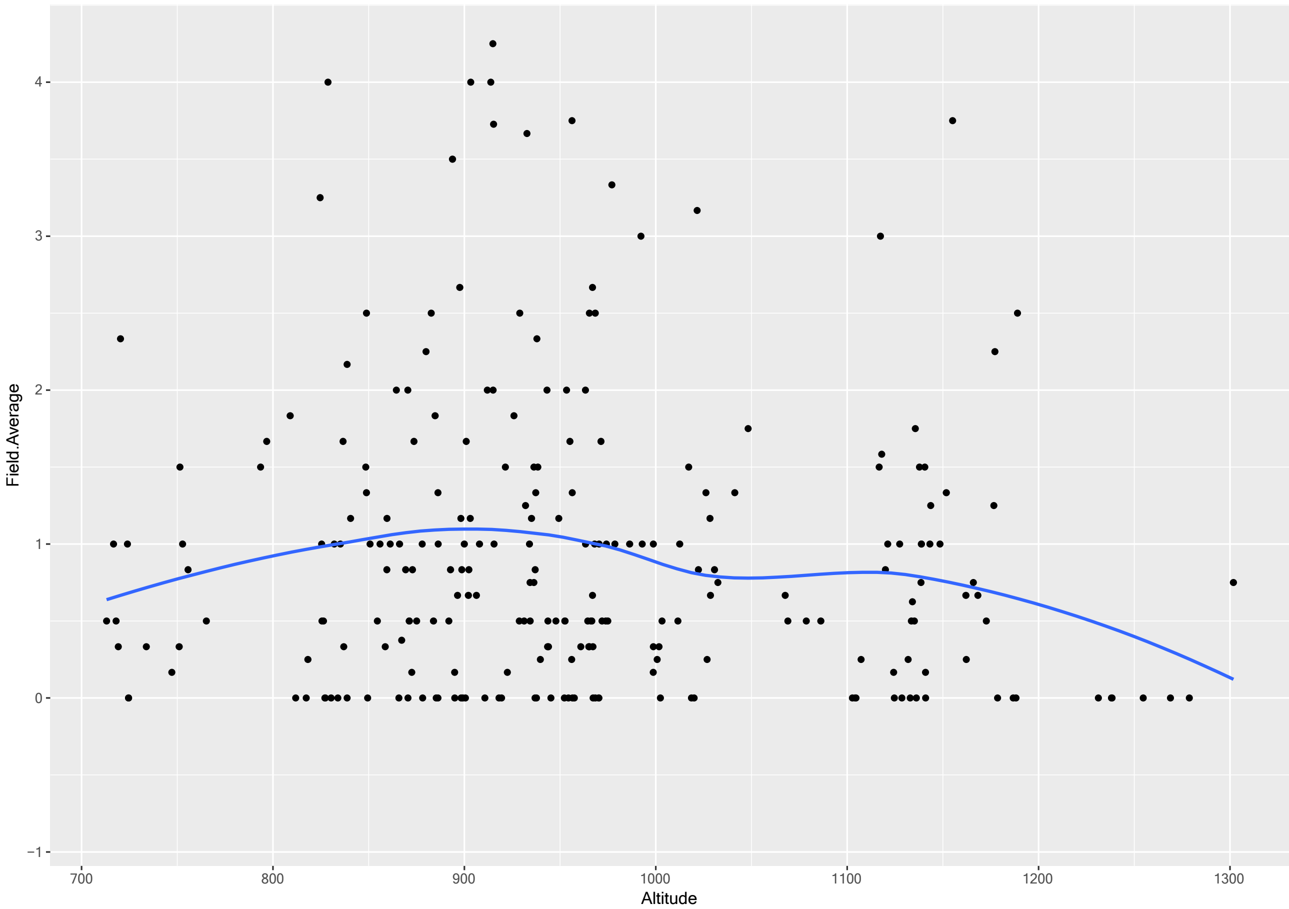
			CCMaize, balahazo 0.47971 0.30405 1.578 0.117581 CCMimosa 0.54219 0.14264 3.801 0.000240 CCNiebe 0.04795 0.42896 0.112 0.911211 CCSoya 0.48501 0.16442 2.950 0.003906 CCSoya, voanjobory, balahazo -0.04726 0.43993 -0.107 0.914659 CCStylosanthes 0.65162 0.30707 2.122 0.036140 CCTsaramaso 1.41963 0.43421 3.269 0.001450 CCTsy asisa 0.80957 0.43116 1.878 0.063153 CCVoanjobory 0.51947 0.17553 2.959 0.003795 CCVoanjolava 0.57283 0.20209 2.834 0.005489 CCVoanjolava, balahazo 0.50922 0.43426 1.173 0.243563 CCVoanzobory 0.53340 0.42897 1.243 0.216417 CCVoatavo, voanjobory 0.78297 0.30956 2.529 0.012887 CCBalahazo *** CCBalahazo, mimosa . CCBalahazo, soya CCBalahazo, voanjobory ** CCBalahazo, voanjolava *** CCMaize *** CCMaize, balahazo CCMimosa *** CCNiebe CCSoya ** CCSoya, voanjobory, balahazo CCStylosanthes * CCTsaramaso ** CCTsy asisa . CCVoanjobory ** CCVoanjolava ** CCVoanjolava, balahazo CCVoanzobory CCVoatavo, voanjobory * --- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 Approximate significance of smooth terms: edf Ref.df F p-value s(Lat,Lon) 4.071 5.331 0.88 0.493 R-sq.(adj) = -0.0257 Deviance explained = 68% GCV = 0.22042 Scale est. = 0.1813 n = 130
Pearson's chi-squared test for independence for Main crop v companion crop	$X^2$1	chisq.test(AD_1R_M_O,AD_1CC)	Pearson's Chi-squared test data: AD_1$R_M_O and AD_1$CC X-squared = 137.08, df = 19, p-value < 2.2e-16
Pearson's chi-squared test for independence for Main crop v previous crop	$X^2$2	chisq.test(AD_1R_M_O,AD_1PC)	Pearson's Chi-squared test data: AD_1$R_M_O and AD_1$PC X-squared = 34.394, df = 18, p-value = 0.01126
Cramer's V test to test for the strength of any observed associations	C1	CramerV(AD_1R_M_O,AD_1PC)	0.7770854

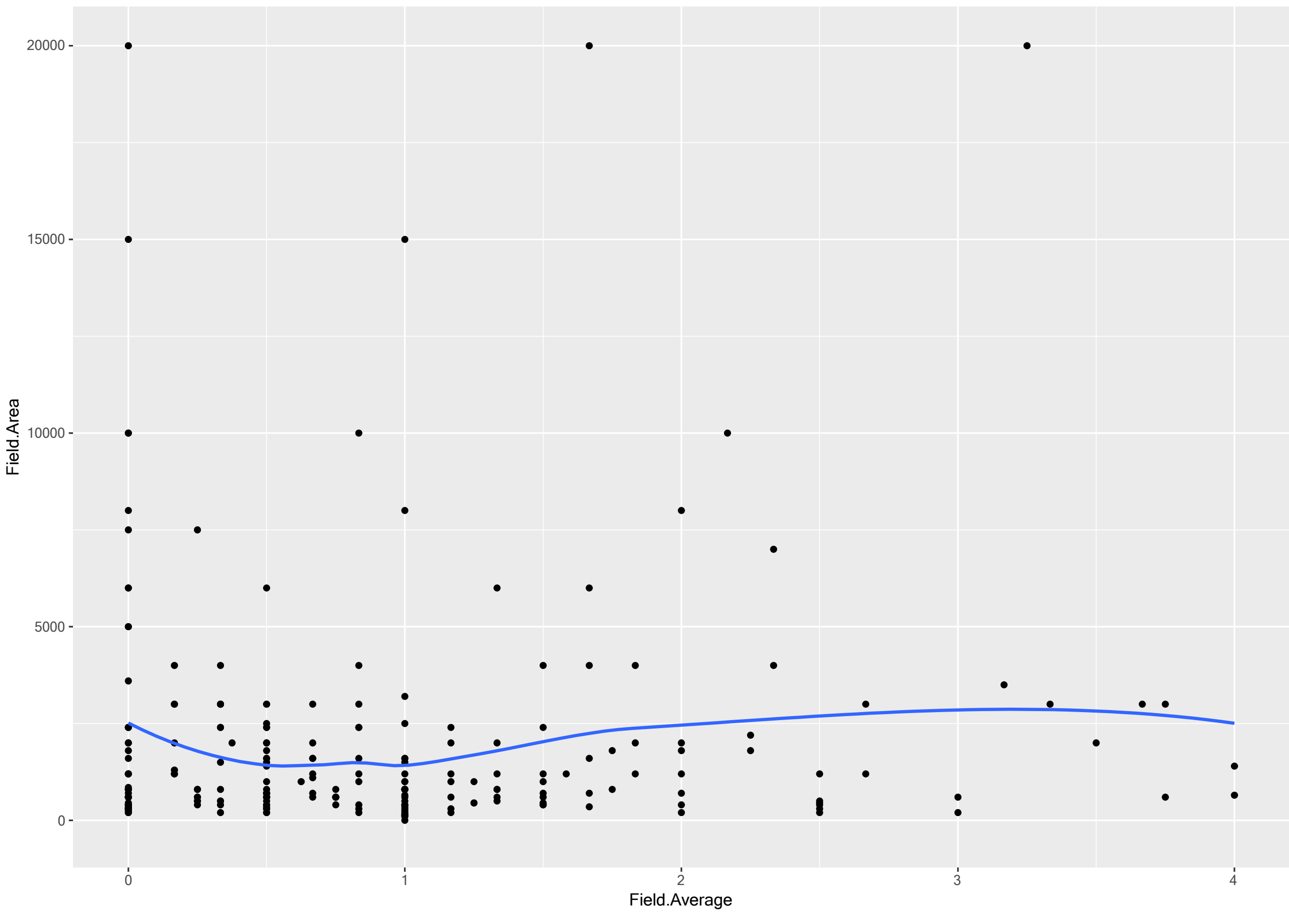
from X^2 1test.			
Cramer's V test to test for the strength of any observed associations from X^2 2test.	C2	CramerV(AD_1R_M_O,AD_1CC)	0.4433248

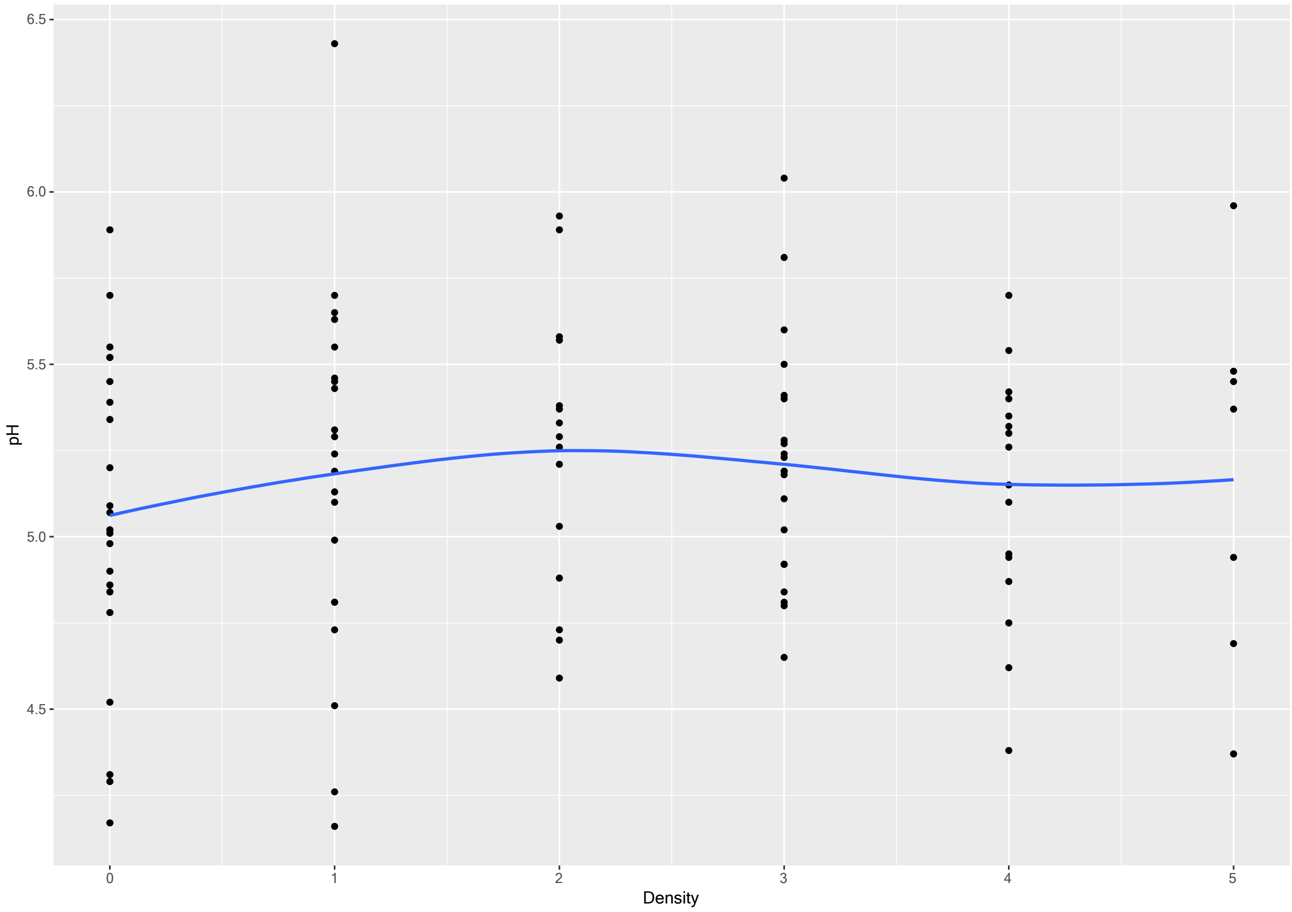
Appendix 2: Scatterplots and boxplots for models

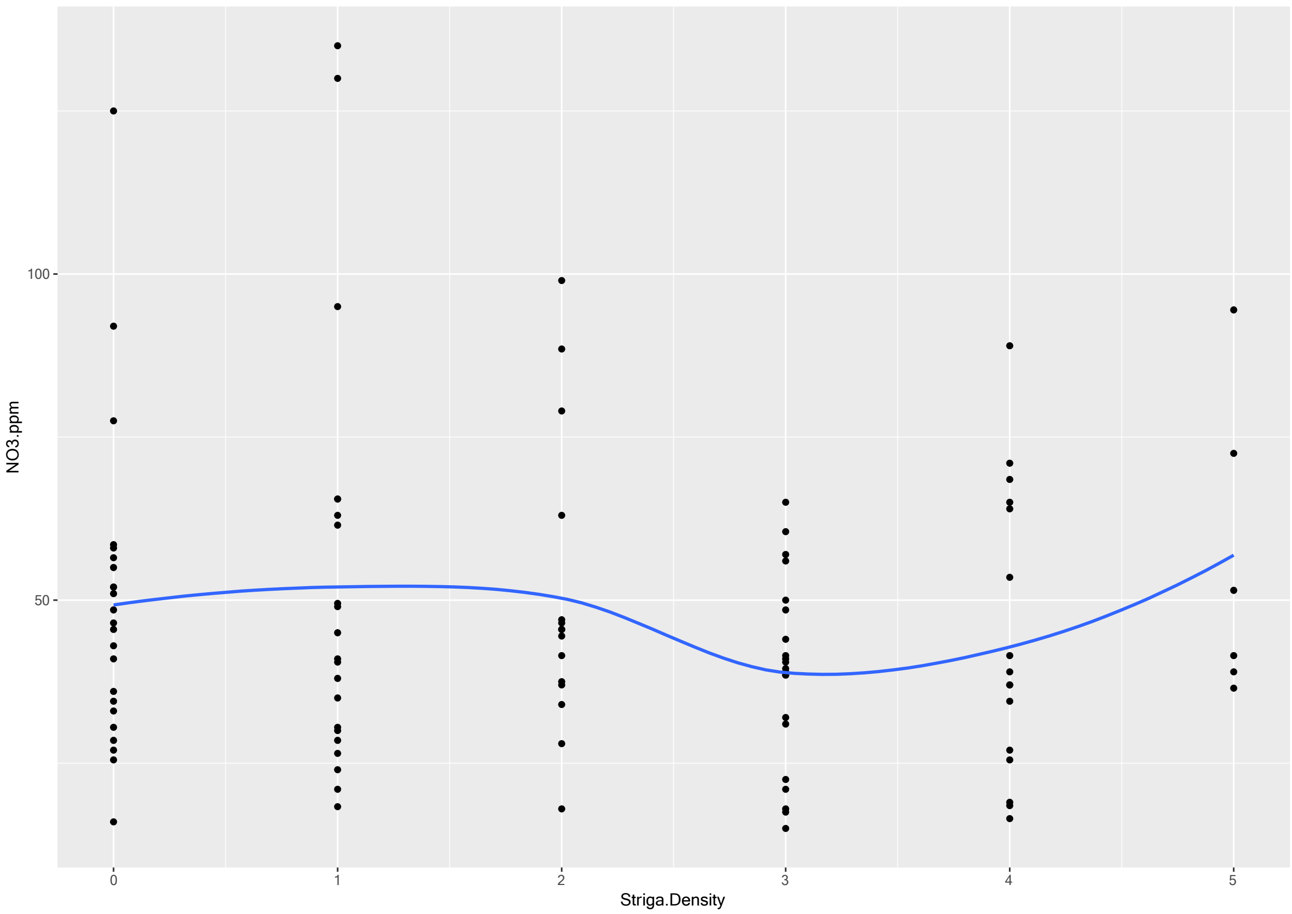


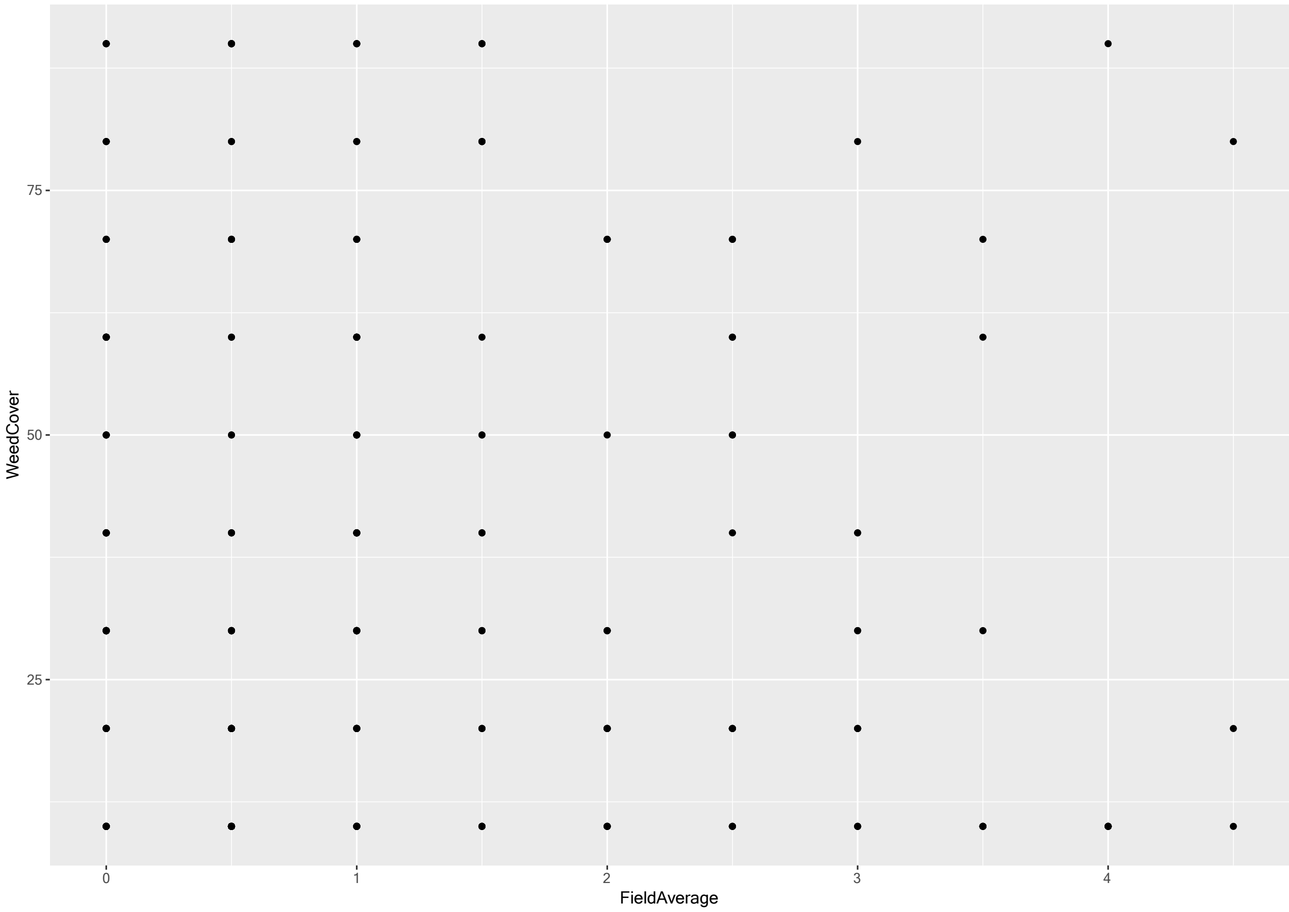


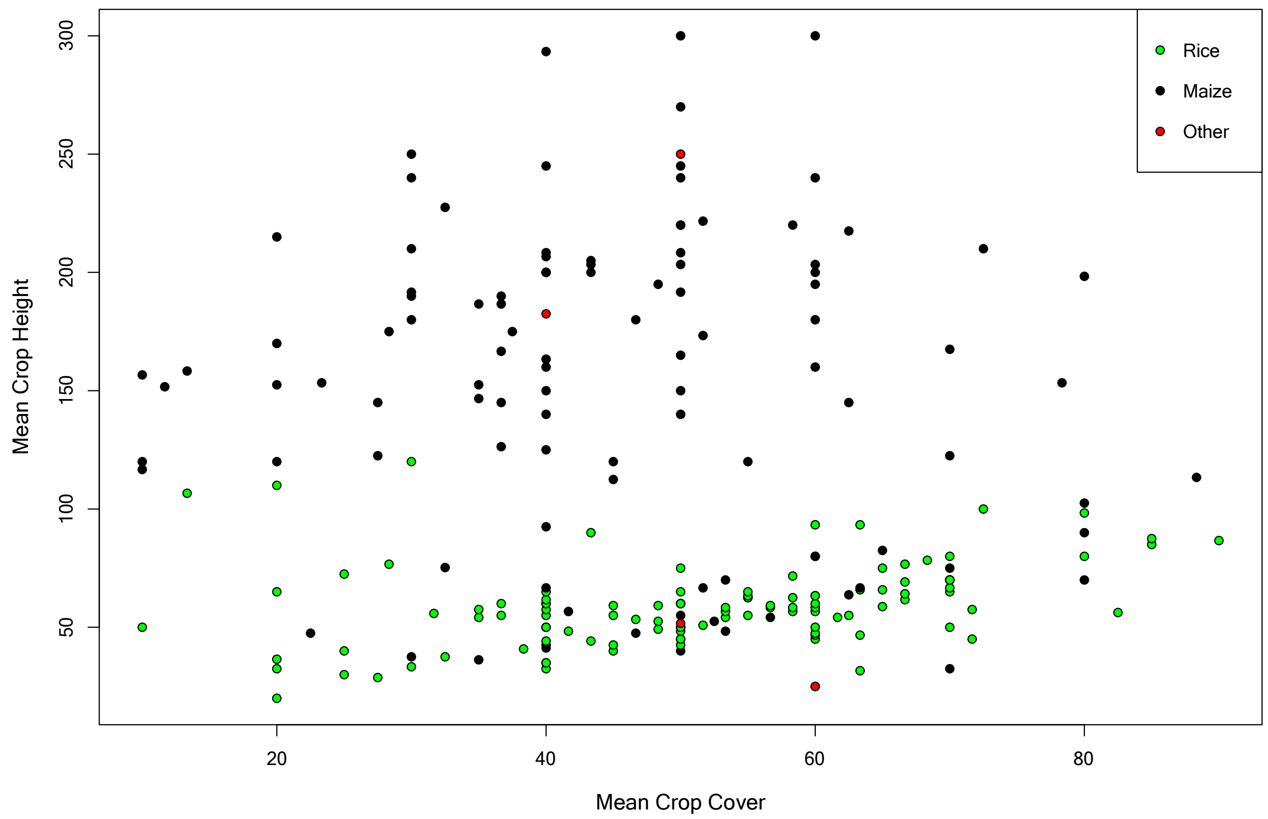

Field.Average
Altitude
4
3
2
1
0
−1
700
800
900
1000
1100
1200
1300

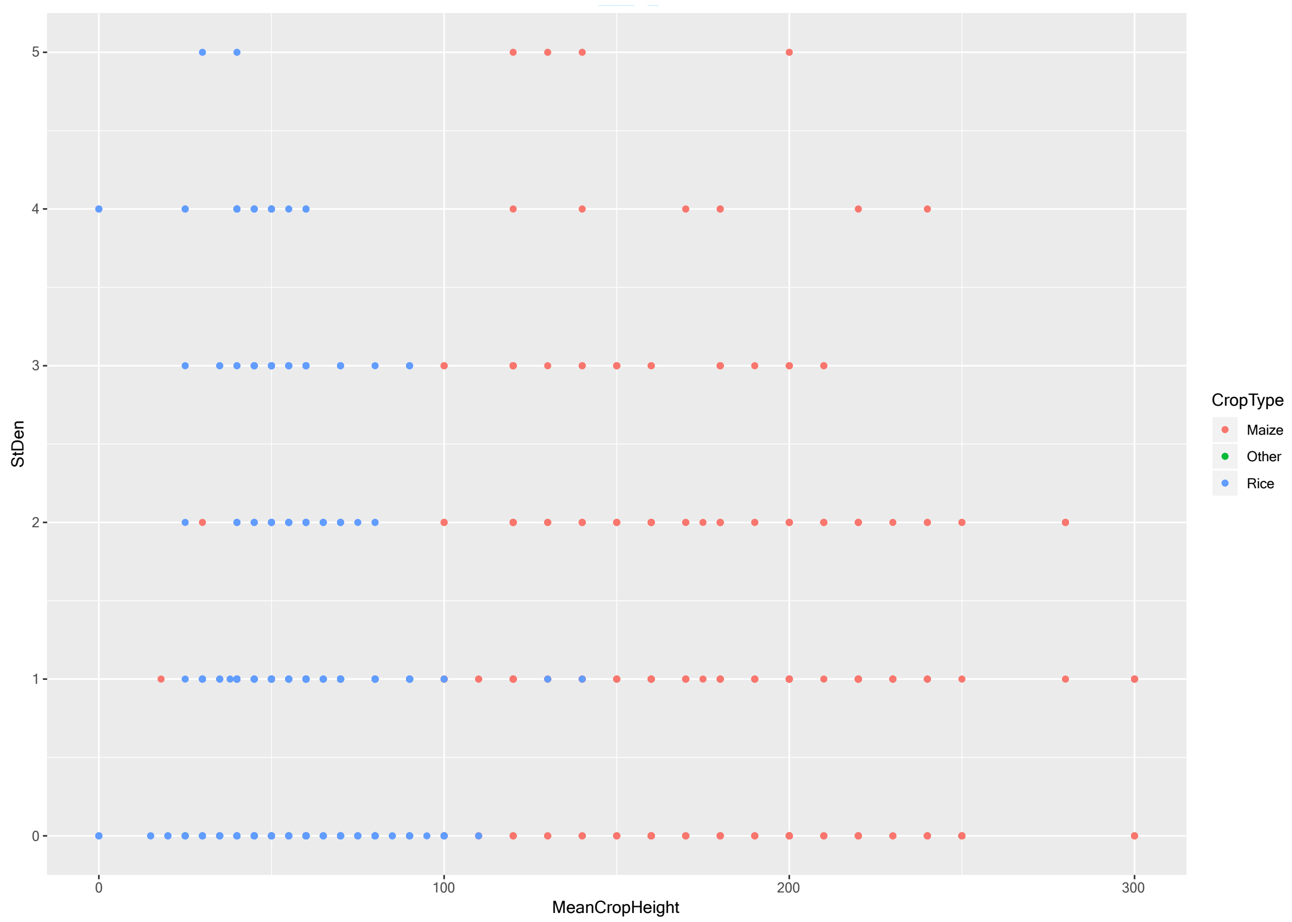

Field.Area
Field.Average
20000
15000
10000
5000
0
0
1
2
3
4


6.5
6.0
5.5
5.0
4.5
pH
0
1
2
3
4
5
Density


100
50
NO3.ppm
0
1
2
3
4
5
Striga.Density


WeedCover
75
50
25
0
1
2
3
4
FieldAverage


Mean Crop Height
Mean Crop Cover
Rice
Maize
Other
50
100
150
200
250
300
20
40
60
80


StDen
MeanCropHeight
CropType
Maize
Other
Rice
0
1
2
3
4
5
0
100
200
300

Appendix 3: Soil sample (pH and NO3) pairs collected within fields containing differing *Striga* densities.

***Striga* density Pair**	**Count**
1:0	5
1:2	3
1:3	11
1:4	2
1:5	0
2:0	3
2:3	3
2:4	4
2:5	2
3:0	3
3:4	3
3:5	1
4:0	3
4:5	4
5:0	0
Zero density (single samples)	10
Total	**104**

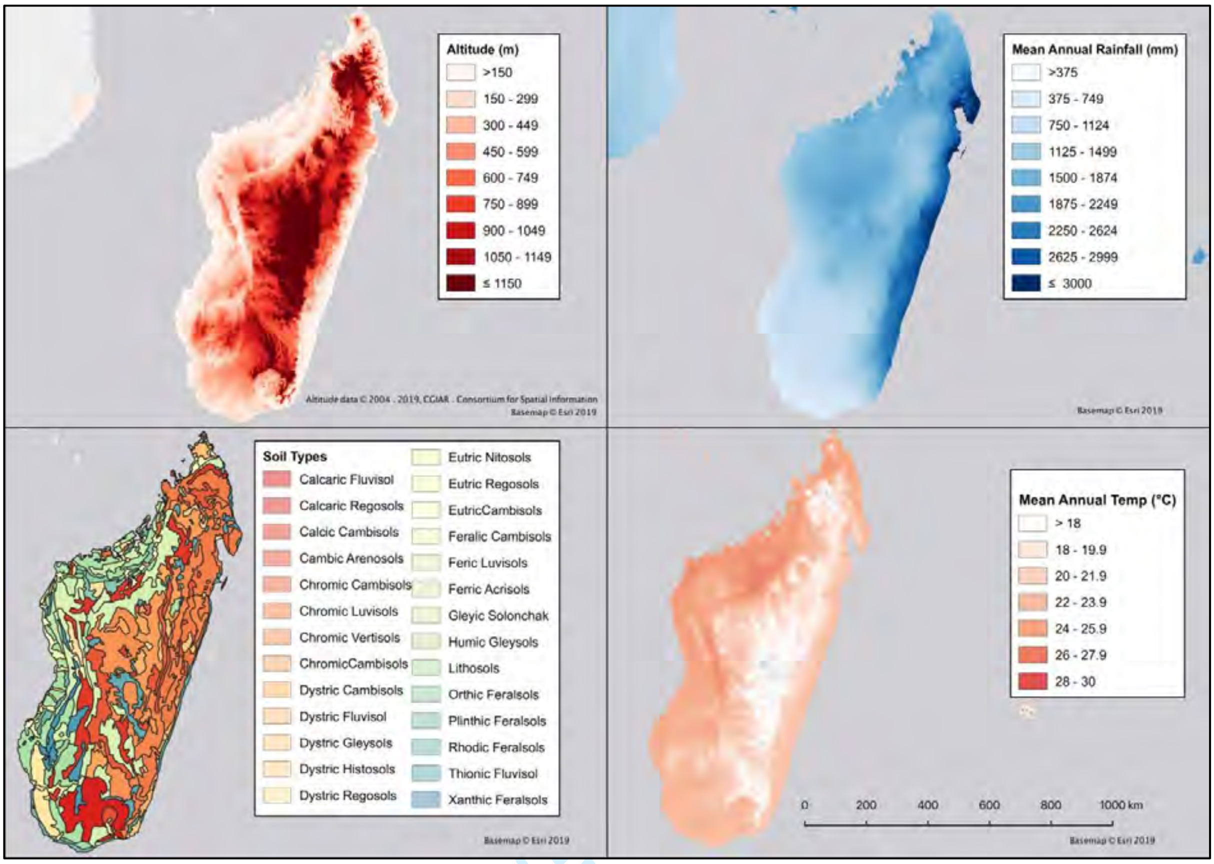


Fig. 1. Altitude (CGIAR-CSI 2019), mean annual rainfall (Fick and Hijmans, 2017), soil types (FAO 2007) and mean annual temperature (Fick and Hijmans, 2017), for Madagascar.

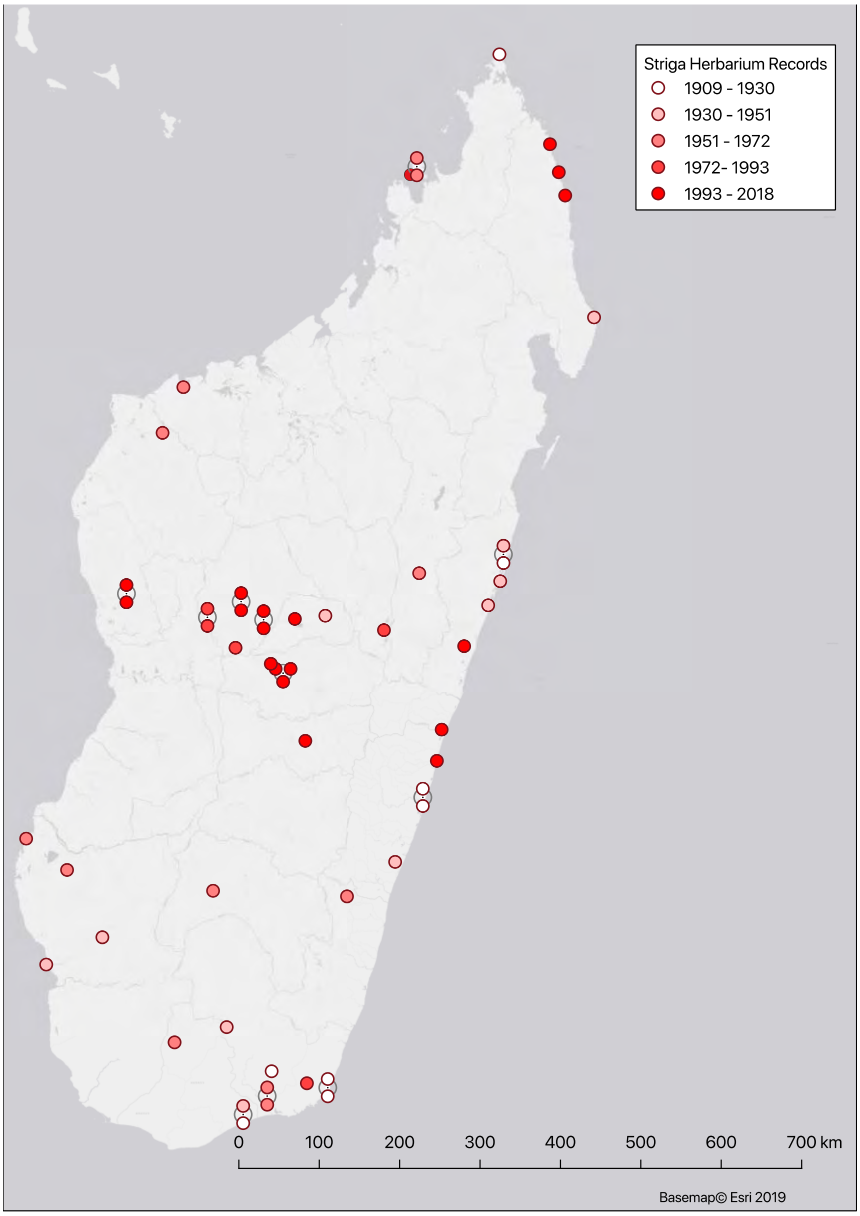


Fig. 2. Herbarium records for *Striga asiatica*. Data from Rodenburg et al (2016).

Fig. 3. Location of transects T1 and T2, located within Vakinakaritra, Itasy and Bongolava provinces in the mid-west of Madagascar.

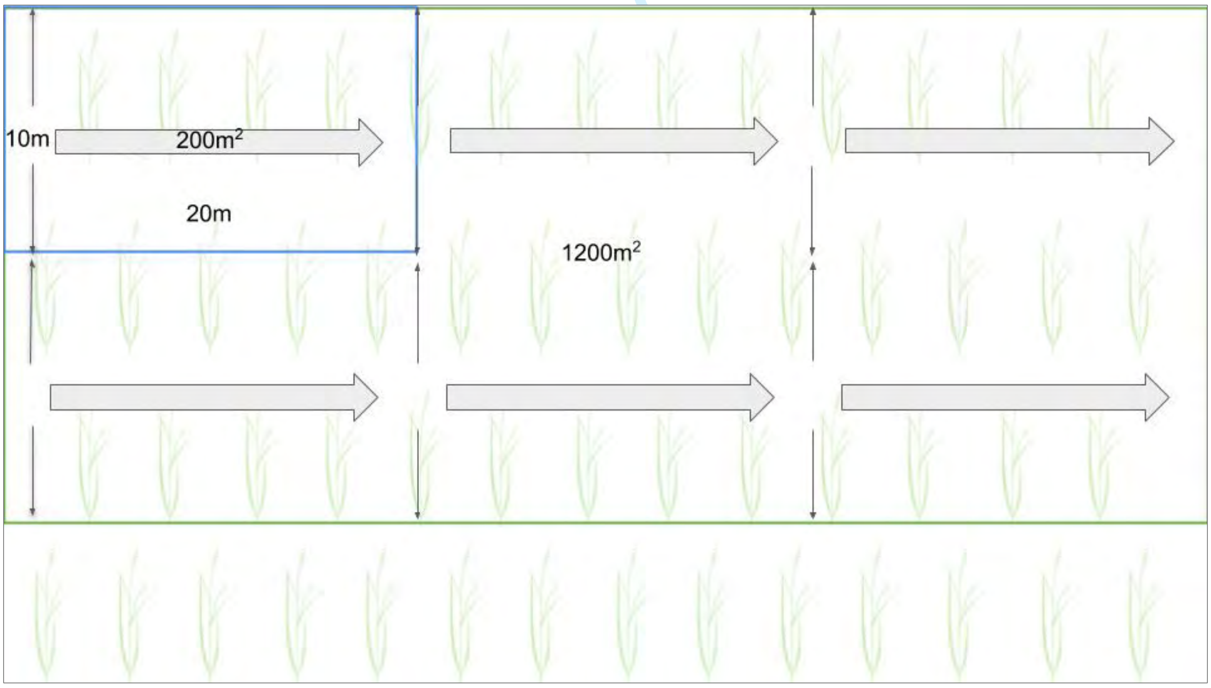


Fig. 4. Illustration of field walking process for two observers, with subdivisions of field into sections for estimation of Striga density.

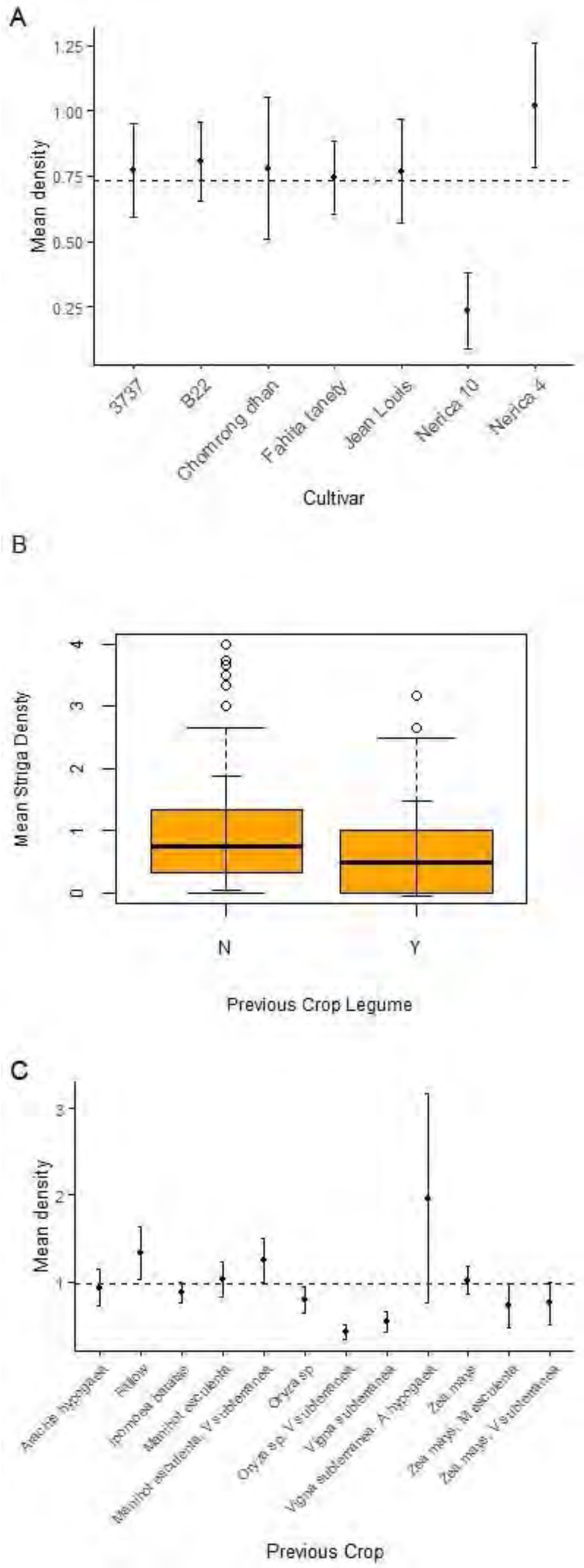


Fig. 5., A: Mean *Striga* density for principle rice varieties with standard errors and grand mean (dashed line), (3737 n=4, B22 n=28, Chomrong dhan n=11, Fahita tanety n=27, Jean Louis n=25, NERICA-10 n=8, NERICA- 4 n=28), B: Mean *Striga* density for previous crop type with standard errors (legume n=65 / non-legume n=120) & C: Mean *Striga* density for previous crop / crop varieties recorded with standard errors and grand mean (dashed line), (*Arachis hypogaea* n=18, Fallow n=14, *Ipomoea batatas* n=4, *Manihot esculenta* n=25, *Manihot*

esculenta, *V subterranea* n=2, *Oryza sp* n=34, *Oryza sp*, *V subterranea* n=2, *Vigna subterranea* n=35, Vigna *subterranea, A hypogaea* n=2, *Zea mays* n=34, *Zea mays, M esculenta* n=7) . Analyses indicated significant effects of rice variety, if the previous crop was leguminous and previous crop / crop combination.

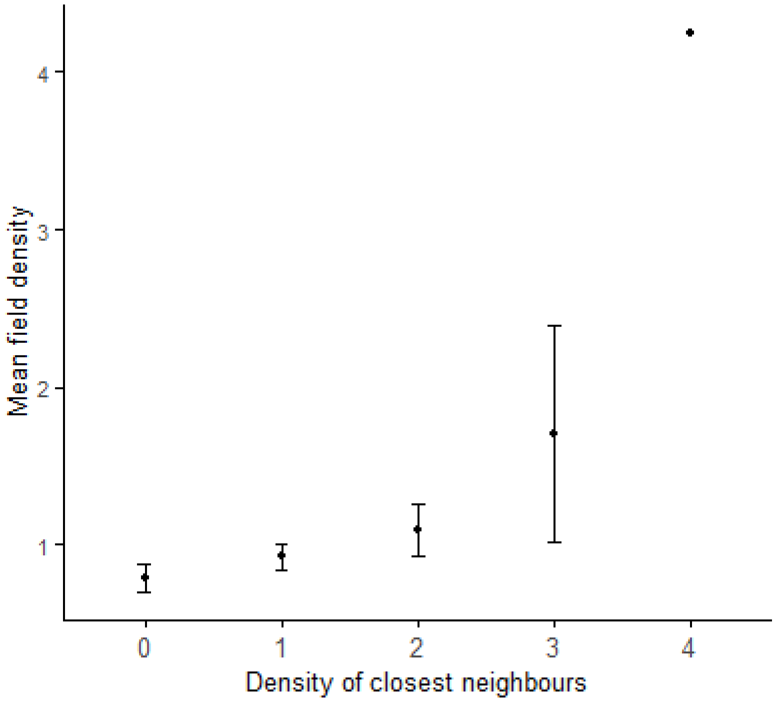


Fig.6. Mean *Striga* density and density of closest neighbouring fields. The effect of density in neighbouring fields on within-field mean *Striga* density was significant for both the linear model and GAM.