Mapping the drivers of parasitic weed abundance at a national scale: a new approach applied to *Striga asiatica* in the mid-west of Madagascar

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**Abstract**

The parasitic weed genus *Striga* causes huge losses to crop production in sub-Saharan Africa, estimated to be 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 *S. 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**

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

1 | 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 caused by *Striga hermonthica* (Del.) Benth and *Striga asiatica* (L) Kuntze (Mohamed et al., 2001). This is due to the significant economic losses caused by these two species to a staple cereal crops grown in SSA (Runo and Kuria, 2018). The *Striga* problem is recognised as an increasingly serious limiting factor on crop production in SSA, primarily affecting rural smallholder farmers (Cairns et al., 2012; Parker, 2012). Reductions in fallow periods and increased monocropping deplete soil organic matter and nitrogen and increase soil erosion, creating conditions favourable for the proliferation of *Striga* (Franke et al., 2006; Parker, 2012).

*Striga* has resulted in reported yield losses of rice between 35% and 80% (Rodenburg et al., 2016), losses of sorghum between 50% and 100% (Abunyewa and Padi, 2003) and losses of maize between 21% and 74% (De Groote, 2007). Estimates of economic losses from *Striga* range between $111 and $300 million per year for rice (Rodenburg et al., 2016) and $383 for maize (Woomer and Savala, 2008). Estimates of areas affected vary between 50 and 100 million ha annually (FAO, http://www.fao.org/). 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 of *Striga* (Scholes and Press, 2008; Hearne, 2009). Ongoing research is being conducted on resistance in rice, and *Striga* management factors. This is due to the significant economic losses caused by these two species to a staple cereal crops grown in SSA, primarily affecting rural smallholder farmers (Cairns et al., 2012; Parker, 2012). Reductions in fallow periods and increased monocropping deplete soil organic matter and nitrogen and increase soil erosion, creating conditions favourable for the proliferation of *Striga* (Franke et al., 2006; Parker, 2012).

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The majority of weed population studies have been conducted on single sites using small (≤1 m²) 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; Tredennick 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 data sets 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 data at the appropriate scale, collection methods to enable such analyses, density-structured techniques, have been developed (Queenborough et al., 2011; Freckleton et al., 2011). 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 (a) develop a rapid and repeatable methodology that would permit the mapping of this weed at a national scale; (b) test the role of management (crop and cropping history) in driving increases in abundance; and (c) analyse the impact of variation in soil nutrients in explaining differences in the distribution of *Striga*.

2 | MATERIALS AND METHODS

Surveys were undertaken by employing a methodology originally developed for the survey of the weed *Alopecurus myosuroides* in the UK (Freckleton et al., 2018b, manuscript in preparation). The method permitted the rapid and accurate assessment of black grass densities at a landscape scale, and robust statistical analyses to identify drivers of abundance. This methodology was modified to take account of morphological differences in detectability between *A. myosuroides* and *Striga* and associated detectability.

2.1 | 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 km² with an elevation between 700 m and 1,000 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 1,100 to 1,900 mm with a mean temperature of 22°C.

2.1.1 | 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 3 km east of Sakay and the outskirts of Tsirano...
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.

### 2.1.2 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 pairs of 10 × 20-m quadrats, in which two observers simultaneously recorded Striga density, by walking at a steady pace along a central transect, and scanning 5 m to either side; in fields >1,200 m², data were recorded from a maximum of three pairs of quadrats (Figure 4). A field corner was randomly selected as the point to begin survey, and Striga density was estimated 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

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**FIGURE 2** Herbarium records for *Striga asiatica* (Rodenburg et al., 2016) [Colour figure can be viewed at wileyonlinelibrary.com]
on fertiliser addition and any other pertinent information on the
general area were recorded (where available). Mean density score,
average crop height and cover, and other weed cover for a quadrat
were called and entered on the mobile app prior to moving to a sub-
sequent quadrat. If no Striga was found in a quadrat, a thorough walk
throughout the entire field was undertaken to verify that Striga was
truly absent.

Where scores varied in excess of one density point between sur-
veyors, 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

![Figure 3: Location of transects T1 and T2 in Vakinakaritra, Itasy and
Bongolava provinces of mid-west of Madagascar (Colour figure can
be viewed at wileyonlinelibrary.com)](image)

![Figure 4: Illustration of Striga density estimation, where two observers simultaneously
surveyed 10 × 20-m quadrats in a field; there was a maximum of three pairs of
quadrats in fields >1,200 m² (Colour figure can be viewed at wileyonlinelibrary.com)](image)
surveyor. As a 10 × 10 m quadrat per surveyor would have negatively affected the speed of repeatability, quadrat dimensions of 200 m² (10 × 20 m) 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.

2.1.3 | Soil samples

The role of available nitrogen in determining S. asiatica densities was addressed through collecting and analysing soil samples for NO₃. 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 S3). 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.

NO₃ analysis was undertaken using a LAQUAtwin NO₃-11 nitrate meter (Horiba Scientific). Owing to low levels of NO₃ within the soil, it was necessary to dilute the standard solution supplied with the meter. Therefore, calibration was undertaken between 15 and 150 ppm NO₃ 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. 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). For each sample, 20 g of soil was mixed with 50 ml of soil preparation solution for 30 s. After 5 min, the soil pH was measured using the meter.

2.2 | 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 climatic and edaphic factors (mean annual temperature, mean annual rainfall, altitude, pH and NO₃) 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 et al., 2015), mgcv (Wood, 2011), lme4 (v0.67-101, Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), MASS (Venables and Ripley, 2002), DescTools (v 0.99.28, Signorelli et al., 2019) and psych (Revelle, 2018, v1.8.12). The full reproducible code is available in Appendix S1.

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 moderately high degrees of collinearity among independent variables (Freckleton, 2011) and violation of normality assumptions for distribution of residuals (Fitzmaurice et al., 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 whether 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 S1). 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 climatic and edaphic factors indicated strong correlation between altitude and mean temperature \((f = 1.860, df = 2, 239, R^2 = 0.93, p < 2.2e−16, VIF: 16.56)\). Potential correlation between mean rainfall and altitude and mean temperature was less evident \((f = 3.40, df = 2, 239, R^2 = 0.03, p = .04, VIF = 1.03)\). However, this interaction was anticipated and is commonplace among analyses using climatic and edaphic data and was therefore not considered a constraint to the analysis undertaken. Smoothed lines fitted to scatterplots for (pH, NO₃, 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 S2).
RESULTS

3.1 | Management factors

Analysis of management data suggests that rice variety had a significant effect on Striga density (linear model $F = 1.72$, $df = 20$, $102$, $p = .04$, GAM $F = 11.14$, $df = 21$, $p < 2e^{-16}$), 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 Figure 5a). A Welch two-sample $t$ test for mean Striga density and previous crop legume (yes/no, Figure 5b) indicated significant differences of means ($t = 2.05$, $df = 141.08$, $p = .02$). The $t$ test for B22 and NERICA-4 did not indicate significant differences of means ($\mu$: B22 = 0.85, NERICA-4 = 1.15, $t = 2.05$, $df = 141.08$, $p = .02$) 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 (Figure 5c) was not significant for a linear model ($F = 1.08$, $df = 25$, $159$, $p = .369$) 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 ($F = 9.015$ $df = 1$, $242$, $p = .01$ and GAM ($F = 10.91$, $df = 1$, $p = .01$). This suggests that spatial factors could be important in determining Striga distribution and spread (see Figure 6). No significant results were obtained from the analyses of mean Striga density used as an explanatory variable for mean crop height ($F = 0.83$, $df = 1$, $223$, $p = .36$) crop cover ($F = 2.329$ $df = 1$, $223$, $p = .13$) and other weed cover ($F = 0.08$ $df = 1$, $151$, $p = .77$).
3.2 | Climatic and edaphic factors

A linear model and GAM combining climatic and edaphic factors to predict Striga density (mean rainfall, mean temperature and altitude) did not produce significant results (linear model: $f = 1.39, df = 3, 238, p = .25$, $\text{GAM} f = 1.297, df = 14.38, p = .19$). A linear mixed model and GAM examining the effects of soil pH and NO$_3$ on Striga density did not produce significant results (linear model: $pH: t = 0.72, df = 92.58, p = .48$, NO$_2$: $t = -1.12, df = 89.33, p = .27$, $\text{GAM} pH: X^2 = 0.72, df = 1, p = .39$, NO$_3$: $X^2 = 0.48, df = 1, p = .49$).

Comparison of variables between transects indicated a high degree of homogeneity (see Table 1). Mean Striga density by transect was similar ($T1 = 0.89, \sigma = 0.93$ and $T2 = 1.01, 1.01 \sigma = 0.97$). Mean rainfall and temperature also showed little variation between transects. Ranges for NO3 were also very similar. Ranges for pH were greater for T1, consistent with a greater distance covered.

4 | DISCUSSION

This paper describes a systematic, landscape-scale agroecological study of the factors driving the occurrence and abundance of Striga. The methodology enabled the rapid collection of statistically robust distribution data to reveal 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.

Previous Striga distribution studies have used a number of other census methods including whole field plant counts (Dugje et al., 2006), plant counts from small quadrats (Kamara et al., 2014), questionnaires (Aflakpui et al., 2008) or preliminary species inventory (Gworgwor et al., 2001). Comparable field-level density estimate methods have been previously used (Kabiri et al., 2015), although these were undertaken on the scale of a few kilometres, without the use of statistical methods to identify ecological factors in determining Striga distribution. Where such statistical analysis has been used, the study employed the much more labour-intensive method of plant counts from multiple quadrats per field (Kamara et al., 2014).

4.1 | Cropping practices

| Transect | Mean Striga density | Mean temperature (°C) | Mean rainfall (mm) | pH range | NO-3 range (ppm) |
|----------|---------------------|-----------------------|-------------------|----------|-----------------|
| T1       | 0.89 ($\sigma = 0.93$) | 21.5                  | 124               | 4.16–6.43 | 15–135          |
| T2       | 1.01 ($\sigma = 0.97$) | 22.3                  | 122               | 4.51–5.81 | 18–130          |

TABLE 1 Mean Striga density (±SD), field area, temperature, rainfall and altitude range for the two transects
detailed above, therefore vary greatly according to 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.

4.2 | 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 et al., 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.

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 Figure 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 Gardner, 2011).

4.3 | 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 and Swanton, 2001). Some previous studies have demonstrated a direct effect of numbers of emerged Striga plants on crop performance (Mumera and Below, 1993; Rodenburg et al., 2017). 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.

4.4 | Climatic and edaphic factors

Climatic and edaphic factors were not significantly correlated with Striga density. This was consistent with previous studies, as S. asiatica has been found to be unresponsive to temperature (Patterson, 1990; Rodenburg et al., 2011). Mean rainfall variation within the study area was low (min: 114 mm, max: 134 mm), which is well within the 50–150 mm range tolerated by Striga species (Mohamed et al., 2006). Similarly, the altitudes encompassed by the current study (713–1,301 m) were well within the cited range of occurrence for S. asiatica (0–2,400 m) (Agnew, 1974). In order to detect effects of climatic or edaphic factors on Striga density, it would be necessary to collect data across a wider section of the above-cited 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.

5 | CONCLUSIONS

The results of this study provide a number of important, wider implications for the study and management of economically important Striga species. 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. The methodology was successfully adapted from blackgrass, which is a morphologically and ecologically very different species. This demonstrates that the methodology 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.

The fact that 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. NERICA-4 has significantly lower resistance to Striga than NERICA-10 and other varieties and landraces. This observation 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. 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 support 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

The authors declare that there is no conflict of interest.

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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