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

Donald Scott[1] | **Julie D. Scholes**[1] | **Meva Tahiry Randrianjafizanaka**[2] | **Jean Augustin Randriamampianina**[3] | **Patrice Autfray**[4] | **Robert P. Freckleton**[1]

[1]Department of Animal & Plant Sciences, University of Sheffield, Sheffield, UK

[2]University of Antananarivo, Antananarivo, Madagascar

[3]FOFIFA, Antananarivo, Madagascar

[4]CIRAD, Paris, France

Correspondence

Donald Scott, Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.

Email: dscott7@sheffield.ac.uk

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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, specifically the NERICA (NEw RIce for Africa) group of varieties. Broad 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*. NERICA-9 and NERICA-4 reduced *S. asiatica* infection levels by 57% and 91%, respectively, compared with levels of infection on 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.

Upland rainfed rice in Madagascar is sown directly following tillage and is grown as a mono-crop or in a mixture with other food crops. Farmers generally do not have access to inorganic fertilisers or herbicides, and weeding is done manually. Therefore, *Striga* management options available to farmers are limited to cropping practices and use of suitable varieties.

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). Continuous monocropping without rotation has been shown to increase levels of infestation and build ups of *Striga* seed within the soil seedbank (Ejeta, 2007).

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 (De Groote, 2007; Rodenburg *et al*., 2016), 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. Figure 1 provides representations of the topography, climate and soil types of Madagascar. Very few studies of *Striga* have been undertaken in Madagascar (Elliot *et al*., 1993; Geiger *et al*., 1996). Herbaria records are also scant, with just one new record submitted since 2014 (see Figure 2).

The first introductions of *S. asiatica* to Madagascar occurred over a century ago (Figure 2), resulting in the spread and establishment of separate populations which exist today. Within infested areas, losses can vary between 20% and 100% (Joyeux, 2014) and 30 and 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, 1998).

The majority of weed population studies have been conducted on single sites using small (≤1 m^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; 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).

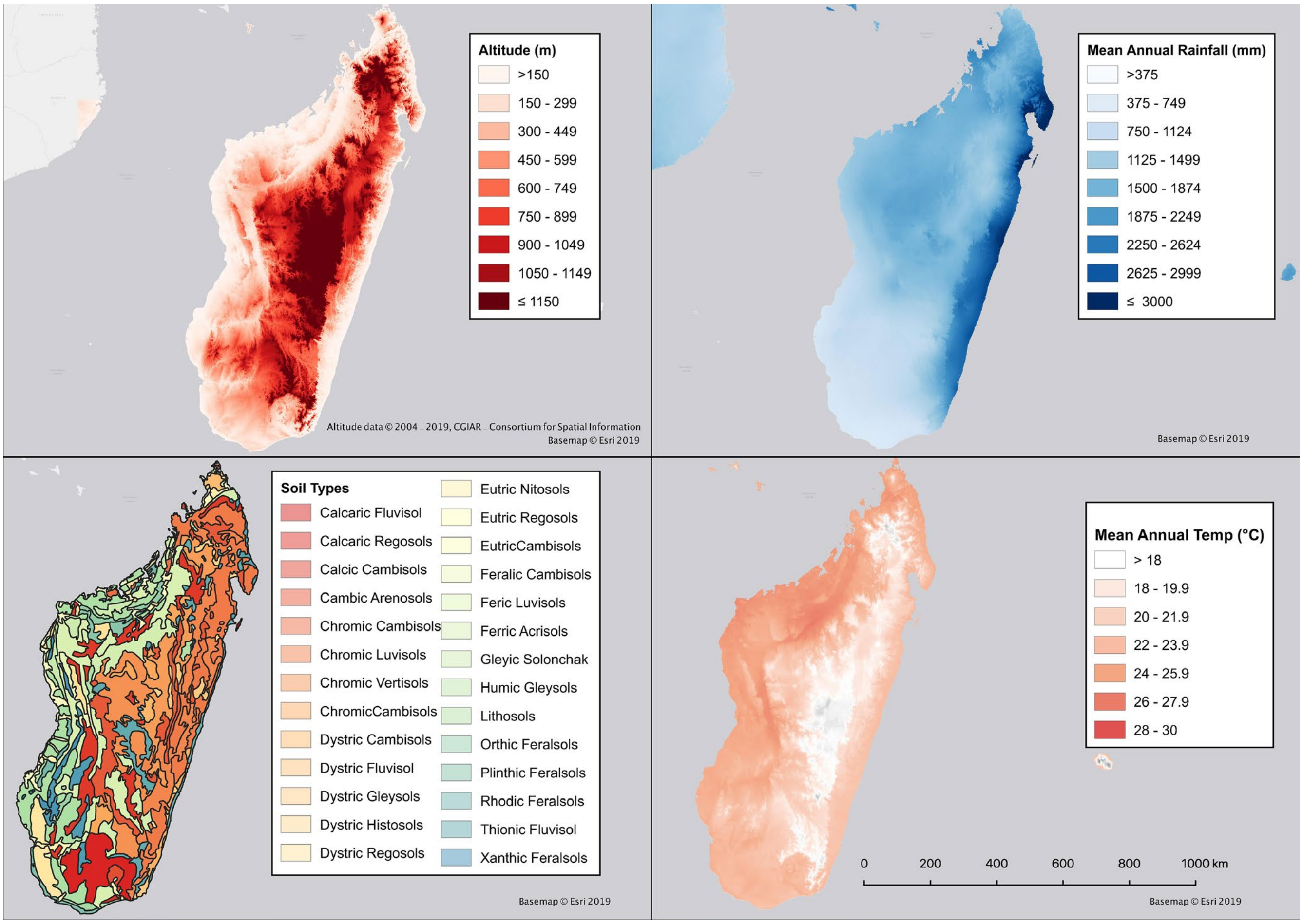

FIGURE 1 Distribution of altitude (CGIAR-CSI, 2019), mean annual rainfall (Fick and Hijmans, 2017), soil type (FAO, 2007) and mean annual temperature (Fick and Hijmans, 2017) across Madagascar

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 km^2 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 3km east of Sakay and the outskirts of Tsiroanomandidy (Figure 3).

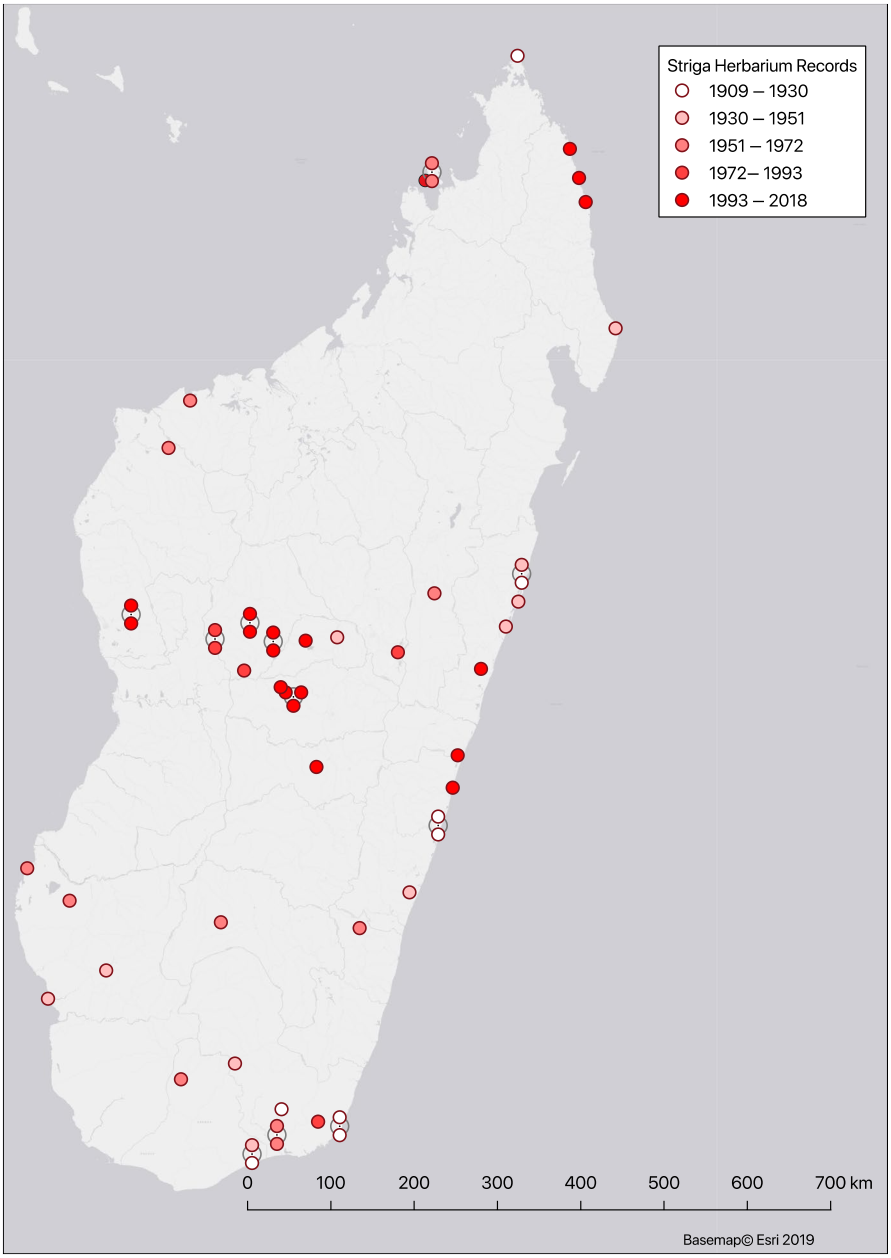

FIGURE 2 Herbarium records for *Striga asiatica* (Rodenburg *et al*., 2016)

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 m^2, 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

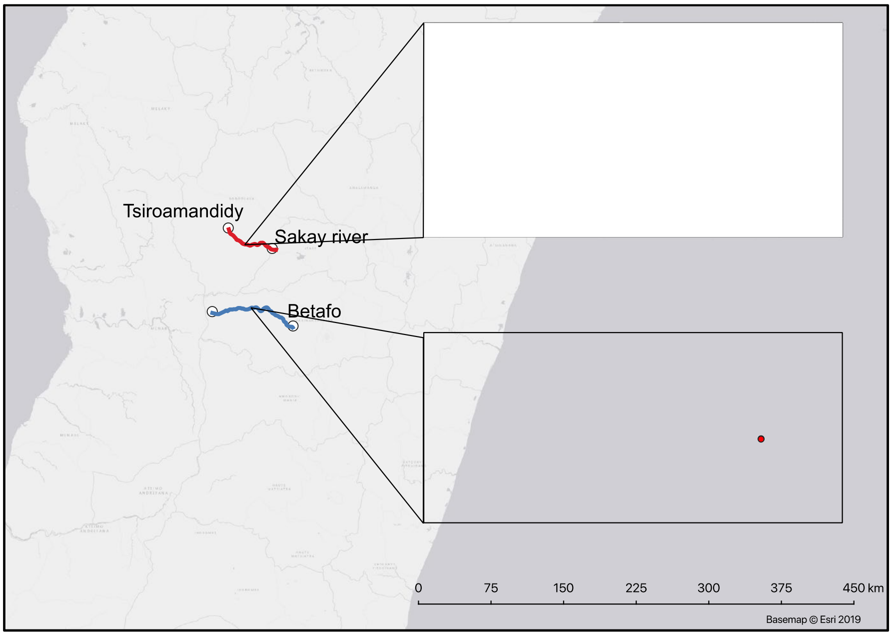

FIGURE 3 Location of transects T1 and T2 in Vakinakaritra, Itasy and Bongolava provinces of mid-west of Madagascar

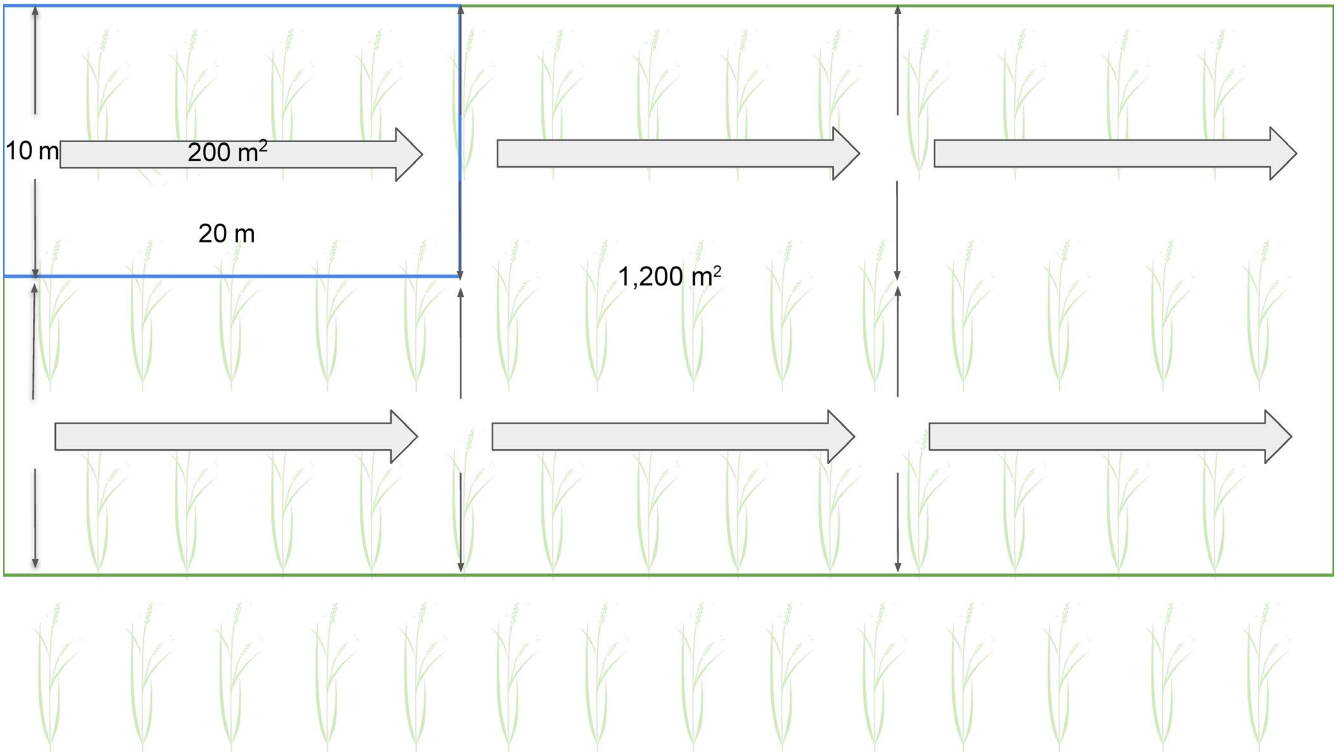

FIGURE 4 Illustration of *Striga* density estimation, where two observers simultaneously surveyed 10 × 20-m quadrats in a field; there was a maximum of three pairs of quadrats in fields >1,200 m^2

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 subsequent 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 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 × 10 m quadrat per surveyor would have negatively affected the speed of repeatability, quadrat dimensions of 200 m^2 (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 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 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.

NO_3 analysis was undertaken using a LAQUAtwin NO_3-11 nitrate meter (Horiba Scientific). 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 NO_3 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). 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 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 *et al.*, 2015), mgcv (Wood, 2011), lme4 (v067.i01, Bates *et al.*, 2015), lmerTest (Kuznetsova *et al.*, 2017), MASS (Venables and Ripley, 2002), DescTools (v 0.99.28, Signorell *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, 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 S2).

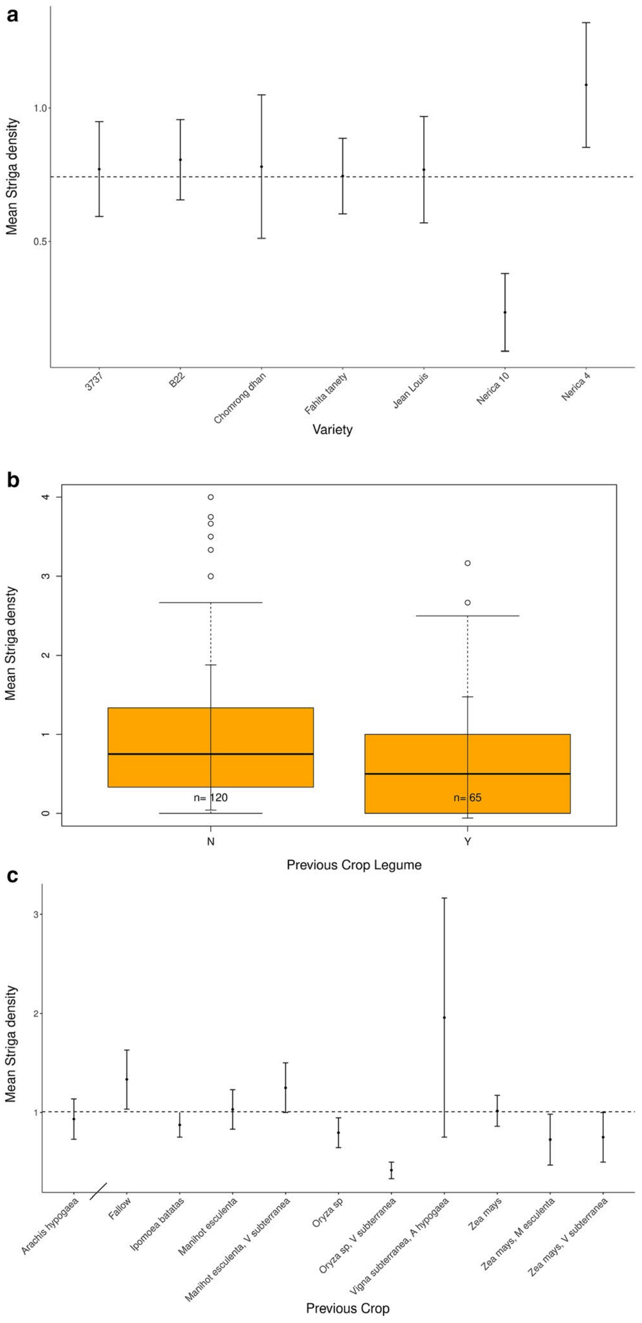

FIGURE 5 (a) Mean ± SE *Striga* density in principal rice varieties (overall mean is dashed line) (3,737: $n = 4$; B22: $n = 28$; Chomrong Dhan: $n = 11$; Fahita tanety: $n = 2$; Jean Louis: $n = 2$; NERICA-10: $n = 8$; and NERICA-4: $n = 28$); (b) mean ± SE *Striga* density of previous crop types (legume: $n = 65$; non-legume: $n = 120$); and (c) mean ± SE *Striga* density of previous crop types and varieties recorded (grand mean is dashed line) (*Arachis hypogaea*: $n = 18$; Fallow: $n = 14$; *Ipomoea batatas*: $n = 4$; *Manihot esculenta*: $n = 25$; *M. esculenta*, *Vigna subterranean*: $n = 2$; *Oryza* sp: $n = 34$; *Oryza* sp, *V. subterranean*: $n = 2$; *V. subterranean*: $n = 35$; *V. subterranean*, *A. hypogaea*: $n = 2$, *Zea mays*: $n = 34$; and *Z. mays*, *M. esculenta*: $n = 7$). Analyses indicated significant effects of rice variety, leguminous and individual previous crops

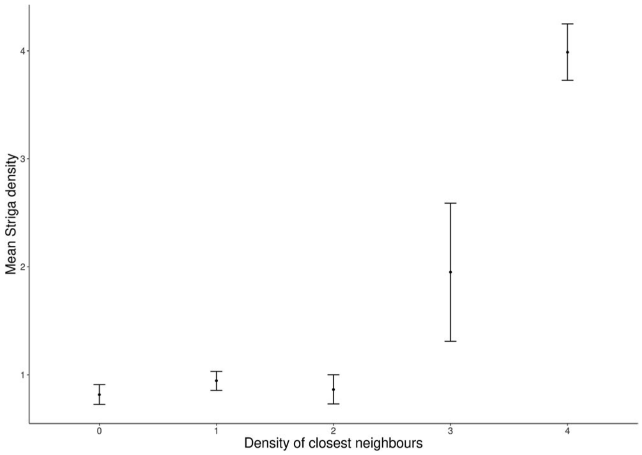

FIGURE 6 Within-study field and neighbouring field mean ± SE *Striga* density. The effect of density in neighbouring fields on within-field mean *Striga* density was significant for the linear model and GAM

3 | 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 $F = 11.14$, $df = 21$, $p < 2e{-}16$p), 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 (μ: 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: $f = 1.39$, $df = 3, 238.$, $p = .25$, 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_3: $t = -1.12$, $df = 89.33$, $p = .27.$, 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

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, similar mean Striga density was recorded for B22 and NERICA-4, with means which 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.* (2018), was not recorded, preventing a complete comparison. The results of Randrianjafizanaka *et al.* (2018) are consistent with regard to the significant effect of previous crop and legumes in reducing Striga infestation. This effect has also been found in other research (e.g., Kureh *et al.*, 2006).

The variance in 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 *et al.*, 2015; Rodenburg *et al.*, 2017). Interactions of environmental factors such as soil composition, nutrients, microclimate, slope and 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

TABLE 1 Mean *Striga* density (±SD), field area, temperature, rainfall and altitude range for the two transects

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

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.

ORCID

Donald Scott https://orcid.org/0000-0001-5936-6558
Robert P. Freckleton https://orcid.org/0000-0002-8338-864X

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SUPPORTING INFORMATION

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

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