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Research

The geography of parasite local adaptation to host communities

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Fitness responses to environment can shape species distributions, though opposing eco-evolutionary processes can obscure environmental effects. For example, host specificity influences parasite dynamics, but is unclear how adaptation of parasites to local host communities may scale up to continental distributions. Here, we develop a macroecological framework to determine how host community structure affects the distribution of specialist and generalist populations of *Striga hermonthica*, an African parasitic plant of cereal crops. Combining data from global crop production and parasite experimental trials, we find that parasites perform best on the host species that is most common in their location of origin. Moreover, niche model contrasts predict parasite specialization on two hosts that evolved alongside *Striga* during domestication (pearl millet and sorghum), indicating that specialist parasites may be most likely to occur where host niches differ most in multivariate environmental space. Our study demonstrates that patterns of parasite local adaptation to host communities can emerge at continental scales and that differential environmental tolerances of hosts indirectly shape the distribution of specialist and generalist parasites. By predicting spatial dynamics of parasite specialization versus generalization directly from environmental data, our approach may help inform current and future management of pests and disease.

Keywords: environmental niche model, host specialization, macroecology

Introduction

Two central questions in biology are what maintains diversity in environmental responses within species and what determines the distribution of organisms across environmental gradients? These two questions are intimately related but often studied separately. A common hypothesis is that adaptation by populations to different local environments is a major source of diversity in environmental responses within species (Clausen et al. 1940, Kawecki and Ebert 2004). Local adaptation is driven by genetic variation in fitness responses to the environment ('environmental preferences') and thus local adaptation may shape abundance patterns across environments. It is often hypothesized that a species' relative abundance in different habitats reflects environmental preferences, but there are many empirical studies where additional processes such as dispersal (Pulliam 1988) obscure or counteract environmental effects.



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Local adaptation is defined as a genotype-by-environment interaction for fitness such that home genotypes have higher fitness than foreign genotypes (Kawecki and Ebert 2004). Local adaptation is common but not ubiquitous (Leimu and Fischer 2008, Hereford 2009) and often difficult to detect in host–parasite systems because parasites may be better adapted to host populations from the recent past than to contemporary host populations (Koskella 2014). The scale of environmental heterogeneity relative to gene flow is one factor determining whether populations adapt to local conditions, evolve generalist strategies (Slatkin 1973, Penczykowski et al. 2016) or specialize on a single environment (Brown and Pavlovic 1992). For example, local adaptation is favored when the size of habitat patches is larger than the characteristic scale of gene flow, while smaller habitat patches may favor adaptation to the average of environments encountered, due to the unpredictability of environments inhabited by offspring (Slatkin 1973). This pattern is readily apparent from empirical studies of host–parasite metapopulations, where the scale of parasite adaptation to local host genotypes depends strongly on habitat configuration and relative scales of gene flow (Thrall and Burdon 1997, Thrall et al. 2002, Laine 2005, Koskella et al. 2011, Tack et al. 2014). However, it is unclear how local adaptation in metapopulations scales up to determine species distribution and abundance (Peterson et al. 2019).

A simple hypothesis about distributions is that population size is greatest where environmental conditions are most favorable (Brown 1984). Yet organisms are often excluded from ideal environments by negative biotic interactions such as competition or predation (Buckley and Roughgarden 2005). Organisms can also persistently occur in poor environments due to immigration (Pulliam 1988). Similarly, high extinction rates of parasite populations followed by recolonization, or high adaptability of hosts, can also limit parasite adaptation to their local hosts (Kaltz and Shykoff 1998). As a result, recent studies have questioned the assumption underlying many macroecological studies that patterns of environmental distribution reflect individual fitness responses to environment (Osorio-Olvera et al. 2019, Holt 2020). Relatedly, parasite fitness may not always be highest in environments where they are most abundant, though several studies suggest parasite abundance is greater on preferred hosts (Krasnov et al. 2004, Poulin 2005). Higher abundance may translate to higher frequencies of parasite occurrence across sampled localities (Poulin et al. 2012), but this trend is rarely linked to patterns of local adaptation.

To address macroecological hypotheses of resource specialization, parasite systems are perhaps some of the most promising (Stephens et al. 2016). For example, the growing availability of host–parasite occurrence data has enabled continent-scale investigations of host specificity (Fecchio et al. 2019, Wells et al. 2019), defined as the number or diversity of hosts a parasite can infect (Wells and Clark 2019). In contrast, host specialization (in the Grinnellian sense) refers to variance in species' performance across a range of environments (Futuyma and Moreno 1988, Devictor et al. 2010). Compared to host specificity (Fecchio et al. 2019),

macroecological studies of host specialization are scarce, perhaps due to the need for quantitative measures of parasite performance which are generally more difficult to obtain than occurrence data.

Here, we investigate continent-scale patterns of host specialization in the parasitic plant *Striga hermonthica*. A root hemiparasite of the broomrape family (Orobanchaceae), *S. hermonthica* is characterized by a complex life cycle. Seeds can remain viable in soils for up to ~14 years (Bebawi et al. 1984) until germination, which requires detection of specific hormones (strigolactones) present in host root exudates (Cook et al. 1966). Other host-derived molecules trigger the formation of the haustorium (Cui et al. 2018), a specialized feeding structure used to invade host tissues and form vascular connections. Through these connections, parasitic plants suppress host immune responses (Shahid et al. 2018) and acquire water and nutrients to support their own development, emergence and reproduction (Clarke et al. 2019). *S. hermonthica* is widespread across diverse abiotic environments in East and West Africa where it parasitizes grasses including maize, pearl millet, sorghum, sugarcane and rice and is a major constraint to food security (Rodenburg et al. 2016, Runo and Kuria 2018). Compared to pearl millet *Pennisetum glaucum* and sorghum *Sorghum bicolor*, which both have centers of domestication in Africa (Winchell et al. 2017, Burgarella et al. 2018), maize is a relatively recent host and has few natural resistances to *Striga* (Rich and Ejeta 2008, Timko et al. 2012).

Parasitic plants offer numerous advantages for studying the eco-evolutionary dynamics of parasitism. *S. hermonthica* hosts are characterized by mating systems from highly outcrossing (pearl millet and maize) to predominately selfing (sorghum) and a diversity of abiotic requirements. Unlike many microbial pathogens and endoparasites, parasite generation times are similar to their hosts (~1 year) potentially leading to more balanced coevolutionary dynamics. The potential for reciprocal coevolution (rather than asymmetrical adaptation of parasites to hosts often assumed in agricultural settings) is supported by a recent study of sorghum and *S. hermonthica*. Bellis et al. (2020) found evidence that *S. hermonthica* prevalence imposed spatially-varying selection on sorghum landraces, promoting among-population diversity in sorghum alleles for *S. hermonthica* resistance. Parasitic plants are large and conspicuous, so excellent occurrence data are available from natural history collections without a need for dissections or molecular diagnostics. Host specialized as well as generalist populations are known (Parker and Reid 1979). However, the eco-evolutionary determinants of specialization are poorly characterized, despite detailed knowledge at the molecular level on parasitic plant response to different hosts (Honaas et al. 2013, Johnson et al. 2019, Lopez et al. 2019).

We synthesize previous experiments on host specialization, combined with continental scale host and parasite distribution data, to ask three questions: Q1) Is regional abundance of a host crop correlated with local specialization by parasites? Q2) Is host specialization associated with observed patterns

of parasite occurrence on different hosts? and Q3) Are abiotic environmental gradients related to the distribution of specialist and generalist parasites, suggesting that future dynamics of specialization versus generalization may be predicted by abiotic change?

Material and methods

Host specialization

To characterize host specialization, we compiled data from four published empirical studies that tested *S. hermonthica* performance (specifically, ‘emergence’ or the number of above-ground parasites per individual host plant at or near crop maturity) on sorghum, millet and maize (King and Zummo 1977, Ramaiah 1983, Bebawi et al. 1986, Kim et al. 1994). These data include *S. hermonthica* populations from 27 locations spanning semiarid regions of East and West Africa between the equator and 14°N (Fig. 2, 3). *Striga hermonthica* populations from empirical studies were

classified into regional groupings based on their location of origin coordinates. Populations from localities with longitudinal coordinates less than 0° were considered ‘Western’, greater than 15°E were considered ‘Eastern’ and greater than 0°W but less than 15°E were considered ‘Central’. Studies of these populations include both pot experiments and field trials (Supporting information) and to our knowledge, represent all studies that have quantified emergence of *S. hermonthica* from geographically distinct populations on multiple genotypes of multiple host species. To account for differences in inoculation pressure and experimental design between studies, for a given *S. hermonthica* population we considered the mean relative emergence on host species *k* as
$$\text{Mean Relative Emergence}_k = \frac{1}{n} \sum_{j=1}^n E_j / E_{\max}$$
 where E_j is the average emergence on host genotype *j*, E_{\max} is the maximum emergence of the parasite population observed on any host genotype of any host species tested at the same location, and *n* is the number of genotypes tested of host species *k*. Mean relative emergence ranges from 0 to 1 where, for example, a mean relative emergence of 0.5 on maize would

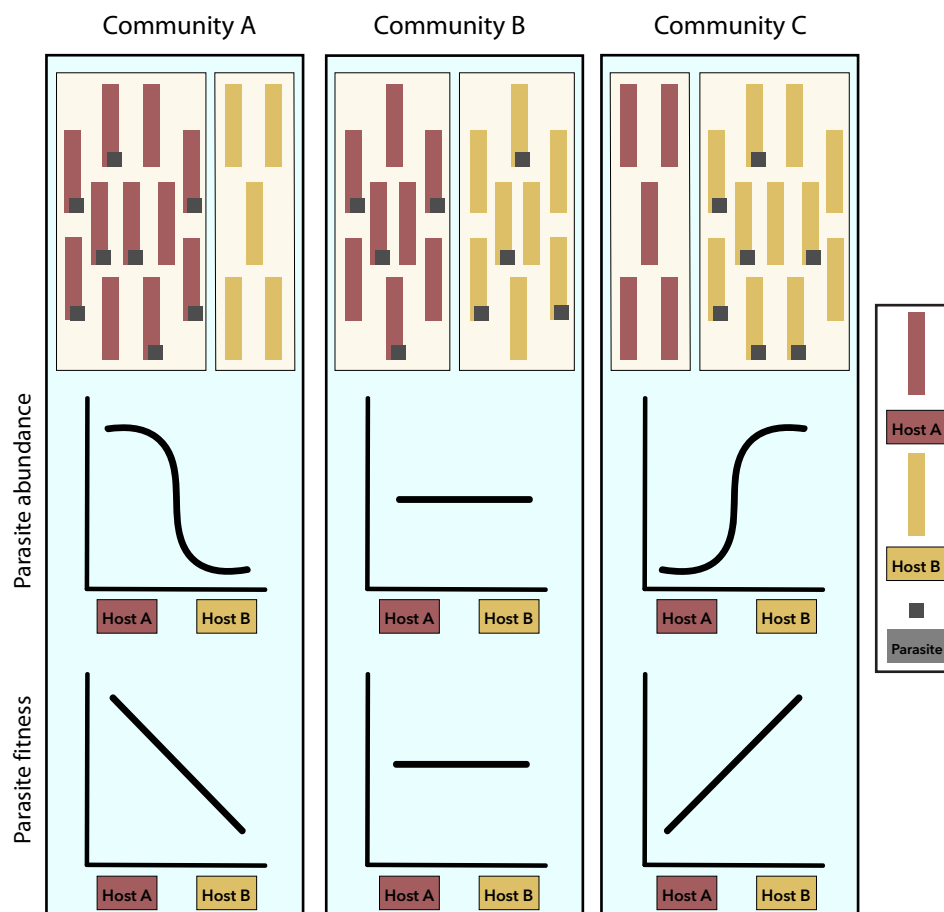


Figure 1. Parasite adaptation to local host community. Predictions are shown for three scenarios. Specialist parasites (characterized by higher fitness on the most abundant host) are selected for in communities A and C, and generalist parasites (with similar fitness on diverse hosts) are selected for in community B. Parasite abundance may decrease more rapidly with decreasing prevalence of alternate hosts due to processes such as dispersal limitation. For community B, intermediate fitness on multiple hosts is shown although other scenarios are possible.

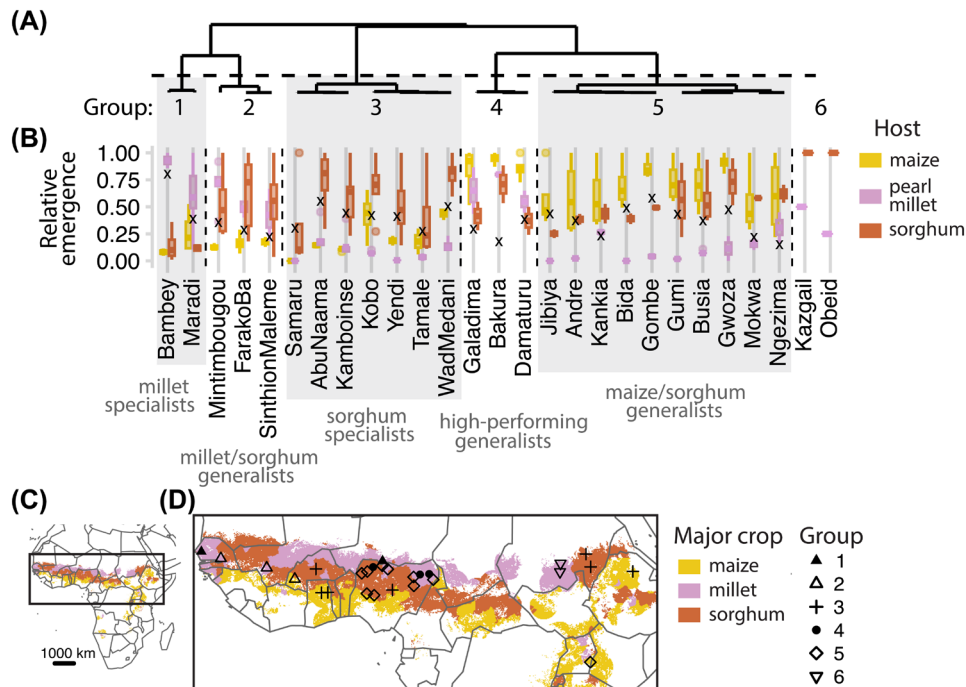


Figure 2. Distribution of generalist and specialist *S. hermonthica* in published studies. Relative emergence was calculated as the mean number of parasites emerged on a particular host species, relative to the highest emergence observed for any tested host genotype. (A) Dendrogram obtained from hierarchical clustering of mean relative emergence values for three hosts. (B) Mean relative emergence on maize, sorghum and pearl millet for *S. hermonthica* from 27 localities. Boxplots represent the distribution of mean relative emergence values across all tested genotypes of a host species. Whiskers extend to the minimum and maximum values and boxes indicate the first and third quartiles. The black 'x' shows the value of the paired difference index (PDI) calculated for each population, where values closer to 1 indicate more specialized populations. Vertical dashed lines demarcate *S. hermonthica* clusters determined in A. Parasites were classified in the following groups: 1) millet specialists, 2) millet/sorghum generalists, 3) sorghum specialists, 4) high-performing generalists (where high emergence is observed across multiple host species), 5) maize/sorghum generalists, and 6) two populations that were excluded from the clustering analysis because emergence on maize was not tested. (C) Host crop production in *S. hermonthica*-prone regions. Colored regions indicate the most abundant host crop based on estimated area harvested in 2000. Note pearl millet is not distinguished from other millets in harvest area data. (D) Inset map. Black symbols (n=27) indicate group assignments from (A) and the location of origin of *S. hermonthica* populations tested for emergence in empirical studies.

indicate that for a given parasite population, on average half of the individuals emerge on genotypes of maize compared to the maximum emergence in an experiment. Similarly, a mean relative emergence close to 1 on sorghum would indicate that a parasite population specializes on sorghum.

Using these values for mean relative emergence, we then classified *S. hermonthica* populations as generalist or specialist using two complementary approaches. First, we used hierarchical clustering, an unsupervised approach, to identify groups of *S. hermonthica* populations with similar mean relative emergence across the three hosts using the 'hclust' function in R (<www.r-project.org>). Clustering was performed using correlation-based distance, which clusters observations with similar profiles, even if there is large variation in the magnitude of feature values (i.e. mean relative emergence). As the measure of cluster dissimilarity, we used 'complete linkage', which considers the maximum distance between any pair of observations in two clusters. We also considered a continuous measure of host specialization, the paired difference index

$$(PDI), \text{ calculated as } PDI = \frac{1}{R-1} \sum_{i=2}^R (P_1 - P_i), \text{ where } P_1$$

is the highest link strength, P_1 is the link strength with the i th resource and R is the number of resources (Poisot et al. 2012). For calculations of PDI, mean relative emergence was used as a measure of link strength on each resource (host).

Distribution of host crop communities

We compiled data on host crop distributions to determine how variation in host ecological communities, i.e. cultivation of specific crops, was associated with parasite specialization (Q1). As a proxy of host abundance, we considered area harvested of the three focal host species: maize, millet and sorghum from global crop production data (Monfreda et al. 2008). These data are based on integration of national, state and county level census statistics with global cropland cover derived from satellite imagery and provide estimates of average hectares harvested for each crop per land area of a 5×5 arcminute grid cell, according to multiple years of data centered on the year 2000 (Monfreda et al. 2008). Although there is a temporal mismatch between crop harvest data and experimental data, the proportion of area harvested of each

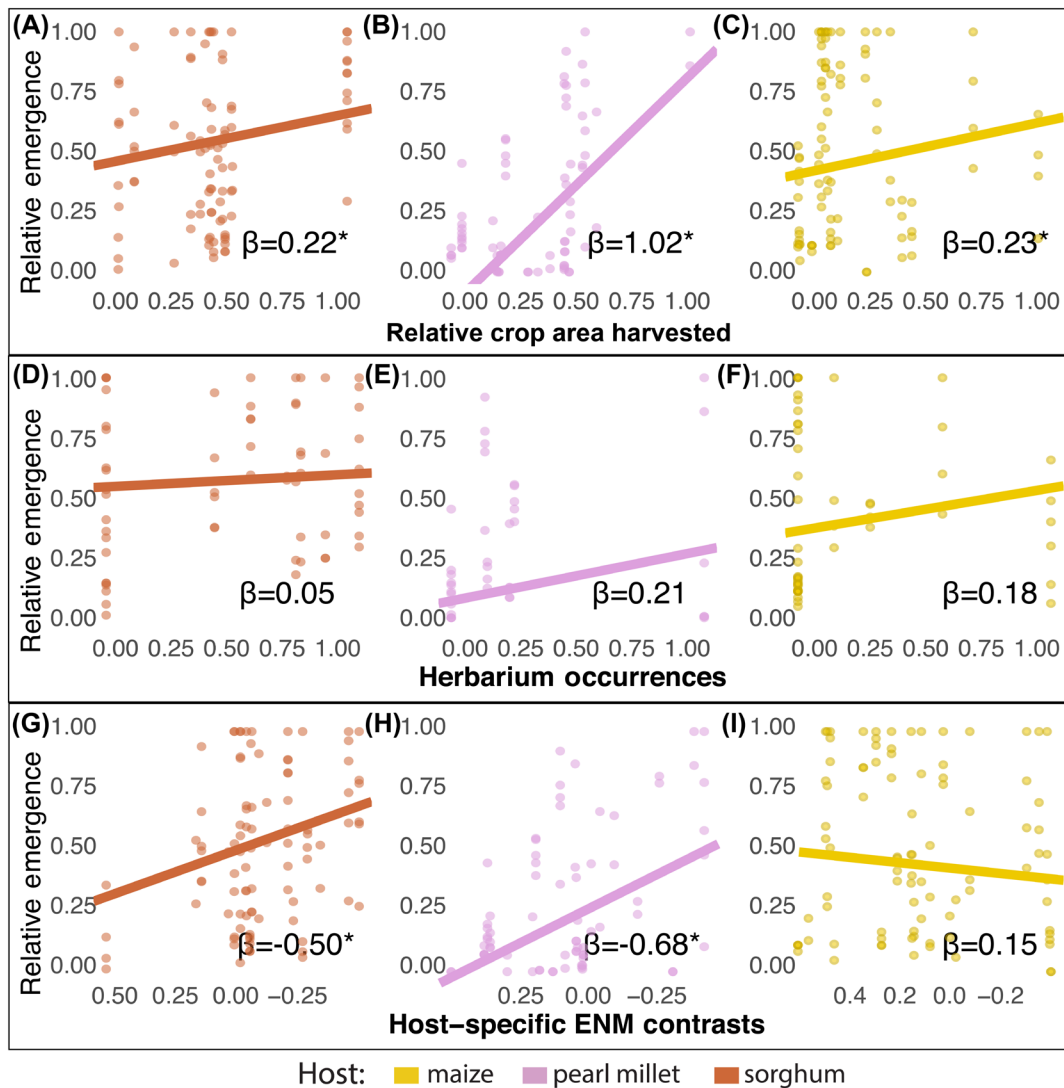


Figure 3. The relationship between mean relative emergence from empirical studies and metrics of predicted specialization for focal hosts. Each point is representative of the relative emergence of a parasite population on a single host genotype and predicted specialization based on either (A–C) relative crop harvested area, (D–F) herbarium occurrences or (G–I) host-specific ENM contrasts and plotted against actualized specialization (mean relative emergence). Lines are shown based on coefficient estimates from linear mixed models. Beta coefficients with an asterisk indicate that the added fixed effect of a specialization parameter is significant for model predictions of mean relative emergence. The axis for host-specific ENM contrasts (G–I) is inverted such that more negative ENMs reflect higher specialization (Materials and methods).

host crop has remained relatively constant in each country, indicating that the harvest data from 2000 are a good proxy for conditions in earlier years (Supporting information). We estimated relative abundance of hosts by calculating the fraction of land planted to a particular host relative to maize, millet and sorghum combined. We also considered productivity (yield per hectare) from the same dataset (Monfreda et al. 2008). Analyses were limited to *S. hermonthica* prone regions, which we defined as regions within 200 km of a known occurrence with habitat suitability scores ≥ 0.1 , according to *S. hermonthica* environmental niche models (ENMs) constructed using occurrences on all hosts (Bellis et al. 2020).

Parasite occurrence

To evaluate whether host specialization is associated with parasite occurrence on different hosts (Q2), we calculated the fraction of parasites observed on a particular host, relative to all parasites with an identified host within 50 km from locations of origin of *S. hermonthica* populations tested in experiments. Starting from an initial set of *S. hermonthica* occurrence records (Bellis et al. 2020), we obtained subsets of records occurring specifically in fields of sorghum ($n=262$), millet ($n=157$) or maize ($n=74$) according to specimen label data. Although millets include several unrelated species, 46 of 47 herbarium specimens with host identified as ‘millet’

and that also gave the name of a genus indicated *Pennisetum* spp. rather than *Eleusine*, *Setaria*, *Digitaria*, *Panicum* or other less common genera of cultivated ‘millets’. Combined with greater overlap in the distribution of pearl millet growing areas and the range of *S. hermonthica* (National Research Council 1996), our analyses are probably most reflective of parasites on pearl millet.

Specialization predicted from environmental niche models

To link abiotic environmental variation with host specialization (Q3), we identified areas with optimal conditions for specialization using environmental niche models (ENMs). ENMs are a widely used tool for characterizing suitable habitat for a species based on correlation between environment and observed occurrences of an organism (Elith et al. 2010). An implicit assumption is that organisms should have higher fitness in locations with higher habitat suitability predicted by ENMs (Nagaraju et al. 2013, Wittmann et al. 2016).

We constructed ENMs based on all parasite occurrences (all-occurrence model) and subsets of occurrences associated with a particular host. ENMs were built using MaxEnt (Phillips et al. 2006), a machine learning based method for modeling distributions based on presence-only data. Models were built using *ENMeval* (Muscarella et al. 2014) to test a variety of tuning parameters. Eight environmental variables were considered, including several associated with differential parasitism on host species (Wilson-Jones 1955, Mohamed et al. 2001), host exudation and production of hormones required for parasite germination (Yoneyama et al. 2013), or parasitism severity (annual rainfall; (Wilson-Jones 1955). Bioclimatic and topographic variables (annual rainfall, mean temperature of the wettest quarter, isothermality, potential evapotranspiration and topographic wetness index) were obtained from CHELSA (Karger et al. 2017) and ENVIREM (Title and Bemmels 2018) datasets. Soil variables (clay content, nitrogen and phosphorus) were obtained from SoilGRIDs250m or AfSoilGrids250m (Hengl et al. 2015, 2017). For AfSoilGrids and SoilGrids250m products, we downsampled to 1-km resolution using bilinear interpolation with the ‘resample’ function of the *raster* package (Hijmans 2020). After downsampling, edaphic variables represent ‘average’ conditions experienced by a parasite and its close relatives, rather than local heterogeneity associated with a single individual. To characterize the background of the study, we randomly sampled 10 000 points from within a 500 km radius of all occurrences; the same background points were used to build each of the host-specific models and the all-occurrence model. Habitat suitability values from an ENM of *S. hermonthica* are associated with a large effect resistance allele in sorghum landraces, supporting both the accuracy of the model and some degree of local host adaptation to *S. hermonthica* (Bellis et al. 2020).

Here, we hypothesized that ENM contrasts, which we define as the difference in habitat suitability between two

different ENMs, might also predict variation in performance on different hosts. We created ENM contrasts by subtracting the logistic-transformed ENM output for parasite occurrence on a focal host species from the all host species-occurrence model for each grid cell. Higher potential for specialization on a given host is indicated by more negative values in ENM contrasts (lower bound of -1) and lower potential for specialization is indicated by more positive values (upper bound of 1). Values close to zero can be interpreted as locations where generalist parasites are likely. We calculated the average value within 50 km of *S. hermonthica* locations from empirical studies as a measure of predicted specialization by ENMs, but similar values were observed at a range of distances (Supporting information).

We investigated the factors most important for predicting overall occurrence in each model using permutation importance. However, environmental factors most important for determining habitat suitability may differ across space; to identify variables that most influence model prediction at each location, we created limiting factor maps (Elith et al. 2010) with *rmaxent* (Baumgartner and Wilson 2017), fitting models based on the optimal regularization multipliers and feature classes parameters determined by *ENMeval* (millet: betamultiplier = 3.5, noproduct, nothreshold; maize: betamultiplier = 0.5, noproduct, nothreshold, nohinge; sorghum: betamultiplier = 3.5, nothreshold). After masking to a 200 km radius of any known *S. hermonthica* occurrence, niche overlap statistics were calculated in *ENMTools* ver. 0.2 (Warren et al. 2010), in environmental space with the ‘env. overlap’ function or in geographic space with the ‘calc.niche. overlap’ function (Warren et al. 2019).

Linking host distributions, parasite specialization and parasite distribution

We used linear mixed effects models (LMMs) to test how parasite specialization in experiments was related to 1) host community variation (relative crop area harvested, Q1), 2) parasite occurrence across hosts (from herbarium records, Q2) and 3) predicted specialization from abiotic environment (host-specific ENM contrasts, Q3). For each of the three predictors of host specialization, we modeled mean relative emergence of an *S. hermonthica* population i , on a focal host as follows:

$$\text{Emergence}_{ij} = \beta_0 + \beta_1 X_i + S_{0j} + I_{0i} + R_{0i} + \epsilon_{ij} \quad (1)$$

where β_0 and β_1 are coefficients, X_i is the value for one of the predictors of specialization (i.e. crop area harvested, observed parasite herbarium occurrence or host-specific ENM contrast), S_{0j} is the random effect of host genotype j , I_{0i} is the random effect of region (western, central or eastern) for *S. hermonthica* population i , R_{0i} is the random effect of study (i.e. publication) for *S. hermonthica* population i , and ϵ_{ij} is the residual error. To assess the significance of our specialization predictors (X_i) as fixed effects, Eq. 1 was compared to the intercept-only model:

$$\text{Emergence}_{ij} = \beta_0 + S_{0j} + I_{0i} + R_{0i} + \epsilon_{ij} \quad (2)$$

using a chi-squared test (Supporting information). Distribution of host genotypes is likely another factor influencing evolution of host specialization, but data that would allow for inclusion of this effect are currently not available.

Models were built with a Gaussian error distribution using the 'lmer' function from the *lme4* package (Bates et al. 2015) and corresponding model summaries and statistical parameters for the fixed effects were calculated with the *lmerTest* package using Satterthwaite's method (Kuznetsova et al. 2017). Normality of residual variation was determined by visually inspecting QQplots. Plots were approximately normal and homoscedastic. Models were confirmed to not have significant spatial autocorrelation through calculation of Moran's I of residuals.

Prediction under future climates

To evaluate potential abiotic driven changes in parasite specialization, we projected ENMs to future climates. We considered relative concentration pathways 4.5 and 8.5, and used climatologies for five CMIP5 models (MPI-ESM-MR, CESM1-BGC, ACCESS-1-0, MIROC5, CMCC-CM) chosen to reduce interdependency (Sanderson et al. 2015). ENMs were projected to 2050 using updated data layers for annual rainfall, mean temperature of the wettest quarter and isothermality. Soil and ENVIREM variables, for which future projections were not available, remained constant. We calculated the average habitat suitability projected under the five different models for 2050. Considering all pixels within 200 km of any occurrence record of *S. hermonthica*, we tested whether the habitat suitability score was significantly different in future compared to 1979–2013 using a Wilcoxon signed rank test.

Results

Complete host specialization is rare

We first characterized levels of host specialization observed in *S. hermonthica* populations across Africa. Degree of host specialization was highly variable across the 27 populations studied (Fig. 2). Populations were characterized by high emergence on either millet or sorghum only, high emergence on two hosts or high emergence on all three hosts (Fig. 2). Hierarchical clustering with a cut-point at 0.5 showed five groups: millet specialists (Group 1; $n=2$), millet/sorghum generalists (Group 2; $n=3$), sorghum specialists (Group 3; $n=7$), high-performing generalists (Group 4; $n=3$) and maize/sorghum specialists (Group 5; $n=10$; Fig. 2). Besides the high-performing generalists, all groups included populations from at least two studies, suggesting that differences among studies did not strongly bias clustering. With the exception of millet specialists from Bambey, Senegal, most populations had modest or low levels of specialization as indicated by pairwise differentiation index values (Fig. 2B). These results suggest that although parasites

may become locally adapted to commonly cultivated host species, complete specialization is rare.

Distribution of host communities shapes specialization

We then investigated whether the distribution of host communities across environments might shape the evolution of host specialization (Q1). *S. hermonthica*-prone regions covered approximately 628 million hectares, of which 80% was estimated to have nonzero production of maize, millet or sorghum. Crop production patterns generally followed rainfall gradients, with greater land area planted to millet in more arid regions of the Sahel, sorghum dominant at lower latitudes and in eastern Sudan, and maize most common in more mesic regions (Fig. 2). In 2000, sorghum or maize were the dominant crop in most *S. hermonthica*-prone areas (38% sorghum; 38% maize), with 24% of areas characterized by millet as the major cereal crop.

Specialization observed in experiments was strongly associated with spatial variation in host crop communities (Fig. 3A–C). For parasites on all three hosts, relative host crop area harvested within a 50 km radius was a strong predictor of mean relative emergence in experimental studies. This finding was especially pronounced for millet ($p_{\text{millet}} < 0.001$; $\beta_{\text{harvest_area}} = 1.02$; LMM; Supporting information). Relative crop area harvested was also a statistically significant predictor of mean relative emergence on sorghum ($p_{\text{sorghum}} = 0.04$; $\beta_{\text{harvest_area}} = 0.22$; LMM) and maize ($p_{\text{maize}} = 0.04$; $\beta_{\text{harvest_area}} = 0.23$; LMM; Supporting information). These results are consistent with the conclusion that parasites adapt to the most abundant host in a particular region and also suggest that relative parasite emergence is a reasonable proxy for fitness (Fig. 1).

Host specialization may structure parasite distributions

Our analyses provided little support for a positive relationship between specialization and parasite occurrence on different hosts (Q2; Fig. 3D–F). Within a 50-km radius of all 27 locations with parasite emergence data, 15 locations had at least one parasite occurrence record with information about host of origin. Proportion of records on a particular host for these 15 *Striga* populations was not a statistically significant predictor of emergence on maize ($p_{\text{maize}} = 0.07$; $\beta_{\text{occurrence}} = 0.18$; LMM), millet ($p_{\text{millet}} = 0.06$; $\beta_{\text{occurrence}} = 0.21$; LMM) or sorghum ($p_{\text{sorghum}} = 0.57$; $\beta_{\text{occurrence}} = 0.05$; LMM; Supporting information). Availability of additional parasite occurrence and performance data could reveal a stronger relationship between specialization and patterns of parasite occurrence on different hosts.

Parasite abiotic niche reflects host environmental tolerance

To characterize the abiotic basis of patterns of host specialization, we built environmental niche models (ENMs) for

potentially host-specialized parasite populations by excluding all occurrences with unknown host or with a non-focal host (Supporting information). Despite a smaller number of observations compared to the all-occurrence model, ENMs had good predictive accuracy for each of the host-specific models. Area under the receiver operating characteristic curve (AUC) for the test set was 0.848 for the all-occurrence model ($n=1049$) compared to 0.850 for the sorghum-only model ($n=262$), 0.908 for the millet-only model ($n=157$) and 0.841 for the maize-only model ($n=74$).

Modeled niches generally reflected known environmental tolerances of hosts, with millet-specific models predicting high habitat suitability in low nitrogen (N), low rainfall environments but maize-specific models predicting higher habitat suitability in environments characterized by more nitrogen-rich soils and higher rainfall (Fig. 4A–D). Across all host species, annual rainfall and soil N were generally among the most important predictors of parasite occurrence (Supporting information). Annual rainfall was the most common factor limiting habitat suitability for maize-parasitizing *S. hermonthica* (59% of all grid cells; 10th–90th percentile for grid cells with habitat suitability ≥ 0.5 : 854–1537 mm yr^{-1}) but was also strongly limiting for parasites of sorghum (41% of cells; 10th–90th percentile: 509–1197 mm yr^{-1}) and millet (32% of cells; 10th–90th percentile: 441–1164 mm yr^{-1}) (Supporting information). Mean temperature of

the wettest quarter was also an important predictor of *S. hermonthica* parasitizing millet (Supporting information) and frequently limited habitat suitability for millet-parasitizing populations (Supporting information). Soil clay content was an important predictor for *S. hermonthica* occurrence on sorghum (Supporting information), but was only limiting for millet-parasitizing populations in eastern Sudan and sorghum-parasitizing populations in western Senegal (Supporting information). Higher soil clay content has been anecdotally associated with parasitism on sorghum in general (Mohamed et al. 2001) and in Sudan (Wilson-Jones 1955).

In agricultural as well as natural ecosystems, more productive environments may be associated with increased availability of alternate hosts, favoring generalists (Thrall et al. 2007). Parasitism on maize was associated with increased environmental quality, with habitat suitability peaking in locations of higher crop productivity (Fig. 4E). Combined crop yield per area harvested was significantly greater where *S. hermonthica* parasitizes maize compared to millet ($p < 0.001$, Wilcoxon rank sum test) but not compared to sorghum ($p=0.2$), consistent with greater niche overlap between maize and sorghum (Supporting information). We observed a weak trend towards reduced parasite specialization with increasing environmental productivity (Fig. 4F; $p=0.15$, chi-square goodness-of-fit test for linear regression model). Taken together, parasite ENMs are highly sensitive to differences in multivariate

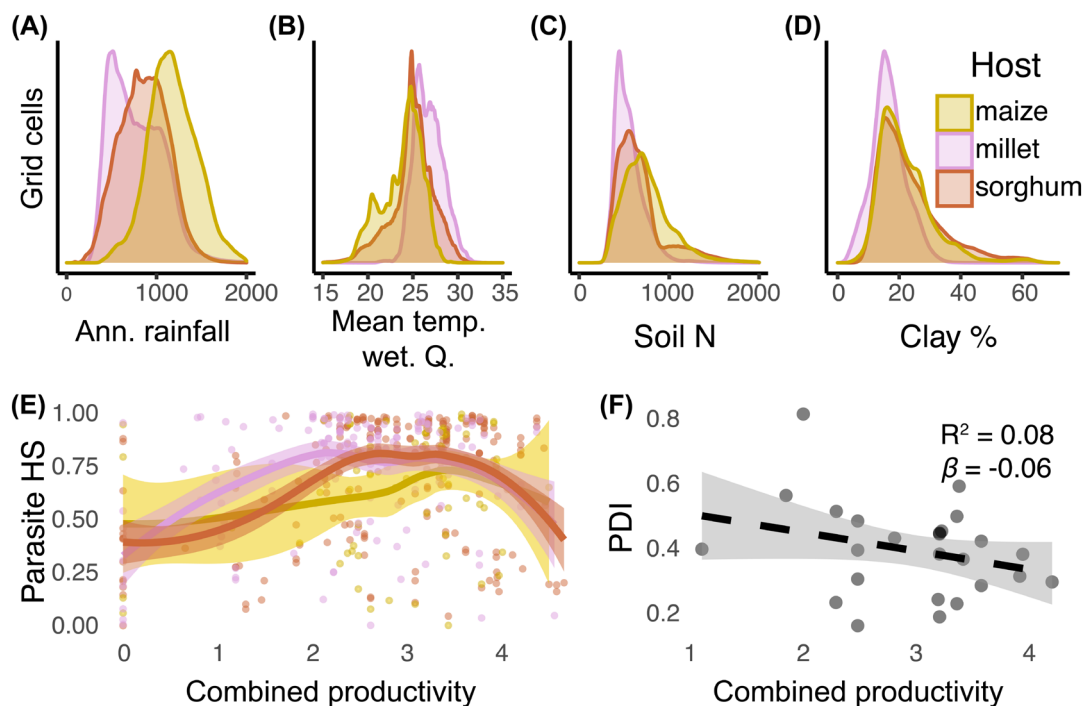


Figure 4. Parasite ENMs reflect host abiotic tolerances. (A–D) Distribution of environmental values for grid cells in core habitat (habitat suitability ≥ 0.5) for ENMs based on subsets on occurrence records on different hosts. (E) Habitat suitability (HS) as a function of combined host productivity (yield per hectare) at locations of maize-, millet- and sorghum-parasitizing *S. hermonthica* from natural history observations. Curves were fit using local polynomial regression. HS peaks in locations of higher productivity for parasites of maize compared to millet or sorghum. (F) Host specialization measured as the paired difference index (PDI) for $n=25$ *S. hermonthica* populations tested for emergence in previous studies. Shaded areas in (E) and (F) indicate 90% confidence intervals. Ann. Rainfall: annual rainfall (mm yr^{-1}); Mean Temp. Wet. Q.: mean temperature of the wettest quarter ($^{\circ}\text{C}$); soil N: soil nitrogen (g kg^{-1}); clay: clay fraction (weight %).

environmental tolerance of hosts, consistent with host cultivation on a gradient from marginal, warm environments (pearl millet) to more productive, cooler environments (maize).

Abiotic gradients shape distribution of millet and sorghum specialists

ENM contrasts show where host niches differ most in multivariate environmental space. If abiotic environment is associated with host specialization, specialists may be most likely where environmental axes most strongly differentiate hosts in niche space (Futuyma and Moreno 1988). Consistent with this idea, ENM contrasts were strongly predictive of variation in *S. hermonthica* performance on host species for which specialist parasite populations have been previously reported (Fig. 3G–H). ENM contrasts were most strongly associated with mean relative emergence on pearl millet ($p_{\text{millet}} < 0.001$; $\beta_{\text{ENM}} = -0.68$; LMM) and were also significantly associated with mean relative emergence on sorghum ($p_{\text{sorghum}} = 0.0067$; $\beta_{\text{ENM}} = -0.50$; LMM) (Supporting information). In contrast, host specialization predicted by ENM contrasts was not strongly associated with mean relative emergence on maize ($p_{\text{maize}} = 0.19$, $\beta_{\text{ENM}} = 0.15$; LMM; Supporting information).

Future change in parasite distributions

To investigate potential changes in host-specialization over time, we projected ENMs to future climates (Supporting information). By 2050, we predicted an overall increase in habitat suitability for *S. hermonthica*, with median increase in habitat suitability in its current range of 0.07 under RCP 4.5 ($p < 0.001$; Wilcoxon signed rank test comparing habitat suitability of grid cells in present versus 2050) and 0.09 under RCP 8.5 ($p < 0.001$; Wilcoxon signed rank test; Supporting information). Habitat suitability increased most for millet-parasitizing populations, followed by maize-parasitizing *S. hermonthica* (Supporting information). Changes in habitat suitability were heterogeneous across space, with many regions in the Sudano-Sahelian zone of west Africa becoming less suitable for *S. hermonthica* and its hosts (Sultan et al. 2013) but central and east Africa generally becoming more suitable (Supporting information).

Discussion

An outstanding goal in evolutionary ecology is understanding how reciprocal host and parasite interactions shape distribution of species. For multi-host parasites, parasite eco-evolutionary dynamics depend on many components including environmental tolerance, host compatibility, genetic diversity and source-sink dynamics (Woolhouse et al. 2001, Dobson 2004, Gandon 2004, Bellis et al. 2020). Although parasite abundance is often constrained by local environment (Wu et al. 2019), it is rarely considered how parasite evolution may also be indirectly affected by host abiotic environmental tolerance. Here we present a framework to

understand broad-scale interactions between *S. hermonthica* and its common hosts across abiotic gradients. Combining host distributional and empirical data from diverse populations of a parasitic plant, we find that regional abundance of a particular host is associated with local specialization on that crop by parasites. By controlling host distributions, abiotic gradients may indirectly shape patterns of parasite local adaptation to host communities and consequently, distributions of generalist and specialist parasites.

Host communities in natural ecosystems can be highly heterogeneous, impacting parasite evolution. In theory, low host heterogeneity favors parasite specialization, whereas high host heterogeneity favors generalism (Futuyma and Moreno 1988). However, strong empirical support for this phenomenon comes from relatively few systems (Legros and Koella 2010, Fecchio et al. 2018, Gibson et al. 2020) and even fewer at continent scale. With well-characterized host community distributions (Monfreda et al. 2008), and host cultivation patterns strongly tied to abiotic gradients (Fig. 2), *S. hermonthica* parasitic plants are a valuable system for developing a predictive framework of host specialization. Unlike well-studied microbial parasites with short generation times (Penczykowski et al. 2016), *S. hermonthica* may be able to maintain long-term adaptive potential due to a long-lived seedbank (> 10 yrs; Bebawi et al. 1984) and substantial genetic diversity from its outcrossing breeding system (Bozkurt et al. 2015, Unachukwu et al. 2017). Whereas repeated selection could exhaust parasite genetic diversity under limited migration and mutation, longer parasite generation times relative to hosts (driven by a long-lived seedbank) help maintain parasite diversity and promote adaptation to changing environments (Gandon and Michalakis 2002).

Our results suggest patterns of host cultivation are strongly associated with parasite adaptation to local host communities (Q1; Fig. 3A–C). Using crop harvest data to approximate relative host abundance (Fig. 2), we found that *S. hermonthica* emergence was highest on the host species most commonly grown at location of origin of parasite populations (Supporting information). This pattern satisfies the ‘home versus away’ criterion described by Kawecki and Ebert (2004), as mean fitness of the parasite is highest in its ‘home’ host environment compared to ‘away’ hosts. Although ‘home versus away’ patterns sometimes conflict with ‘foreign versus local’ genotype contrasts when one environment is relatively higher quality, we did not see evidence for such a conflict. Instead different parasite populations performed best on different hosts. Higher fitness on ‘home’ hosts was apparent despite the fact that we were not able to find high resolution crop distributional data prior to the year 2000, whereas empirical studies were based on *S. hermonthica* populations from field and pot trials that were sampled or tested 12–25 years earlier. This may be because host community composition (relative area planted to each host crop) remained roughly constant in East and West Africa during this period, although total area harvested increased dramatically (Supporting information). Evidence supporting a link between specialization and patterns of parasite occurrence on different hosts (Q2)

was weaker, likely due to the small number of parasite records with host annotations that were also near the origin of *S. hermonthica* populations tested in experiments (Fig. 3D–F).

If parasite populations adapt to local host communities, it follows that the abiotic environments which shape host communities also shape distributions of generalist and specialist parasites (Q3). In support of our ENM-based approach, we found that host-specific ENMs readily distinguished parasite populations along environmental axes associated with differences in host performance (Fig. 4A–D). These axes may correspond to a multivariate ‘optimum’ that differs for parasites on different host species, possibly due to host environmental tolerances (Reynolds et al. 2015). Parasites may perform best on hosts that are stressed enough to exude chemical signals for recruitment of mycorrhizae, signals which are also required for parasites to sense hosts and germinate (Yoneyama et al. 2010). However, parasite reproductive fitness may be low if hosts are too stressed to provide adequate nutrition. Supporting an important role of abiotic environment in shaping distribution of specialist parasites, we found significant associations between ENM contrasts and relative parasite emergence on pearl millet and sorghum observed in common garden experiments and in pot trials (Fig. 3G–H; Supporting information).

We did not, however, observe an association between ENM contrasts and mean relative emergence for parasites of maize (Fig. 3I). Given that relative crop area harvested did predict emergence on maize (Fig. 3C; Supporting information), it may be that ENM contrasts perform poorly if alternate hosts are common. Alternate hosts may be particularly common in areas with the highest quality environments, which are also those predicted to have highest habitat suitability for parasites of maize (Fig. 4). For example, ENM contrasts predicted high suitability for maize specialization in central Nigeria (Fig. 5). However, sorghum was the dominant crop in this area in 2000 and other hosts are commonly grown (Supporting information); indeed, most tested parasite populations from Nigeria appear to be maize/sorghum generalists (Fig. 2). In addition to increased diversity of hosts in higher quality environments (Thrall et al. 2007), the observed lack of parasite specialization on maize could result from coevolutionary history. Both

sorghum and pearl millet originated in Africa, with evidence for centers of domestication for sorghum in eastern Sudan (Winchell et al. 2017) and for pearl millet in the western Sahara (Burgarella et al. 2018). In contrast, maize was domesticated in Mexico about 9000 years ago (Matsuoka et al. 2002, Piperno et al. 2009) and improved varieties bred specifically for African environments were not available until the 1980s and 1990s (Evenson and Gollin 2003).

Consequently, parasite populations in published experiments may not yet have reached a local fitness optimum with respect to performance on maize. For example, low or no emergence was recorded on maize for *S. hermonthica* from two locations (Abu Naama, Sudan and Samuru, Nigeria), although both locations had high predicted habitat suitability for parasitism on maize (Supporting information). However, in the year of each respective trial, only 2% (Sudan, 1979) or 12% (Nigeria, 1975) of total crop area harvested of maize, millet and sorghum was planted to maize (Food and Agriculture Organization of the United Nations 2020). Thirteen years later, when relative area of maize harvested in Nigeria had more than doubled (Supporting information), Kim et al. (1994) observed higher emergence on maize than either sorghum or pearl millet in 10 of 12 locations. Kim et al. (1994) also described poor reproductive success (post emergence) of parasites on maize relative to sorghum. If contemporary *S. hermonthica* populations are better adapted to maize, for example through evolution of reduced virulence but increased seed set, ENM contrasts might show stronger associations with emergence.

Taken together, our study suggests that abiotic environmental gradients shape parasite adaptation to cultivated host communities across continental Africa. Our results indicate that parasites specialize on abundant hosts in environments that strongly distinguish hosts in multivariate niche space or generalize where diverse hosts are available. If underlying abiotic drivers can predict host specialization, one promising application is the potential to inform management efforts. For example, if pearl millet production increases in the Guinean region of West Africa (Supporting information), shifting patterns in host cultivation could provide a ‘window of opportunity’ for intensive management before parasite populations

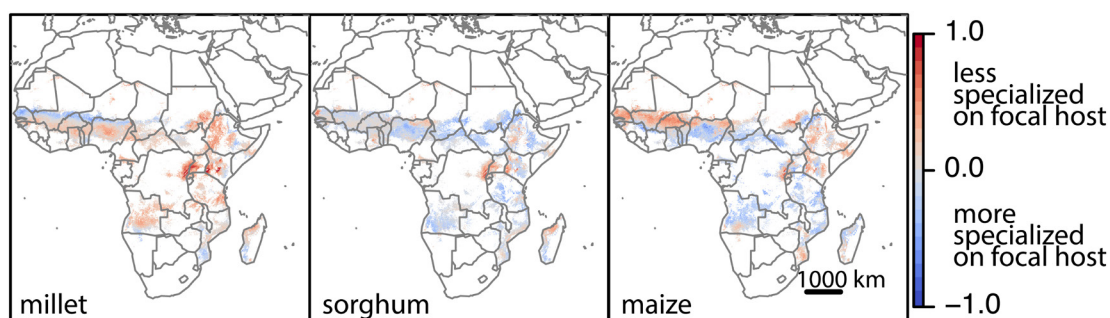


Figure 5. ENM contrasts to predict host specialization by *S. hermonthica*. Logistic output from each of the host-specific models was subtracted from the all-occurrence model, so that values close to 0 indicate similar predicted habitat suitability, negative values indicate higher habitat suitability in the host-specific model, and positive values indicate higher habitat suitability in the all-occurrence model. Pixels with habitat suitability in the all-occurrence model < 0.2 are not shown.

become locally adapted to host species or genotypes new to a region. Complete prevention of parasite reproduction on new hosts, through hand-weeding or other means, would be critical to take advantage of any 'lag' in population dynamics. The modeling framework developed here could be further extended to tailor management strategies for *S. hermonthica* and other parasites under shifting abiotic gradients linked to climate change.

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Data accessibility statement

No new data were generated. Code needed to reproduce results of the manuscript are available at <<https://github.com/em-bellis/StrigaMacroecologyMS>>.

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