Macroecology of host specialization in a parasitic plant

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Abstract

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 specialization of individual parasites or populations scales up to continental distributions. Here, we develop a macroecological framework to determine how host community structure affects continent-scale specialization in *Striga hermonthica*, an African parasitic plant of cereal crops. We find regional abundance of hosts in cultivated cereal communities is associated with parasite specialization observed in experiments. Moreover, abiotic environment at location of origin predicts parasite performance on pearl millet and sorghum but not maize, possibly due to the shorter coevolutionary history for maize and *Striga*. 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.

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ESB, CWD, and JRL conceived of the study. ESB designed geographic and environmental analyses. CMM developed linear mixed models. ESB, CMM, and JRL wrote the manuscript with input from CWD.

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Abstract:

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 specialization of individual parasites or populations scales up to continental distributions. Here, we develop a macroecological framework to determine how host community structure affects continent-scale specialization in *Striga hermonthica,* an African parasitic plant of cereal crops. We find regional abundance of hosts in cultivated cereal communities is associated with parasite specialization observed in experiments. Moreover, abiotic environment at location of origin predicts parasite performance on pearl millet and sorghum but not maize, possibly due to the shorter coevolutionary history for maize and*Striga* . 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.

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 & Ebert 2004). Local adaptation is driven by genetic variation in fitness responses to 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 (*e.g.* dispersal limitation, Pulliam 1988) obscure or counteract environmental effects.

Local adaptation is defined as a genotype-by-environment interaction for fitness such that home genotypes have higher fitness than foreign genotypes (Kawecki & Ebert 2004). Local adaptation is common but not ubiquitous, and often not detected in experiments (Leimu & Fischer 2008; Hereford 2009; 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 & 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; Fig. 1). 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 & 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; Fig. 1). Yet organisms are often excluded from ideal environments by negative biotic interactions such as competition or predation (Buckley & Roughgarden 2005). Organisms can also persistently occur in poor environments due to immigration (i.e. source-sink dynamics, 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 & 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 & Clark 2019). In contrast, host specialization (in the Grinnellian sense) refers to variance in species' performance across a range of environments (Futuyma & 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. S. hermonthica* is widespread across diverse abiotic environments in East and West Africa where it parasitizes grasses including the staple crops maize, pearl millet, and sorghum and is a major constraint to food security (Runo & Kuria 2018). Compared to pearl millet (*Pennisetum glaucum*) and sorghum (*Sorghum bicolor*), which both have centers of domestication in Africa, maize is a relatively recent host and has few natural resistances to *Striga* (Rich & Ejeta 2008; Timko *et al.* 2012). 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) leading to more balanced coevolutionary dynamics. Parasitic plants are also large and conspicuous, so excellent occurrence data are available from natural history collections. Host specialized as well as generalist populations are known (Parker & 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) Does regional abundance of a host crop lead to local specialization by parasites?, Q2) Is host specialization associated with patterns of parasite occurrence on different hosts?, and Q3) Do abiotic environmental gradients shape the distribution of specialist and generalist parasites, suggesting that future dynamics of specialization vs. generalization may be predicted by abiotic change?

Materials 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 & Zummo 1977; Ramaiah 1983; Bebawi*et al.* 1986; Kim *et al.* 1994; Appendix I). 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). They involve both pot experiments and field trials (Table S1) 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 relative emergence on host species k asRelative 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 tested host species, and n is the number of genotypes tested of host species$k$.

Using these relative emergence values, 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 relative emergence across the three hosts using the 'hclust' function in R (R Core Team 2020). 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.* 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), calculated as$PDI = \frac{1}{R-1}\sum_{i=2}^{R}(\mathbf{P}_1 - \mathbf{P}_i)$, where $\mathbf{P}_1$ is the highest link strength,$\mathbf{P}_1$ is the link strength with the i th resource, and R is the number of resources (Poisot *et al.*2012). For calculations of PDI, 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 x 5 arcminute grid cell, according to multiple years of data centered on the year 2000 (Monfreda *et al.* 2008). 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 also to 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 (soil clay content; Wilson-Jones 1955; Mohamed *et al.* 2001), host exudation and production of hormones required for parasite germination (soil nitrogen and phosphorus; 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 & 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 down-sampled to 1-km resolution using bilinear interpolation with the 'resample' function of the *raster*package (Hijmans 2020). 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. We previously found that habitat suitability values from an ENM of *S. hermonthica*were 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 (Fig. S2).

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 & Wilson nd), 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* version 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 generalized linear mixed effects models (GLMMs) to test how parasite specialization in experiments was related to 1) host community variation (crop area harvested, Q1), 2) parasite occurrence across hosts (from recorded natural history collections, Q2), and 3) predicted specialization from abiotic environment (ENM contrasts, Q3). For each of the three predictors of host specialization, we modeled relative emergence of an *S. hermonthica* population i , on a focal host as follows:

$$Emergence_{ij} = \beta_0 + \beta_1 \Xi_\imath + S_{0j} + ?_{ij} ,$$

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 occurrence, or ENM contrast), S_{0j} is the random effect of host genotype j , and $?_{ij}$is the irreducible error. Models were built 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).

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 distinct groups: millet specialists (n=2), millet/sorghum generalists (n=3), sorghum specialists (n= 7), virulent generalists (n =3), and maize/sorghum specialists (n= 10; Fig. 2). Besides the 'virulent generalists', all groups included populations from at least two studies, suggesting that differences among studies did not strongly bias clustering. 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. 3). 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. For parasites on all three hosts, relative host crop area harvested within a 50 km radius was a strong predictor of relative emergence in experimental studies. This finding was especially pronounced for millet(p_{millet}<0.001; $\beta_{\text{harvest\_area}}$=0.85; GLMM; Table S2-S3). Relative crop area harvested was also a statistically significant predictor of relative emergence on sorghum (p_{sorghum}=0.03; $\beta_{\text{harvest\_area}}$=0.25; GLMM) and maize ($p_{\text{maize}}$=0.02; $\beta_{\text{harvest\_area}}$=0.25; GLMM; Table S2-S3). 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 mixed support for a positive relationship between specialization and parasite occurrence on different hosts (Q2). 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 also a statistically significant predictor of emergence for maize (p_{maize}< 0.001; $\beta_{\text{occurrence}}$= 0.31; GLMM) but not millet (p_{millet} =0.26; $\beta_{\text{occurrence}}$=0.14; GLMM) or sorghum (p_{sorghum}=0.96; $\beta_{\text{occurrence}}$= -0.01; GLMM; Table S2). Availability of additional parasite oc-

currence 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 (Fig. S1). 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 (Table S4). 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) but was also strongly limiting for parasites of sorghum (41% of cells; 10th-90th percentile: 509-1197 mm/yr) and millet (32% of cells; 10th-90th percentile: 441-1164 mm/yr) (Fig. S3). Mean temperature of the wettest quarter was also an important predictor of *S. hermonthica* parasitizing millet (Table S4) and frequently limited habitat suitability for millet-parasitizing populations (Fig. S3). Soil clay content was an important predictor for*S. hermonthica* occurrence on sorghum (Table S4), but was only limiting for millet-parasitizing populations in eastern Sudan and sorghum-parasitizing populations in western Senegal (Fig. S3). 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 (Table S5). 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 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 & Moreno 1988; Fig. 5). Consistent with this idea, ENM contrasts were strongly predictive of variation in *S. hermonthica* performance on hosts native to Africa. ENM contrasts were most strongly associated with relative emergence on pearl millet (p_{millet}<0.001; β_{ENM} = -0.70; GLMM) and were also significantly associated with relative emergence on sorghum (p_{sorghum}=0.003; β_{ENM} = -0.52; GLMM) (Table S2, S6). In contrast, host specialization predicted by ENM contrasts was not strongly associated with relative emergence on maize (p_{maize}=0.82, β_{ENM} = 0.02; GLMM; Table S2, S6).

Future change in parasite distributions

To investigate potential changes in host-specialization over time, we projected ENMs to future climates (Fig. S4). 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 vs. 2050) and 0.09 under RCP 8.5 ($p < 0.001$; Wilcoxon signed rank test; Table S7). Habitat suitability increased most for millet-parasitizing populations, followed by maize-parasitizing *S. hermonthica* (Table S7). Changes in habitat suitability were heterogenous 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 (Fig. S4).

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 several 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 leads to 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 & Moreno 1988). However, strong empirical support for this phenomenon comes from relatively few systems (Legros & 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. 3), *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 & Michalakis 2002).

Our results suggest patterns of host cultivation are strongly associated with parasite adaptation to local host communities (Q1). Using crop harvest data to approximate relative host abundance (Fig. 3), we found that relative crop area harvested demonstrated a strong, positive association with *S. hermonthica* emergence for all three hosts considered (Table S3). These patterns were 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 (Food and Agriculture Organization of the United Nations 2020). 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.

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 also found significant associations between ENM contrasts and relative parasite emergence on pearl millet and sorghum. We did not, however, observe this trend for parasites of maize. Given that relative crop area harvested did predict emergence on maize (Table S2), ENMs may be poorly representative of realized host environment for maize. Both sorghum and pearl millet originated in Africa, with evidence for centers of domestication for sorghum in eastern Sudan (~6000 years ago; Winchell*et al.* 2017) and for pearl millet in the western Sahara (Burgarella *et al.* 2018). In contrast, maize was domesticated in Mexico about 9,000 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 & Gollin 2003).

Consequently, parasite populations in published experiments may not yet have reached a local fitness optimum with respect to maize pathogenicity traits. 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 (Fig. S1). 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 (FAO 2020). Thirteen years later, when relative area of maize harvested in Nigeria had more than doubled (to 28%; FAO 2020), Kim*et al.* (1994) observed higher emergence on maize than either sorghum or pearl millet in 10 of 12 locations. However, 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 (Fig. S4), shifting patterns in host cultivation could provide a 'window of opportunity' for intensive management before parasite populations 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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Figure Legends

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Fig. 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.

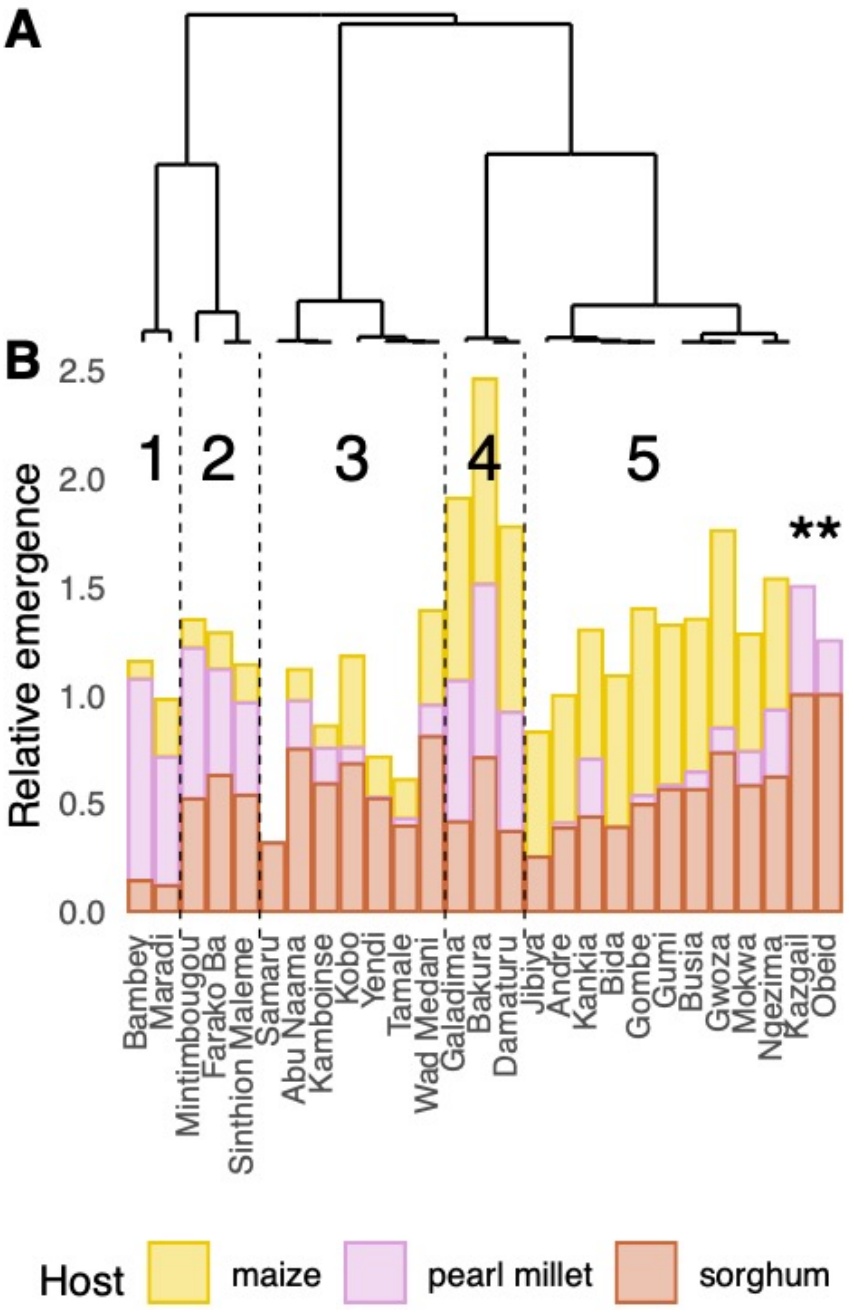

Fig. 2. Emergence of *S. hermonthica* in published studies. Relative emergence for each parasite population was calculated as the mean number of parasites across all genotypes of a particular host species, relative to the highest emergence observed for any tested host genotype. A) Dendrogram obtained from hierarchical clustering of relative emergence on three hosts. B) Relative emergence on maize, sorghum, and pearl millet for *S. hermonthica* from 27 localities. Vertical dashed lines demarcate *S. hermonthica* clusters determined in A. Asterisks indicate two populations that were excluded from the clustering analysis because emergence on maize was not tested.

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Fig. 3. 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. Black symbols (n =27) indicate group assignments from Figure 2 and the location of origin of*S. hermonthica* populations tested for emergence in empirical studies. Group 6 includes two populations that were not tested on maize.

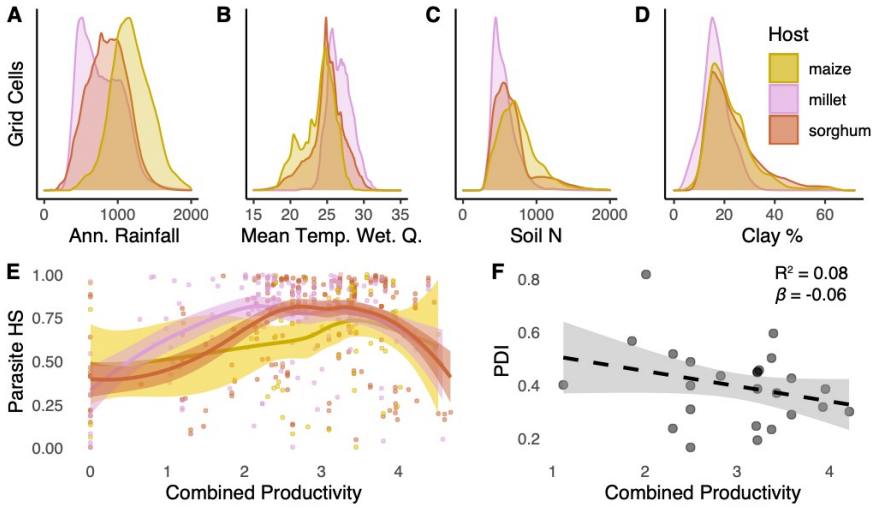

Fig. 4 . Parasite ENMs reflect host abiotic tolerances. A-D) Distribution of environmental values for grid cells in core habitat (habitat suitability [?] 0.5) for ENMs based on subsets on occurrence records on different hosts. E) Habitat suitability (HS) as a function of combined host productivity (yield 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); Mean Temp. Wet. Q.: mean temperature of the wettest quarter (°C); soil N: soil nitrogen (g/kg); clay: clay fraction (weight %)

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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.