

# Spatial patterns of persistence for environmentally transmitted parasites: Effects of regional climate and local landscape



Tyler R. Bonnell<sup>a,\*</sup>, Ria R. Ghai<sup>b</sup>, Tony L. Goldberg<sup>c</sup>, Raja Sengupta<sup>d</sup>, Colin A. Chapman<sup>e,f</sup>

<sup>a</sup> Department of Psychology, University of Lethbridge, Lethbridge, Canada

<sup>b</sup> Odum School of Ecology, University of Georgia, Athens, USA

<sup>c</sup> Department of Pathobiological Sciences and School of Veterinary Medicine, University of Wisconsin-Madison, Madison, USA

<sup>d</sup> Department of Geography, McGill University, Montreal, Canada

<sup>e</sup> Department of Anthropology and McGill School of Environment, McGill University, Montreal, Canada

<sup>f</sup> Wildlife Conservation Society, Bronx, NY, USA

## ARTICLE INFO

### Article history:

Received 8 January 2016

Received in revised form 19 July 2016

Accepted 21 July 2016

Available online 9 August 2016

### Keywords:

Climate change

Geographic information system

Helminths

Macroparasite transmission model

Primate

## ABSTRACT

Both regional climatic conditions and local landscape characteristics can affect the ability of environmentally transmitted parasites to persist outside their host. In general, implications of shifting climate conditions on the persistence and spread of parasites have been examined in the absence of interactions with local landscape characteristics (e.g., forest fragmentation). Here, we test the utility of a model that includes regional climate and local landscape characteristics to model environmental persistence of parasites. We used a system with both a well-studied landscape and data-rich host-parasite relationship and investigated how regional and local conditions affected the transmission of a parasitic whipworm (*Trichuris* spp.) within a population of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. We model persistence of a whipworm deposit in the environment as a function of both regional climate suitability and its sensitivity to the local conditions in which it was deposited. Our simulation suggests that changes to regional climate suitability impacts prevalence patterns in hosts to a larger extent than sensitivity to local landscape characteristics, with no evidence of an interaction effect. However, we find that in landscapes that offer fewer suitable sites for egg persistence (i.e., high sensitivity to local landscape characteristics), our model predicts greater variability in parasite prevalence among host groups, and a shift to source-sink parasite dynamics. Our results suggest that when modeling environmentally-transmitted parasites, explicitly considering spatial patterns of environmental persistence and host movement behaviour provides insight into transmission dynamics of specific landscape-host-parasite systems.

© 2016 Elsevier B.V. All rights reserved.

## 1. Introduction

Host-parasite systems with a parasite life stage outside the host are considered particularly susceptible in the face of climate change, as the survival of the parasite is often linked to the suitability of the climate for persistence (Brooker et al., 2004; Chammartin et al., 2014; Pullan and Brooker, 2012). Soil transmitted helminths (STHs) are one such group of parasites; eggs are shed in the feces of an infected host, where they must persist in the environment until ingested by, or come in contact with, a susceptible host (Bowman et al., 2003). STHs are also increasingly recognized as a public health

concern, given that an estimated 5.3 billion people worldwide suffer from these infections (Anderson et al., 2013; Pullan and Brooker, 2012).

In general, STH prevalence tends to increase under warm and moist conditions in both human and animal populations, as these conditions may expedite development and prevent desiccation (Chammartin et al., 2014; Chapman et al., 2010b; Pullan and Brooker, 2012). Climatic conditions have long been used to predict where a parasite can persist, and when outbreaks might occur (Gordon, 1948). For example, bioclimatographs, descriptions of the climatic envelop in which disease occurs, have been developed to predict outbreaks of STH in domesticated animals (Dobson and Carper, 1992; Gordon, 1948; Swarnkar and Singh, 2011). Changing climatic conditions and shifting patterns of seasonality have also been shown to have significant impacts on transmission (Altizer et al., 2006; Dobson and Carper, 1992; Kenyon et al., 2009). How-

\* Corresponding author.

E-mail addresses: [tyler.bonnell@uleth.ca](mailto:tyler.bonnell@uleth.ca), [tyler.bonnell@mail.mcgill.ca](mailto:tyler.bonnell@mail.mcgill.ca) (T.R. Bonnell).

ever, regional climatic conditions may not be solely accountable for changes in STH transmission. Studies examining local environmental conditions of landscapes, such as vegetation, shading, and soil type, show that these fine scale variables are also important for environmental persistence of parasites (Berbigier et al., 1990; Brown, 1927; Larsen and Roepstorff, 1999). For instance, early experiments show that microhabitats with long grass cover moderated temperature fluctuations, which improved the survival of a parasitic nodule worm larvae (*Oesophagostomum dentatum*) (Rose and Small, 1981).

While the regional effects of climate change and local microclimatic effects have been studied independently, they are infrequently considered together. Given the empirical evidence for impacts of climate and landscape characteristics on longevity of environmentally-transmitted parasites, and widespread changes in both climates and landscapes globally (Ellis and Ramankutty, 2008), there is a need to understand how changes in both of these variables are likely to alter patterns of transmission in environmentally-transmitted parasites. For example, under conditions where daily maximum temperatures increase beyond suitable ranges for a STH, the longevity of eggs in the environment are likely to be increasingly tied to the amount of vegetation in the microhabitat (Pebsworth et al., 2012). Conversely, landscape changes that reduce favorable microhabitats might have larger consequences when climate changes negatively affect longevity – such as forest fragmentation in dry, hot areas which reduce the buffering effect of high temperatures (Ewers and Banks-Leite, 2013). Changes in landscape are also likely to impact host movement patterns, which may subsequently alter deposition and uptake of environmentally transmitted parasites (Bonnell et al., 2010; Stoner, 1996). However, integrating climate, landscape, and host behaviour into a single quantitative approach presents a significant challenge due to the different scales and the dynamic nature of the variables involved (Brearley et al., 2013).

Developments in epidemiology have led to models that are able to consider spatially-explicit variables and host behavior (Ostfeld et al., 2005). One such modeling approach, spatially-explicit agent-based models, circumvent many shortcomings of traditional infectious disease models, such as assuming homogenous contact rates between hosts (i.e., compartment models). Spatially-explicit agent-based models can also include the behaviour of individual hosts, which are represented by an algorithm, and can include detailed representations of the environment in which host and parasite co-occur. The contact structure among hosts can then be considered as the result of the interactions of hosts with other hosts, as well as hosts with their environment (e.g., Lane-deGraaf et al., 2013; Nunn et al., 2014; Nunn et al., 2011). This approach offers the potential to extend models based solely on climate, by including the potential mediating effects of a heterogeneous local environment and the specific behaviours of the hosts.

Here, we develop a spatially-explicit epidemiological model to determine how regional climate and local environment interact to affect STH transmission by explicitly modeling environmental persistence of the parasite. In this model we allow environmental persistence of the STH to be a function of regional climate and local environmental characteristics in which a STH is deposited. Modifying either assumptions about the suitability of the regional climate for a STH deposit or its sensitivity to local environments conditions generates alternative scenarios of environmental persistence. The interactions between STH persistence and the movement and grouping behaviours of the host then produce alternative spatial patterns of environmental contamination, which can be associated with alternative regional climate and local landscape scenarios. As a model system, we use the endangered red colobus monkey (*Procolobus rufomitratus*) as the host and whipworm (*Trichuris* spp.), an environmentally transmitted STH, as the parasite. This system

was selected due to the availability of over four decades of data from the study site (Kibale National Park, Uganda) (Chapman et al., 2015, 2005; Goldberg et al., 2012; Jacob et al., 2014; Struhsaker, 1997), and because whipworm infection is known to be common in this population (Ghai et al., 2014; Gillespie et al., 2005). To evaluate this model, a sensitivity analysis was performed to quantify the strength of association between transmission parameters and infection prevalence at the population level. We then infected a naïve host population under alternative regional climate and local environmental scenarios, to: 1) quantify the rate at which infections spreads through a naïve host population, and 2) measure changes in the distribution of parasite infections throughout the landscape. By simulating transmission of a STH under alternative regional climate and local landscape scenarios we compare the relative effects of climate change and landscape suitability, and test for their interactions on the transmission of environmentally transmitted parasites.

## 2. Materials and methods

### 2.1. Overview

We use a spatial epidemiological model to define: 1) the landscape, 2) host behaviour, and 3) the parasite (Fig. 1). We extend similar models proposed by Nunn et al. (2014, 2011) for environmentally transmitted parasites, using empirical data to develop host behaviours and landscape structure. Our model used remotely sensed data to represent the vegetation landscape on which simulated hosts forage. Long-term behavioural data (Chapman et al., In Review; Chapman et al., 2010c; Chapman unpublished data; Snaith and Chapman, 2008) were used to develop a host movement model, simulating patterns of habitat use of red colobus. A parasitic agent with *Trichuris*-like life history parameters was then introduced into the simulated population. Our model description follows the ODD protocol: Objectives, Design concepts, and Details section (Grimm et al., 2010), which uses a standard structure, consisting of specific sections and subsection, designed to facilitate communication and comparison of agent-based models.

### 2.2. Study system

Kibale National Park (hereafter Kibale), is an isolated protected area in Uganda (795 km<sup>2</sup>) that is entirely surrounded by subsistence farmers inhabiting small villages. The park is largely composed of moist-evergreen forest (74%), grasses/shrubs (22%), and wetland areas (4%) (Chapman and Lambert, 2000; Jacob et al., 2014) and harbours exceptionally high primate biodiversity and density. One endangered primate, the red colobus, is commonly infected with whipworm (Ghai et al., 2014; Gillespie and Chapman, 2008; Gillespie et al., 2005; Goldberg et al., 2012), and show clinical signs of infection through changes in activity and feeding during periods of infection (Ghai et al., 2015). In addition, sequencing of ribosomal DNA suggests that red colobus whipworm is transmissible to other wild primates and people living adjacent to the park (Ghai et al., 2014). *Trichuris* reproduces sexually within the large intestine of its host, subsequently passing eggs in the host feces upon defecation. The eggs develop (embryonate) into infective stages within the environment, where they persist in soil and surrounding vegetation (Bowman et al., 2003). Infection of a susceptible host occurs through the ingestion of an infectious egg. Since red colobus are mostly arboreal, *Trichuris* infections most likely occur through the ingestion of contaminated leaves or the use of contaminated branches and subsequent hand-to-mouth transmission. Red colobus occasionally come to the ground to ingest soil, particularly in forest fragments (Goldberg et al., 2008, 2012), and infection may occur at this time.

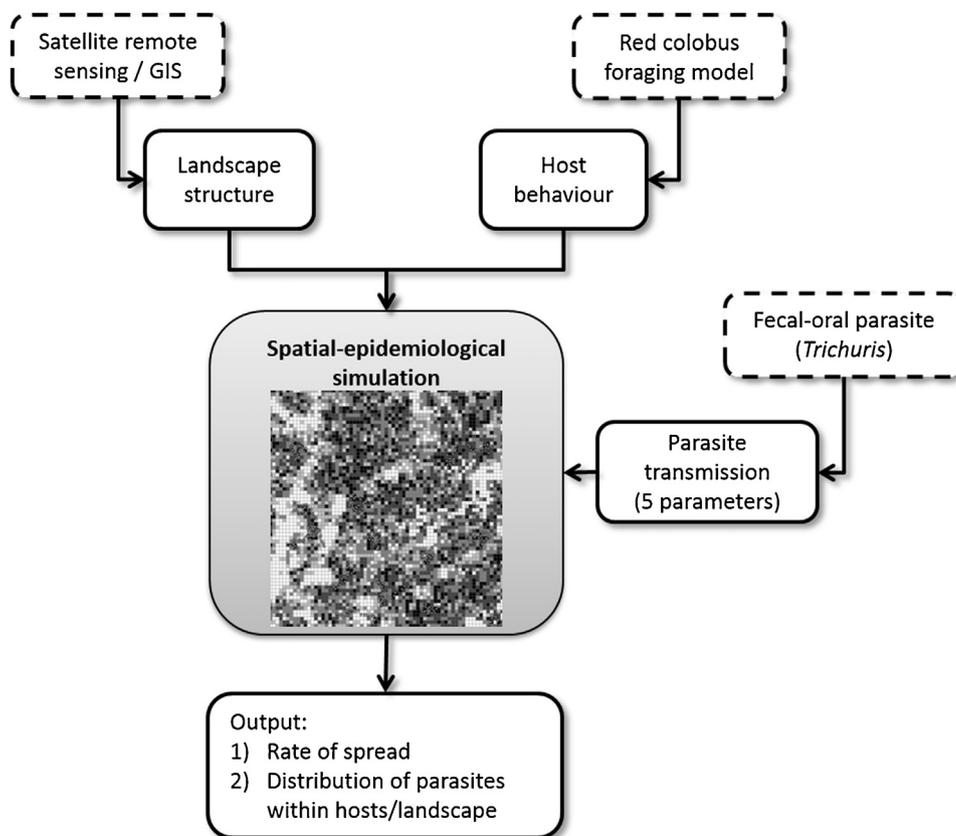


Fig. 1. Overview of model construction: incorporating landscape, host behavioural, and parasitological data.

To parameterize our model we collected data on *Trichuris* infections in red colobus. During ~5200 h of observation, we collected fecal samples deposited by focal animals and an individual was sampled only once per month. Fecal samples were collected in sterile tubes, and we recorded the date, time of collection, species, sex, individual, location, and habitat. At the end of each day, 1 g of feces was fixed in 2 ml of 10% formalin. Samples were shipped to McGill University for analysis. To identify *Trichuris*, we used a modified formalin-ethyl acetate concentration method, as recommended by the Clinical and Laboratory Standards Institute for the recovery of intestinal parasites (Garcia et al., 2005; Young et al., 1979). The entire sediment, typically 5–15 slides, was examined under 10× objective magnification and the presence of *Trichuris* eggs was recorded (Gillespie et al., 2005; Greiner and McIntosh, 2009; Hodder and Chapman, 2012). From these data (n=98 individuals), prevalence of infection was found to be 43.7%.

### 2.3. The model

#### 2.3.1. Purpose

The model was designed to quantify the consequences of varying parasite longevity, that could result from regional climate change and changing landscape characteristics, on transmission of an environmentally transmitted parasite in a population of red colobus.

#### 2.3.2. Entities, state variables, and scales

The model was composed of red colobus agents that foraged on a gridded resource landscape as points in continuous space. *Trichuris* was modeled as discrete groups representing the 4 stages of their lifecycle: 1) non-infective eggs in the environment, 2) infective eggs in the environment, 3) larvae developing in the red colobus

host, and 4) adults in the large intestine of red colobus. Red colobus agents had state variables: desired number of nearby group mates, group identity, energy level, and the presence or absence of larvae and adult stage parasites in their gut. Landscape grid cells had state variables: resource level, number of non-infectious egg, and number of infectious egg deposits. *Trichuris* deposits (i.e., defecations containing *Trichuris* eggs) had state variables: age and life cycle stage.

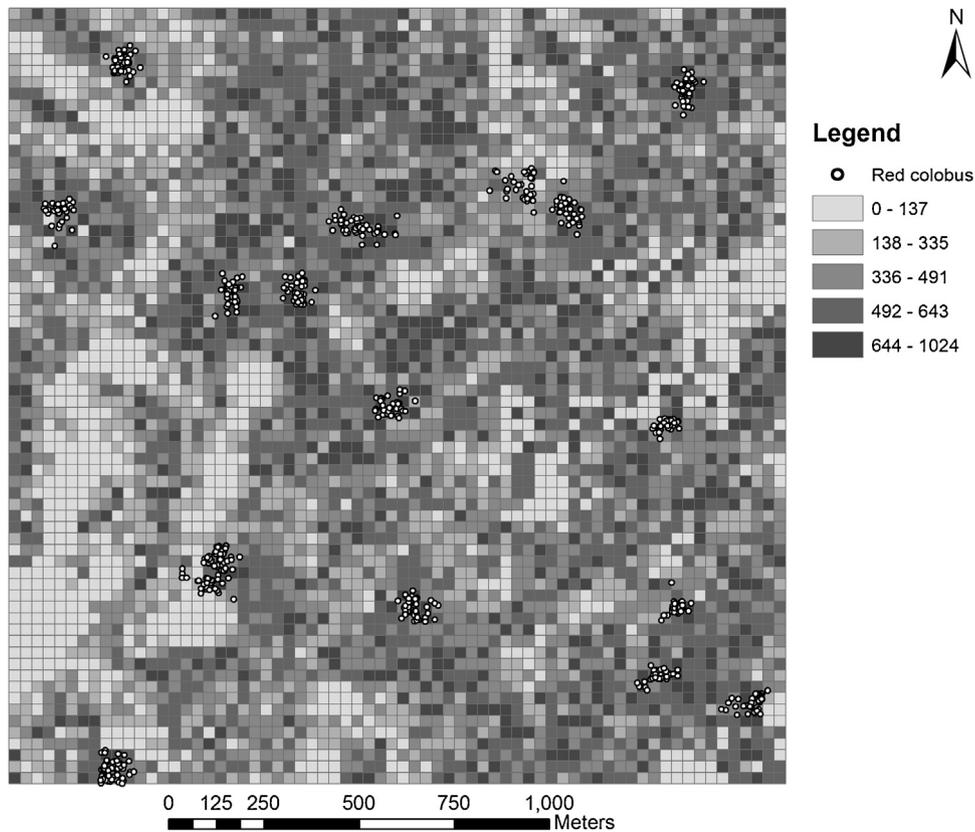
The model covered a 2 × 2 km area encompassing 17 red colobus groups (see Section 2.3.3, “Input Data”) and was run to simulate 5 years, in which each day was represented by 26 half-hour steps (Fig. 2). Half-hour steps were chosen as this was the frequency with which behavioural data were recorded (Snaith and Chapman, 2008). Red colobus are generally active from 06:30 to 19:30 (Struhsaker, 2010), resulting in 26 half-hour steps per day. The period of 5 years was chosen as this was found to be sufficient time for the model to converge around a steady mean prevalence (with some random fluctuations).

#### 2.3.3. Process overview and scheduling

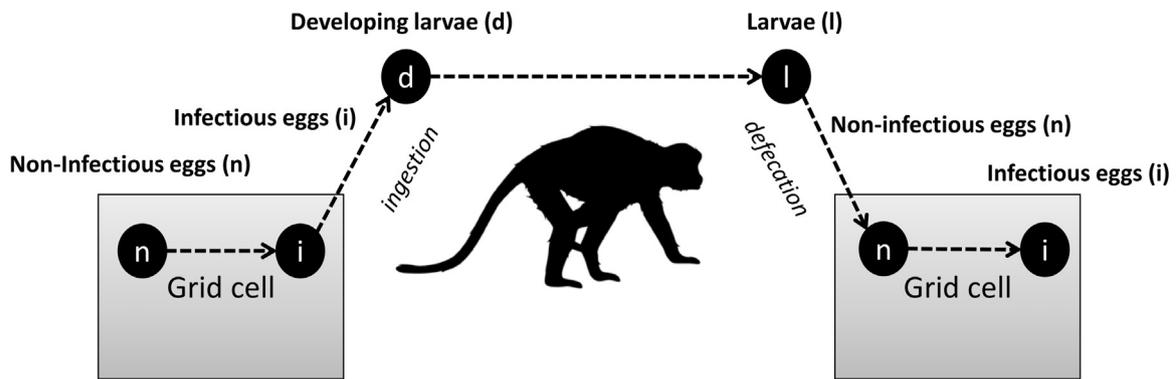
At each time step all primate agents updated their information about their local external environment, as did the parasite populations within the gut of the host. Each primate agent then performed an action based on a behavioural algorithm, responding to its particular surroundings and internal states (see submodel: *Red-colobus-movement*). At the end of each step, all grid cells in the landscape regrew at a constant rate and parasite populations within grid cells were updated.

#### 2.3.4. Design concepts

**Basic principles:** The model was composed of three main parts: landscape, host, and parasite. The goal of our host model was



**Fig. 2.** Model environment for simulating the spread of an environmentally transmitted parasite. Grid cells are shaded light to dark based on the amount of resources, and red colobus agents are represented as points organized into groups.



**Fig. 3.** Model used to represent the life-cycle of a fecal-oral parasite. The progression of a parasite is presented, maturing from an initial group of non-infectious eggs in the environment to a reproduction stage within a host to defecation and formation of a new parasite deposit.

to reproduce the spatial-temporal habitat use of the host population. To do so, we simulated the movement and grouping behaviour of red colobus (see submodel: *Red-colobus-movement*) on a spatially-explicit environment derived from satellite remote sensing data (see details section: input data). Transmission of parasites through this simulated population depended on five parameters that reflect a fecal-oral mode of transmission: maturation time in the environment, life expectancy in the environment, probability of host ingesting a parasite, maturation time in the host, and life expectancy in the host (Fig. 3, see submodel: *parasite-transmission*).

**Host contact structure:** Red colobus were organized into distinct groups. Individuals within the group were able to see food sites within a 50 m food-search-radius, as well as other red colobus within a larger radius of 200 m. When a red colobus moved, it

affected the safety and foraging choices of others in its group, resulting in grouping and range use patterns similar to those observed red colobus in nature (Bonnell et al., 2013).

**Model Output:** We recorded the speed of spread and the distribution of parasites within the host population. To monitor spread, we recorded the number of infected hosts and grid cells at each time step, and estimated a growth rate based on logistic function using the *grofit* package (Kahm et al., 2010) in the R programming environment (R Core Team, 2015). To monitor the distribution of parasites in hosts, we measured prevalence at the population and group level. At the landscape level, we estimated final area contaminated by the parasite (i.e., grid cells holding egg deposits). We also recorded the total number of eggs deposited, the total number of transmission events, and the total number of visits to each grid cell.

### 2.3.5. Initialization/Input data

Input data were used to represent landscape characteristics and host density patterns. Satellite imagery from the SPOT-5 sensor (Satellite Pour l'Observation de la Terre) (November 2008) were used to develop a resource landscape for the red colobus. The image was geo-referenced and unscaled to radiance values in Envi 4.8, without atmospheric correction. Radiance measures in the remote sensing data were compared with forest data comprised of 26 vegetation plots (10 × 200 m) containing measures of total DBH of red colobus food trees (Chapman et al., 2010a). Linear models comparing the total DBH of red colobus food to average pixel values within these transects were created. Using the “leaps” package in the R programming environment (Lumley, 2009; R Core Team, 2015) and comparing models using Bayesian Information Criterion (BIC), a final model was selected. BIC is a model selection criterion to choose among a set of models, based in part, on a likelihood function. It is closely related to Akaike information criterion (AIC). The final model used the green spectral band and the variance in the NIR (near infrared) spectral band (9 × 9 window) from the SPOT-5 sensor, and showed an adjusted r-squared value of 0.41,  $p < 0.001$ .

$$DBH = -5.6(Var_{nir}) - 76.3(Green) + 4440.6 + \varepsilon(N(0, 248)) \quad (1)$$

The residuals of this model comparing the 26 vegetation plots to satellite spectral measures were found to be normally distributed (Shapiro-Wilk,  $W = 0.97$ ,  $p = 0.63$ ), and not heteroskedastic (Studentized Breusch-Pagan test,  $BP = 3.94$ ,  $df = 2$ ,  $p = 0.14$ ). The independent variables were also not significantly correlated (Pearson's product-moment correlation:  $r = 0.33$ ,  $t = 1.7$ ,  $df = 24$ ,  $p = 0.10$ ). The use of the green band and the variance in the NIR band is consistent with other linear models using the SPOT-5 sensor to quantify forest biophysical characteristics, such as above ground biomass and basal area (Castillo-Santiago et al., 2010).

To extrapolate this linear model to areas surrounding vegetation plots, the SPOT-5 image was used to classify land cover. An unsupervised classification algorithm was used to identify 5–10 spectrally similar land covers (ISODATA, ENVI 4.8). Seven land covers were identified by the unsupervised classification algorithm. The best classification, testing against ground reference data, augmented by points taken from Google Earth imagery (geo-eye 2010), resulted when these spectrally similar land covers were re-grouped into 4 types: forest, agriculture/shrub, bare soil, and water. Finally, swamp land cover was separated from land cover classified as forest using a decision tree approach, classifying forest pixels as swamp if:  $EVI < 0.26$  (enhanced vegetation index),  $NIR < 100$ , and topography was classified as a plane, channel, or pit. Topographic classification was achieved using ENVI's topographic feature extraction tool (ENVI 4.8), and plane, channel, and pit were selected as important features as they suggest landscape topography which facilitates swamp formation (i.e., as opposed to peaks, or ridges). Our chosen values produced a land cover classification with an overall fit of 84% (Supp. Table 1). An estimate of the total DBH of red colobus food trees per forest pixel was calculated using the linear model Eq. (1). Other land cover classes were assigned a value of zero, as these habitats were either not used by red colobus groups (i.e., swamp, bare land, water) or very rarely used (i.e., agriculture/shrub – CAC unpublished data).

The DBH surface derived from the remotely sensed data was then used in the simulation model to estimate red colobus food availability. To convert DBH values to food availability and to select food regrowth rates, we compared movements of simulated groups to observed groups. We found that a conversion of 0.58 energy/DBH (resulting in an average energy per forest grid cell of 500), a regrowth rate of 1.7 energy/step, and memory of high resource sites within 500 m of their starting location reproduced observed home range sizes: 4 groups (size: 25, 40, 45 and 52) in the study area showed an average monthly home range of 35.5 ha

(Snaith and Chapman, 2008), compared to 33.7 ha from the simulated groups. The regrowth rate of 1.7 energy/step resulted in a recovery time of an average site to be approximately 11 days. This fits well with what is known of the regrowth of young leaves (the primary red colobus food source) in tropical forests, which are generally in expansion (from bud to mature leaf) for only 1–3 weeks (Coley and Barone, 1996).

Population density was defined as the number of groups within the 4 km<sup>2</sup> area. Line transect data estimated a density of groups in the study area of 4.2 groups per km<sup>2</sup> (Chapman et al., In Review; Chapman et al., 2010c). To match these data we populated the simulation with 17 groups (4.2 groups/km<sup>2</sup> \* 4 km<sup>2</sup> = 16.8), where each group size was selected from a probability distribution based on group size counts of known groups in the region (~N (mean = 47, sd = 4)) (Gogarten et al., 2014). This resulted in an average of 200 individuals/km<sup>2</sup> (47 individuals/group \* 17 groups/4 km<sup>2</sup>), which compares well with empirical estimates of approximately 176–219 individuals/km<sup>2</sup> (Struhsaker 2010 pp.76, Chapman unpublished data). Groups were placed in set starting locations in the landscape at the beginning of each simulation. These set locations were randomly chosen, where all starting locations were at least 100 m apart and within grid cells classified as forested.

### 2.3.6. Submodels

*Red-colobus-movement and intergroup dispersal:* We used a movement model developed in Bonnell et al. (2013), where various individual-based movement models were tested against observed red colobus group movement patterns. In this model we selected the movement model that was most successful in representing observed movement patterns: leader led groups. Here, individuals use a landmark-based memory in which agents can remember up to 20 food sites. We initialized the memory of individuals within groups at the start of each simulation by giving them knowledge of the highest value food sites within 35.5 ha (average observed home range size) (Snaith and Chapman, 2008). Individuals in this model chose to move by balancing competing goals of safety and foraging. Specifically, agents attempt to limit feeding competition by lowering the number of group mates nearby, and to maximize safety by being near as many group mates as possible. Priority between these competing goals shifted based on individual foraging success, maximizing safety when feeding was good and lowering safety when feeding was low. Resulting group movements resembled observed patterns (Bonnell et al., 2010).

We added two additional behaviours to the model that are thought to be important for helminth transmission: the use of sleeping sites and dispersal of individuals between groups. Returning to the same sleeping sites may influence exposure to a parasite with an immobile life-stage in the external environment (Gilbert, 1997; Hausfater and Meade, 1982; Markham et al., 2015). We thus added the requirement each night that the group seek out a sleeping site. Two hours before the end of the day (18:00) the leaders' safety was made dependent on being in a sleeping site. Sleeping sites were assigned as any remembered site which had resources remaining, which agrees with natural history observations.

Dispersal of individuals between groups can play an important role in parasite spread (Cross et al., 2009). We included dispersal within the model by introducing a probability that an individual will disperse from a group ( $P_{\text{dispersal}}$ ). If dispersal occurs, the individual no longer considers group mates while foraging and forages on its own until it sees another non-native group to which it can join. Detailed behavioural observations have identified ~3 immigrations per year (Struhsaker, 2010). By varying the probability of dispersal in our model and monitoring the average number of immigration events into each group per year, we selected a dispersal probability that yielded an average of 3.45 (sd = 0.21) annual immigrations per group.

**Table 1**  
Parameters used to describe transmission of nematode groups, and the range of values tested.

Location	Parameter	(min, max)	Units	Description (Refs.)
Environment	$M_{n,i}$	(14,28)	Days	Maturation time (Acha and Szyfres, 2003)
	$D_{env}$	(28,84)	Days	Life expectancy (Acha and Szyfres, 2003)
	$P_{i,l}$	(0.000001, 0.0001)	%	Probability of being ingested
Host gut	$M_{l,a}$	(56,84)	Days	Maturation time (Acha and Szyfres, 2003)
	$D_{host}$	(0.5,1.0)	Years	Life expectancy (Anderson et al., 2013)

**Parasite Transmission:** The basic unit in the parasite model was chosen as a group of *Trichuris* parasites. Within a group, age, time to maturation, and life stage was assumed to be homogeneous. Each fecal deposition of eggs into the environment created a new parasite group. Subsequent transmission, survival, and reproduction were modeled at the level of these groups. Each group contained an age, and current life stage: non-infectious eggs (n), infectious eggs (i), developing larvae (l), and adult (a) (Fig. 3).

A newly deposited group of non-infectious eggs passed through a latent period ( $M_{n,i}$ ), before eggs were considered infectious. Groups in the environment had a life expectancy of  $D_{env}$ , where eggs were considered to have died or to have become unavailable to red colobus hosts (e.g., washed away by rainfall), modeled by a negative binomial distribution. The negative binomial distribution allows for over-dispersion in the death rate, such that most groups are removed fairly quickly (mean longevity =  $D_{env} = p/(1-p)$ ), but some groups remain available in the environment for extended periods. Ingestion by a local host (i.e., within the same grid cell) was modeled as a random probability of ingestion ( $P_{i,d}$ ). If ingestion occurred, a new developing larvae group was introduced into the host's gut. This group passed through a latent period ( $M_{d,l}$ ), after which it matured to the adult stage. An adult group in the host intestine then had a life expectancy of  $D_{host}$ , after which point it was removed from the host. While alive in the host, non-infectious groups were passed when defecation occurred, creating a new *Trichuris* group in the environment. Individual defecation rate was determined by a set random probability ( $P_{defecation}$ ) with a mean of 5 defecations per day (Chapman unpublished data).

#### 2.4. Analyses

We set the range of parasite parameters based on empirical data on *Trichuris* transmission derived from other host systems (Acha and Szyfres, 2003; Petkevicius et al., 2007; Roepstorff and Murrell, 1997) (Table 1) and used a Latin Hypercube Sampling (LHS) regime to select 100 points from the parameter space. LHS is a statistical method of choosing stratified-random parameter values from a range of possible values (Blower and Dowlatabadi, 1994). The model was then run for each parameter set, where one individual of a group living on the edge of our landscape was infected with 10 adult larvae at the start of each simulation. We then monitored prevalence of the parasite population under each parameterization at the end of a 5 year simulation. To quantify sensitivity of model results to individual parameters, we estimate standardised regression coefficients and estimated standard errors by bootstrapping ( $n = 1000$ ) (Pujol et al., 2012).

To select the best-fit parameterization we compare simulated and observed prevalence from the red colobus population. An optimization algorithm, BOBYQA from the nloptr package in R (Johnson, 2015; Powell, 2009), was run to find the parameterization which minimized the total distance between the observed prevalence and simulated prevalence. A measure of uncertainty around the best-fit parameterization was estimated by running the model using the optimal parameterization 30 times.

With the best fit parameterization we then tested the effects of changing the mean longevity of *Trichuris* deposition in the environment. Mean longevity of a parasite deposit was determined by

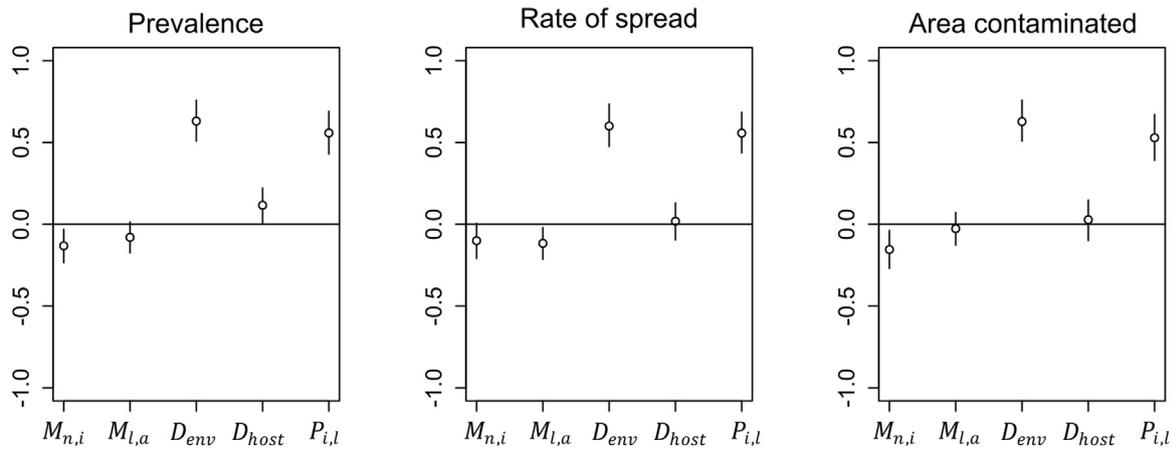
a function of both the regional climate and of the local landscape characteristics in which it was found. By altering the suitability of the regional climate or the sensitivity to local landscape characteristics we then generate various environmental persistence scenarios. For example, a scenario in which there is low climate suitability and high sensitivity to local landscape characteristics might reflect hot dry regional climate conditions, where a deposit of eggs in the open sun might die faster than that of a deposit under heavy vegetation. Similarly, high regional climate suitability and low sensitivity to local landscape characteristics might reflect warm moist climatic conditions, where being deposited under vegetation might have less of an effect on longevity. We thus vary both regional climate suitability ( $S_R$ ) for the parasite in the external environment, as well as the sensitivity to local landscape characteristics ( $S_L$ ). We treat regional climate suitability as the average number of days a deposited group of *Trichuris* eggs will persist in the environment under ideal local landscape conditions. Any variation from local landscape ideals resulted in decreased longevity, where the magnitude of this decrease was determined by the degree of sensitivity to landscape characteristics ( $S_L$ ). In our model ideal conditions represent heavily forested regions and variation away from this ideal was measured as the difference between the maximum observed DBH and the DBH of the grid cell in which the parasite was deposited. We varied regional climate suitability  $S_R$  between 5 and 34 days, and vary the sensitivity to reduction in vegetation  $S_L$  from 0.01 to 0.1 days/ $\Delta$ DBH. Thus mean longevity of a  $D_{env,j} = S_R - S_L (DBH_{max} - DBH_j)$  deposit in grid cell  $j$  ( $D_{env,j}$ ) was determined by eq 2:

Where  $DBH_{max}$  was the maximum estimated DBH value in the landscape. To compare the relative effects of regional climate suitability and sensitivity to local vegetation we vary both (e.g., Fig. S1), selecting 100 values from a Latin-hypercube sample, and tested for interactions using linear regression. Separate regression lines were fit for each model outcome: rate of propagation of infections, final population prevalence, and final area contaminated. Regression models were fit in R using model outcomes as a dependent variable, and  $S_R$ ,  $S_L$  and an interaction term ( $S_R * S_L$ ) as dependent variables. In cases where non-linearity was an issue, the dependent variable was corrected using a boxcox power transformation to normalize the model residuals. Data points in which the parasite population went extinct were excluded from the regression analyses ( $N = 13$ ).

### 3. Results

#### 3.1. Model sensitivity analysis and best-fit parameterization

By running the model with the 100 parameter sets chosen by LHS and estimating the standardized regression coefficient for each parameter, we were able to quantify the sensitivity of model results to each parameter. Changes in the transmission probability ( $P_{i,l}$ ) and mean parasite longevity in the environment ( $D_{env}$ ) resulted in the largest changes in the final area contaminated by the parasite. Similarly, transmission probability and the longevity of the parasite in the environment were also most influential with respect to rate at which infections increased in the population and final infection



**Fig. 4.** Sensitivity analysis of transmission parameters on infection outcomes. Parameters varied were: maturation in the environment ( $M_{n,i}$ ), maturation in the host ( $M_{l,a}$ ), death in the environment ( $D_{env}$ ), death in the host ( $D_{host}$ ), and transmission probability ( $P_{i,l}$ ).

prevalence. In all cases, increasing transmission and longevity had positive effects (Fig. 4). To a lesser degree, egg maturation time in the environment ( $M_{n,i}$ ) had a negative effect on prevalence and final area contaminated. The duration of the infection in the host ( $D_{host}$ ) showed no significant effects on the final area contaminated or rate of spread, but did show a small positive effect on final prevalence. Finally, maturation of the infection from a larval state to an adult state in the host ( $M_{l,a}$ ) also showed a small negative effect on the rate of spread of infections in the population.

The parameterization that deviated least from observed prevalence in red colobus (43%) was used as the starting value for the optimization algorithm (i.e., minimizing the difference between observed prevalence and prevalence in the simulation). The algorithm converged at a best fit parameterization of:  $M_{n,i}$  = 27 days,  $D_{env}$  = 16 days,  $M_{l,a}$  = 77 days,  $D_{host}$  = 225 days,  $P_{i,l}$  =  $9.03 \times 10^{-5}$ . Running this best fit parameterization 30 times resulted in a mean prevalence of 46% (standard deviation of 2%), and a mean area contaminated of 271 ha (standard deviation of 6 ha).

### 3.2. Distribution of parasites within hosts

The population level prevalence at the end of five years showed a sigmoidal response to changes in regional climate suitability (Fig. 5a) and a linear decline in response to increased sensitivity to the amount of vegetation (Fig. 5b). Comparing the relative effects of both, our results suggest that shifts in regional climate suitability were more influential on final prevalence compared with shifts in sensitivity to local vegetation, with no evidence of an interaction effect (standardized coefficients:  $S_R$  = 0.99,  $S_L$  = -0.34,  $S_R * S_L$  = 0.002) (Table 2). Comparing the variability in prevalence between red colobus groups, we find that the changes in sensitivity to local vegetation lead to more variability in group level prevalence when compared to changes in regional climate suitability (Fig. 5c and d).

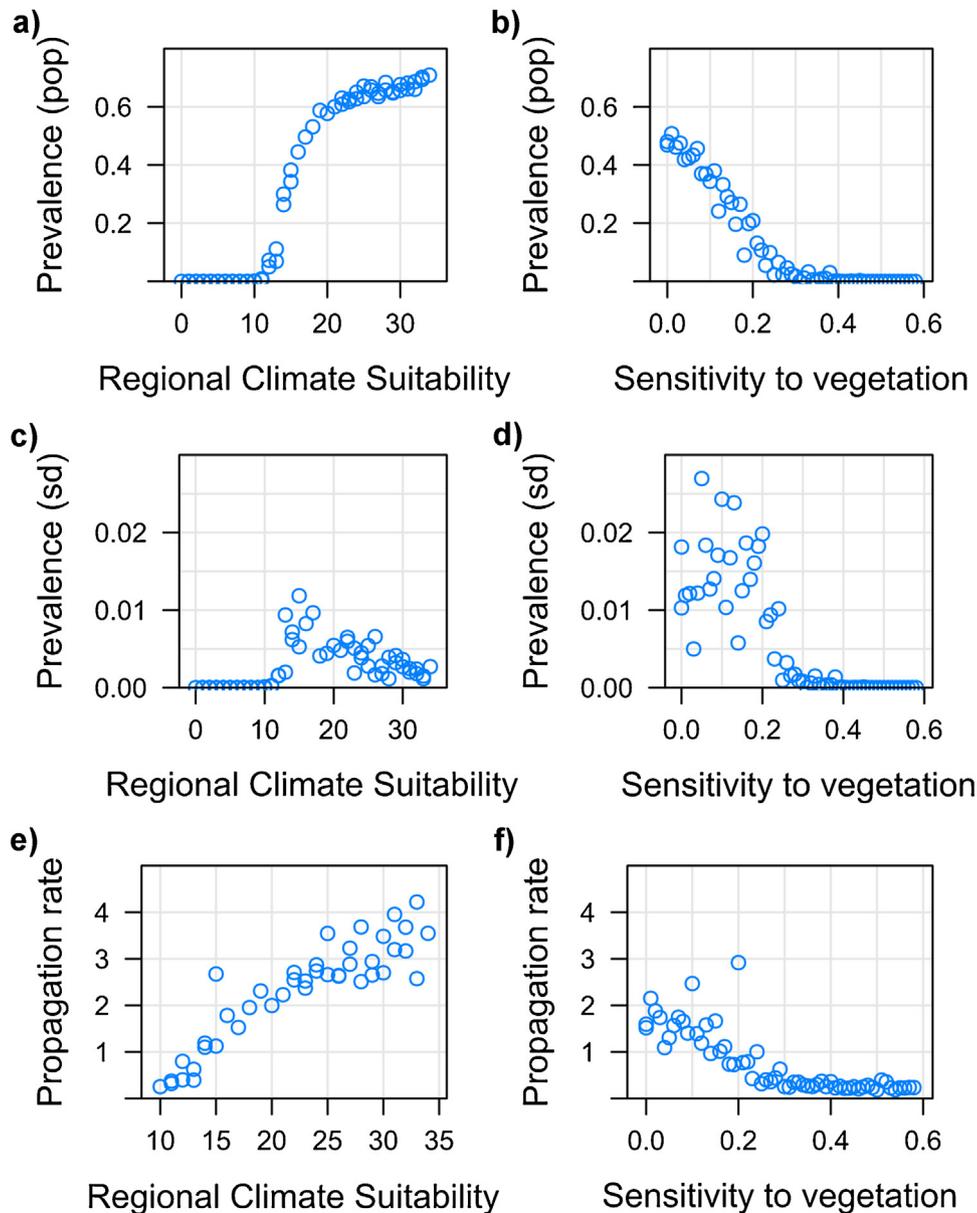
Starting from the initial infection of one individual, varying regional climate suitability resulted in a linear relationship with the speed at which the parasite spread through the host population (Fig. 5e). When sensitivity to local vegetation was increased the speed of propagation was reduced (Fig. 5f). Considered together we find that variability in regional climate suitability resulted in much larger impacts on propagation compared to sensitivity to local vegetation, again with no evidence of an interaction effect (standardized coefficients:  $S_R$  = 0.85,  $S_L$  = -0.29,  $S_R * S_L$  = 0.09) (Table 2).

### 3.3. Distribution of parasites on the landscape

The total area contaminated by parasitic eggs at the end of the simulation followed a sigmoidal response as regional climate suitability was varied and a relatively linear decline as parasites became more sensitive to local vegetation (Fig. 6a and b). The combined effects of regional climate suitability and sensitivity local vegetation on the final area contaminated indicated that regional climate suitability had the largest effect and again there was no evidence of an interaction (standardized coefficients:  $S_R$  = 0.95,  $S_L$  = -0.39,  $S_R * S_L$  = 0.07) (Table 2). Variation in regional climate suitability resulted in a sharp sigmoidal curve in the magnitude of correlation between the total egg deposits within a grid cell and total number of successful transmission events in that same grid cell. In response to increased sensitivity to local vegetation, the correlation between eggs deposited and transmission events occurring in a grid cell showed a linear decline (Fig. 6c and d).

## 4. Discussion

The results of our model suggest that changes to the suitability of the regional climate had the largest effects on infection prevalence, rate of propagation, and area contaminated, when compared to changes in sensitivity of the parasite to local landscape characteristics (i.e., amount of vegetation). In scenarios where environmental persistence was highly sensitive to local landscape characteristics, resulting in landscapes that presented few suitable locations for egg persistence, we found high resilience of the simulated parasite to both persist and spread. The few locations on the landscape that provided suitable conditions for parasite longevity delivered adequate exposure to the host population to both maintain and spread the parasite. However, under the condition of high sensitivity to landscape characteristics the correlation between the number of eggs deposited in a given grid cell and the number of transmission events occurring in that same grid cell were reduced (Fig. 6). This suggests that the population dynamics of the parasite increasingly resembled a source-sink pattern as sensitivity to vegetation increased, such that a few grid cells (sources) generated the majority of transmission events, and the majority (sinks) resulted in very few transmission events as deposits quickly died off (Fig. 7). This heterogeneous pattern of spatial contamination subsequently resulted in more heterogeneous patterns of infection, where differences in prevalence measured between groups increased (Fig. 5). This increase in variation between groups largely depended on the landscape characteristics within each group's home range (e.g.,



**Fig. 5.** Distribution of parasites within the host population: a-b) final population prevalence resulting from changes to regional climate suitability ( $S_R$ ) and sensitivity to local landscape characteristics (i.e., vegetation) ( $S_L$ ), c-d) variation in prevalence between groups resulting from changes to  $S_R$  and  $S_L$ , and e-f) estimated rate at which prevalence increased based on changes to  $S_R$  and  $S_L$ .

**Table 2**

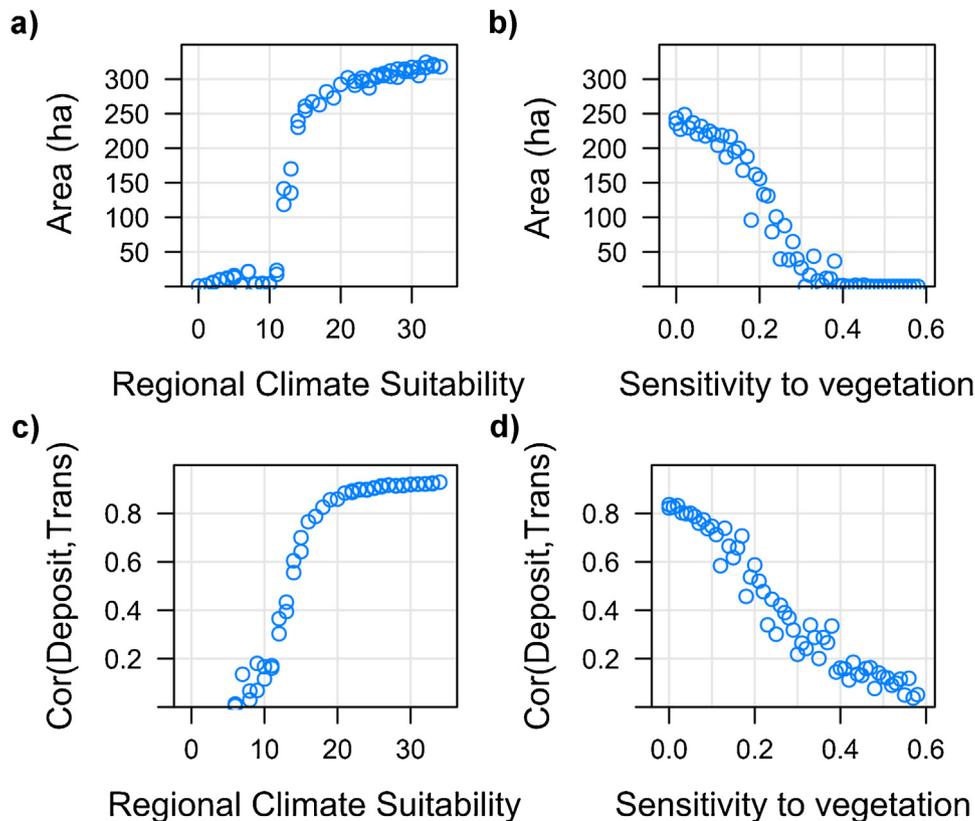
Comparing the strength of regional climate and local landscape parameterization on the distribution of parasites: prevalence in the host population, propagation speed through the host population, and area contaminated with parasites at the end of the simulation. Coefficients presented are standardized to be comparable.

Parameter	Prevalence (se)	Propagation (se)	Contamination (se)
Regional climate suitability ( $S_R$ )	0.99 (0.03)	0.85 (0.07)	0.95 (0.04)
Local landscape suitability ( $S_L$ )	-0.34 (0.03)	-0.29 (0.07)	-0.39 (0.04)
Interaction ( $S_R * S_L$ )	0.002 (0.002)	0.09 (0.07)	0.07 (0.04)
F-statistic	$F_{3,83} = 358$	$F_{3,83} = 54$	$F_{3,83} = 165$
p-value	<0.01	<0.01	<0.01
Adj r-squared	0.93	0.65	0.85

suitability for egg longevity) and group location within the larger population (e.g., isolated groups).

Using a similar spatially-explicit agent-based modelling approach, Nunn et al. (2014, 2011) examined the spread of gastrointestinal parasites through a socially structured population in a uniform environment and a more seasonal environment. Using this approach, these authors varied group movement and trans-

mission parameters and quantified their effects on the spread of an environmentally transmitted parasite. Similar to our sensitivity analysis, they found that the duration of the infectious period in the soil (i.e., environmental persistence) was an important parameter in determining transmission within the simulated hosts. Our results suggest that the inclusion of regional and local influences on persistence in the environment can significantly alter the pat-



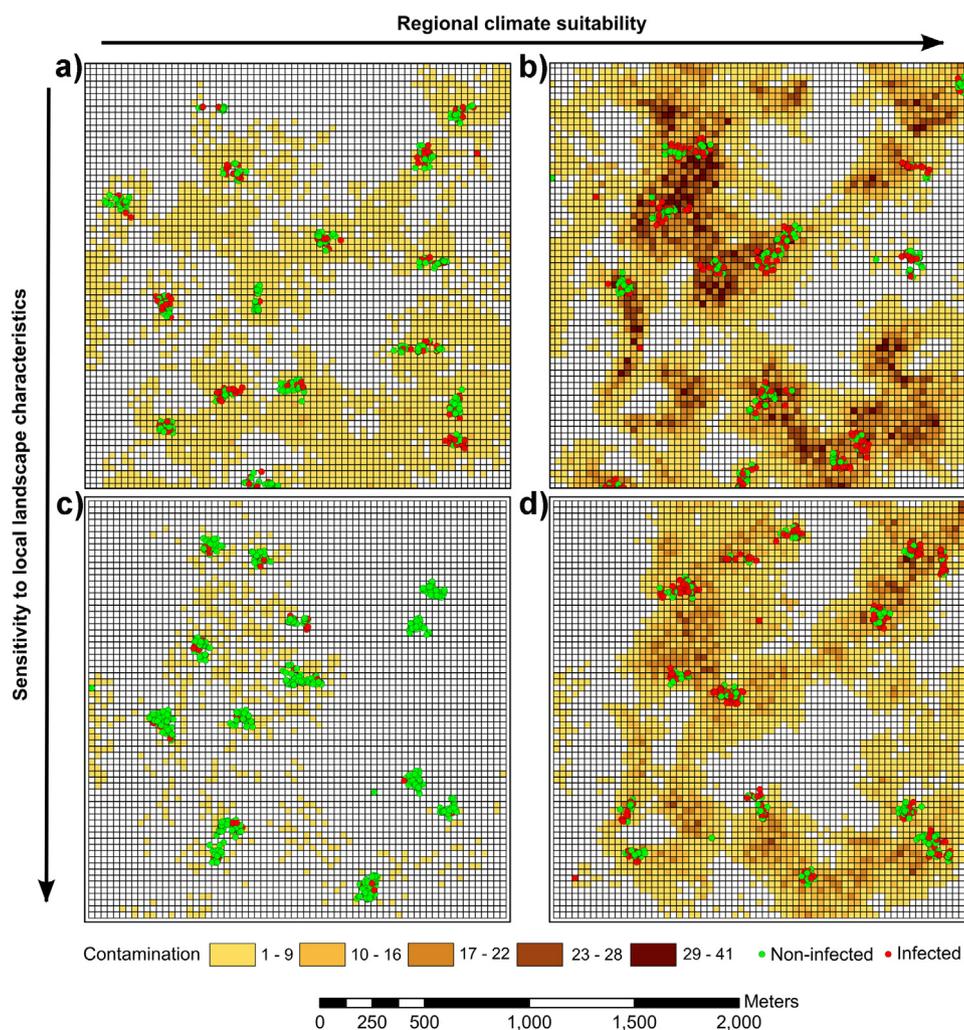
**Fig. 6.** Distribution of parasites on the landscape: a–b) total area containing parasites at the end of the simulation resulting from changes to regional climate suitability ( $S_R$ ) and sensitivity to local landscape characteristics (i.e. vegetation) ( $S_L$ ), and c and d) magnitude of the correlation between the amount of parasite deposits within a grid cell and the number of transmission events occurring in that grid cell as a result of changes in  $S_R$  and  $S_L$ .

terns of environmental contamination, and can have implications for infection patterns in the host (e.g., higher infection variability between groups). Additionally, Nunn et al. (2014, 2011) found that altering the ranging behaviour of the host altered subsequent transmission of the parasite. In our model behaviour was fixed, parameterized to movement data collected on the red colobus of Kibale. However, there is evidence that behaviour changes with infection status. Specifically, in our host population, *Trichuris* infections are known to be associated with increased resting, decreased energetic activity, and changes in foraging behaviour (Ghai et al., 2015). In addition, climate may also be associated with behavioural changes that may influence risk of infection. For example, temperature and precipitation have been associated with the length of travel by primate groups during a day (Johnson et al., 2015). This suggests that further work could include behavioural changes of hosts made in response to infection and climate.

Climate data from Kibale shows long-term, temporal variation in rainfall and temperature. Longer drought events, more time between rainfall events, and a warming trend have been identified (Hartter et al., 2012; Saulnier-Talbot et al., 2014) and an increase in rainfall suggested (Chapman et al., 2011). The development and survival of *Trichuris* sp., in the environment is negatively affected by high temperatures (max survival at 37–40 °C), temperature variation (Chammartin et al., 2014), and low relative humidity (Pullan and Brooker, 2012; Weaver et al., 2010). Drier, more prolonged drought periods would then be expected to 1) decrease regional climate suitability of STH reducing the mean life-expectancy of eggs outside the host, and 2) increase differences in life-expectancy of eggs due to spatial variation in microclimate conditions resulting from local landscape characteristics (e.g., open vs. vegetated areas). Our model suggests that a reduction in the suitability of regional climate conditions will have a larger effect on host prevalence levels

than local landscape characteristics. Similarly, our model suggests that increases in the degree to which persistence depends on local landscape characteristics will lead to more heterogeneous patterns of infection within the host population.

Given that greater variation in microclimates occur in more fragmented landscapes (Kapos, 1989), it is probable that changes in climate will have more of an impact on patterns of transmission in fragmented and more heterogeneous landscapes. Indeed, identifying refugia from climate change at fine scales has been recently suggested as a useful management tool for conservation (Ashcroft, 2010; Dobrowski, 2011; Keppel and Wardell-Johnson, 2012). In which microhabitats are identified where species can persist due to buffering effects of landscape characteristics on changes in climate (Keppel and Wardell-Johnson, 2012; Varner and Dearing, 2014). For example, regional climate scenarios suggest that East Africa will become wetter and hotter (Chapman et al., 2010b; Christensen et al., 2007) suggesting that landscape characteristics which buffer against high temperatures (desiccation) and runoff (non-availability to hosts) will increasingly provide refugia for STH eggs outside the host. In the context of environmentally transmitted parasites, this search for safe-haven habitats might be useful for identifying sources and sinks on the landscape from the point of view of the parasite, particularly when combined with movement and grouping patterns of hosts (e.g., Kays et al., 2015). Indeed, advances in recent technology has facilitated the collection of movement data (e.g., GPS), as well as landscape data both at the regional (e.g., satellite remote sensing) and the local scales (e.g., micro climate stations: HOBO). We suggest that the combination of more precise microhabitat mapping and monitoring of host movement and grouping patterns could lead to better management of environmentally transmitted parasites and host population health.



**Fig. 7.** Spatial patterns of contamination resulting from: a) best fit model ( $S_R = 16$  days,  $S_L = 0$  days/ $\Delta$ DBH), b) increased regional climate suitability ( $S_R = 24$  days,  $S_L = 0$  days/ $\Delta$ DBH), c) increased sensitivity to local landscape characteristics ( $S_L = 0.2$  days/ $\Delta$ DBH), and d) increased regional climate suitability and sensitivity to local landscape characteristics ( $S_R = 24$  days,  $S_L = 0.2$  days/ $\Delta$ DBH).

## 5. Data accessibility

Model code is available from ([https://github.com/tbonne/Landscape\\_Host\\_Parasite](https://github.com/tbonne/Landscape_Host_Parasite)).

## Acknowledgements

We gratefully acknowledge the Uganda National Council for Science and Technology and the Uganda Wildlife Authority for permission to conduct this research. Funding for the research was provided by the Canada Research Chairs Program, Natural Science and Engineering Research Council of Canada, Fonds Québécois de la Recherche sur la Nature et les Technologies, National Geographic and by NIH grant TW009237 as part of the joint NIH-NSF Ecology of Infectious Disease program and the UK Economic and Social Research Council. TRB was supported by an FQRNT Fellowship. We thank Melanie Lefebvre for helpful editorial comments on the writing of this manuscript.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.07.018>.

## References

- Acha, P.N., Szyfres, B., 2003. *Trichuriasis of Animal Origin, Zoonoses and Communicable Diseases Common to Man and Animals*, 3rd ed. Pan American Health Organization, Washington D.C.
- Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M., Rohani, P., 2006. Seasonality and the dynamics of infectious diseases. *Ecol. Lett.* 9, 467–484.
- Anderson, R.M., Truscott, J.E., Pullan, R.L., Brooker, S.J., Hollingsworth, T.D., 2013. How effective is school-based deworming for the community-wide control of soil-transmitted helminths? *PLOS Negl. Trop. Dis.* 7, e2027.
- Ashcroft, M.B., 2010. Identifying refugia from climate change. *J. Biogeogr.* 37, 1407–1413.
- Berbigier, P., Gruner, L., Mambri, M., Sophie, S.A., 1990. Faecal water content and egg survival of goat gastro-intestinal strongyles under dry tropical conditions in Guadeloupe. *Parasitol. Res.* 76, 379–385.
- Blower, S.M., Dowlatabadi, H., 1994. Sensitivity and uncertainty analysis of complex models of disease transmission: an HIV model, as an example. *Int. Stat. Rev. Int. de Stat.* 62, 229–243.
- Bonnell, T.R., Sengupta, R.R., Chapman, C.A., Goldberg, T.L., 2010. An agent-based model of red colobus resources and disease dynamics implicates key resource sites as hot spots of disease transmission. *Ecol. Modell.* 221, 2491–2500.
- Bonnell, T.R., Campenni, M., Chapman, C.A., Gogarten, J.F., Reyna-Hurtado, R.A., Teichroeb, J.A., Wasserman, M.D., Sengupta, R., 2013. Emergent group level navigation: an agent-based evaluation of movement patterns in a folivorous primate. *PLoS One* 8, e78264.
- Bowman, D.D., Lynn, R.C., Eberhard, M.L., 2003. *Georgis Parasitology for Veterinarians*. Saunders, St. Louis.
- Brearley, G., Rhodes, J., Bradley, A., Baxter, G., Seabrook, L., Lunney, D., Liu, Y., McAlpine, C., 2013. Wildlife disease prevalence in human-modified landscapes. *Biol. Rev.* 88, 427–442.

- Brooker, S., Kabatereine, N.B., Tukahebwa, E.M., Kazibwe, F., 2004. Spatial analysis of the distribution of intestinal nematode infections in Uganda. *Epidemiol. Infect.* 132, 1065–1071.
- Brown, H.W., 1927. Studies on the rate of development and viability of the eggs of *Ascaris lumbricoides* and *Trichuris trichiura* under field conditions. *J. Parasitol.* 14, 1–15.
- Castillo-Santiago, M.A., Ricker, M., de Jong, B.H.J., 2010. Estimation of tropical forest structure from SPOT-5 satellite images. *Int. J. Remote Sens.* 31, 2767–2782.
- Chammartin, F., Guimarães, L.H., Scholte, R.G., Bavia, M.E., Utzinger, J., Vounatsou, P., 2014. Spatio-temporal distribution of soil-transmitted helminth infections in Brazil. *Parasite Vector* 7, 1–16.
- Chapman, C.A., Lambert, J.E., 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50, 169–185.
- Chapman, C.A., Struhsaker, T.T., Lambert, J.E., 2005. Thirty years of research in Kibale National Park, Uganda, reveals a complex picture for conservation. *Int. J. Primatol.* 26, 539–555.
- Chapman, C.A., Chapman, L.J., Jacob, A.L., Rothman, J.M., Omeja, P., Reyna-Hurtado, R., Hartter, J., Lawes, M.J., 2010a. Tropical tree community shifts: implications for wildlife conservation. *Biol. Conserv.* 143, 366–374.
- Chapman, C.A., Speirs, M.L., Hodder, S.A.M., Rothman, J.M., 2010b. Colobus monkey parasite infections in wet and dry habitats: implications for climate change. *Afr. J. Ecol.* 48, 555–558.
- Chapman, C.A., Struhsaker, T.T., Skorupa, J.P., Snaith, T.V., Rothman, J.M., 2010c. Understanding long-term primate community dynamics: implications of forest change. *Ecol. Appl.* 20, 179–191.
- Chapman, C.A., Chapman, L.J., Ghai, R.R., Hartter, J., Jacob, A.L., Lwanga, J.S., Omeja, P.A., Rothman, J.M., Twinomugisha, D., 2011. Complex responses to climate and anthropogenic changes: an evaluation based on long-term data from Kibale National Park. In: Plumptre, A.J. (Ed.), *The Ecological Impact of Long-term Changes in Africa's Rift Valley*. Nova Science Publishers, Hauppauge, New York, pp. 70–87.
- Chapman, C.A., Schoof, V.A., Bonnell, T.R., Gogarten, J.F., Calmé, S., 2015. Competing pressures on populations: long-term dynamics of food availability, food quality, disease, stress and animal abundance. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 370, 20140112.
- Chapman, C.A., Struhsaker, T.T., Paim, F.P., Bortolamiol, S., Valenta, K., 2016. Primate population dynamics: variation over space and time. *Biol. Conserv.* (In Review).
- Christensen, J.H., Hewitson, B., Busuioac, A., Chen, A., Gao, X., Held, R., Jones, R., Kolli, R.K., Kwon, W., Laprise, R., 2007. Regional Climate Projections. *Climate Change, 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. University Press, Cambridge 847–940 (Chapter 11).
- Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27, 305–335.
- Cross, P.C., Drewe, J., Patrek, V., Pearce, G., Samuel, M.D., Delahay, R.J., 2009. *Wildlife Population Structure and Parasite Transmission: Implications for Disease Management, Management of Disease in Wild Mammals*. Springer, pp. 9–29.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biol.* 17, 1022–1035.
- Dobson, A., Carper, R., 1992. Global warming and potential changes in host-parasite and disease-vector relationships.
- Ellis, E.C., Ramankutty, N., 2008. Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* 6, 439–447.
- Ewers, R.M., Banks-Leite, C., 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS One* 8, e58093.
- García, L.S., Campbell, J., Fritsche, P.T.R., Hummert, B., Johnston, S.P., Rachford, F.W., Rocha, A.J., Shimizu, R., Smith, J., 2005. Procedures for the recovery and identification of parasites from the intestinal tract, Approved guideline, Second ed.
- Ghai, R.R., Fugère, V., Chapman, C.A., Goldberg, T.L., Davies, T.J., 2015. Sickness behaviour associated with non-lethal infections in wild primates. *Proc. R. Soc. Lond. B: Biol. Sci.*, 282.
- Ghai, R.R., Simons, N.D., Chapman, C.A., Omeja, P.A., Davies, T.J., Ting, N., Goldberg, T.L., 2014. Hidden population structure and cross-species transmission of whipworms (*Trichuris* sp.) in humans and non-human primates in Uganda. *PLOS Negl. Trop. Dis.* 8, e3256.
- Gilbert, K.A., 1997. Red howling monkey use of specific defecation sites as a parasite avoidance strategy. *Anim. Behav.* 54, 451–455.
- Gillespie, T.R., Chapman, C.A., 2008. Forest fragmentation, the decline of an endangered primate, and changes in host–parasite interactions relative to an unfragmented forest. *Am. J. Primatol.* 70, 222–230.
- Gillespie, T.R., Greiner, E.C., Chapman, C.A., 2005. Gastrointestinal parasites of the colobus monkeys of Uganda. *J. Parasitol.* 91, 569–573.
- Gogarten, J.F., Jacob, A.L., Ghai, R.R., Rothman, J.M., Twinomugisha, D., Wasserman, M.D., Chapman, C.A., 2014. Group size dynamics over 15+ years in an african forest primate community. *Biotropica* (n/a–n/a).
- Goldberg, T.L., Gillespie, T.R., Rwego, I.B., Estoff, E.L., Chapman, C.A., 2008. Forest fragmentation as cause of bacterial transmission among nonhuman primates, humans, and livestock, Uganda. *Emerg. Infect. Dis.* 14, 1375–1382.
- Goldberg, T.L., Paige, S.B., Chapman, C.A., 2012. The Kibale eco health project. In: Aguirre, A.A., Ostfeld, R.S., Daszak, P. (Eds.), *New Directions in Conservation Medicine*. Oxford University Press, New York.
- Gordon, H.M., 1948. The epidemiology of parasitic diseases, with special reference to studies with nematode parasites of sheep. *Aust. Vet. J.* 24, 17–45.
- Greiner, E.C., McIntosh, A., 2009. Collection methods and diagnostic procedures for primate parasitology. In: Huffman, M.A., Chapman, C.A. (Eds.), *Primate Parasite Ecology: The Dynamics and Study of Host–parasite Relationships*. Cambridge University Press, Cambridge, UK, pp. 3–28.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol A review and first update. *Ecol. Modell.* 221, 2760–2768.
- Hartter, J., Stampono, M.D., Ryan, S.J., Kirner, K., Chapman, C.A., Goldman, A., 2012. Patterns and perceptions of climate change in a biodiversity conservation hotspot. *PLoS One* 7, e32408.
- Hausfater, G., Meade, B.J., 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23, 287–297.
- Hodder, S.A.M., Chapman, C.A., 2012. Do Colobus monkeys on humanized forest edges exhibit more severe parasite infections than those on non-humanized forest edges? *Int. J. Primatol.* 33, 845–859.
- Jacob, A.L., Bonnell, T.R., Dowhaniuk, N., Hartter, J., 2014. Topographic and spectral data resolve land cover misclassification to distinguish and monitor wetlands in western Uganda. *Isprs J. Photogramm.* 94, 114–126.
- Johnson, C., Piel, A.K., Forman, D., Stewart, F.A., King, A.J., 2015. The ecological determinants of baboon troop movements at local and continental scales. *Mov. Ecol.* 3, 1–13.
- Johnson, S.G., 2015. The NLOpt nonlinear-optimization package.
- Kahm, M., Hasenbrink, G., Lichtenberg-Frate, H., Ludwig, J., Kschischo, M., 2010. Grofit: fitting biological growth curves with R. *J. Stat. Softw.* 33, 1–21.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185.
- Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. *Science*, 348.
- Kenyon, F., Sargison, N., Skuce, P., Jackson, F., 2009. Sheep helminth parasitic disease in south eastern Scotland arising as a possible consequence of climate change. *Vet. Parasitol.* 163, 293–297.
- Keppel, G., Wardell-Johnson, G.W., 2012. Refugia: keys to climate change management. *Global Change Biol.* 18, 2389–2391.
- Lane-deGraaf, K.E., Kennedy, R.C., Arifin, S.M.N., Madey, G.R., Fuentes, A., Hollocher, H., 2013. A test of agent-based models as a tool for predicting patterns of pathogen transmission in complex landscapes. *BMC Ecol.*, 13.
- Larsen, M.N., Roepstorff, A., 1999. Seasonal variation in development and survival of *Ascaris suum* and *Trichuris suis* eggs on pastures. *Parasitology* 119, break 209–220.
- Lumley, T., 2009. leaps: regression subset selection. R package version 2.9.
- Markham, A.C., Alberts, S.C., Altmann, J., 2015. Haven for the night: sleeping site selection in a wild primate. *Behav. Ecol.*, arv118.
- Nunn, C.L., Thrall, P.H., Kappeler, P.M., 2014. Shared resources and disease dynamics in spatially structured populations. *Ecol. Modell.* 272, 198–207.
- Nunn, C.L., Thrall, P.H., Leendertz, F.H., Boesch, C., 2011. The spread of fecally transmitted parasites in socially-structured populations. *PLoS One*, 6.
- Ostfeld, S.R., Glass, E.G., Keesing, F., 2005. Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends Ecol. Evol.* 20, 328–336.
- Pebsworth, P., Archer, C., Appleton, C., Huffman, M., 2012. Parasite transmission risk from geophagic and foraging behavior in chacma baboons. *Am. J. Primatol.* 74, 940–947.
- Petkevicius, S., Thomsen, L.E., Knudsen, K.E.B., Murrell, K.D., Roepstorff, A., Boes, J., 2007. The effect of inulin on new and on patent infections of *Trichuris suis* in growing pigs. *Parasitology* 134, 121–127.
- Powell, M.J., 2009. The BOBYQA algorithm for bound constrained optimization without derivatives.
- Pujol, G., looss, B., Janon, A., 2012. <http://cran.r-project.org/web/packages/sensitivity/index.html>. In: *Sensitivity: Sensitivity Analysis*.
- Pullan, R.L., Brooker, S.J., 2012. The global limits and population at risk of soil-transmitted helminth infections in 2010. *Parasite Vector*, 5.
- R Core Team, 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roepstorff, A., Murrell, K.D., 1997. Transmission dynamics of helminth parasites of pigs on continuous pasture: *Ascaris suum* and *Trichuris suis*. *Int. J. Parasitol.* 27, 563–572.
- Rose, J., Small, A., 1981. The relationship between pasture herbage and the development and survival of the free-living stages of *Oesophagostomum dentatum*. *J. Helminthol.* 55, 109–113.
- Saulnier-Talbot, É., Gregory-Eaves, I., Simpson, K.G., Efitre, J., Nowlan, T.E., Taranu, Z.E., Chapman, L.J., 2014. Small changes in climate can profoundly alter the dynamics and ecosystem services of tropical crater lakes. *PLoS One* 9, e86561.
- Snaith, T.V., Chapman, C.A., 2008. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behav. Ecol.* 19, 1289–1296.
- Stoner, K.E., 1996. Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: implications for conservation biology. *Conserv. Biol.* 10, 539–546.
- Struhsaker, T.T., 1997. Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation. University Press of Florida, Gainesville, Florida.
- Struhsaker, T.T., 2010. *The Red Colobus Monkeys: Variation in Demography, Behavior, and Ecology of Endangered Species*. Oxford University Press, Oxford.

- Swarnkar, C., Singh, D., 2011. Role of bioclimatographs in forecasting of strongyle infection in Rajasthan. *Indian J. Anim. Sci.* 81, 216.
- Varner, J., Dearing, M.D., 2014. The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS One* 9, e104648.
- Weaver, H.J., Hawdon, J.M., Hoberg, E.P., 2010. Soil-transmitted helminthiasis: implications of climate change and human behavior. *Trends Parasitol.* 26, 574–581.
- Young, K.H., Bullock, S.L., Melvin, D.M., Spruill, C.L., 1979. Ethyl-Acetate as a substitute for diethyl-ether in the formalin-ether sedimentation technique. *J. Clin. Microbiol.* 10, 852–853.