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An agent-based model to simulate tsetse fly distribution and control techniques: a case study in Nguruman, Kenya

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Abstract

Background—African trypanosomiasis, also known as “sleeping sickness” in humans and “nagana” in livestock is an important vector-borne disease in Sub-Saharan Africa. Control of trypanosomiasis has focused on eliminating the vector, the tsetse fly (*Glossina*, spp.). Effective tsetse fly control planning requires models to predict tsetse population and distribution changes over time and space. Traditional planning models have used statistical tools to predict tsetse distributions and have been hindered by limited field survey data.

Methodology/Results—We developed an Agent-Based Model (ABM) to provide timing and location information for tsetse fly control without presence/absence training data. The model is driven by daily remotely-sensed environment data. The model provides a flexible tool linking environmental changes with individual biology to analyze tsetse control methods such as aerial insecticide spraying, wild animal control, releasing irradiated sterile tsetse males, and land use and cover modification.

Significance—This is a bottom-up process-based model with freely available data as inputs that can be easily transferred to a new area. The tsetse population simulation more closely approximates real conditions than those using traditional statistical models making it a useful tool in tsetse fly control planning.

Keywords

Individual-based model; Tsetse fly control; Agent Based Models; African Trypanosomiasis

1 Introduction

African trypanosomiasis is a parasitic disease transmitted to both humans and animals by the tsetse fly (*Glossina* spp.). It is estimated that trypanosomiasis reduces the production of meat

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and milk from those cattle by at least 50% in tsetse-infested areas (Swallow, 1999). There were three major epidemics of Human African Trypanosomiasis (HAT) in Africa over the last century, one between 1896 and 1906, one in 1920, and the other one between 1970 and late 1990s (WHO, 2014). In 1998, 40, 000 cases were reported with estimation of 300, 000 cases undiagnosed (WHO, 2014). In 2009, the number of cases reported dropped below 10, 000 (*i.e.*, 9, 878) for the first time in 50 years; fewer cases (7, 216) were reported in 2012 with 20, 000 estimated actual cases and 70 million people at risk (WHO, 2014). The WHO NTD Roadmap has targeted the elimination of HAT as a public health problem by 2020 (WHO, 2014). Current treatments for African Trypanosomiasis are often antiquated, highly toxic, and frequently ineffective (Kennedy, 2008). Not surprisingly, more attention has been paid to the control of the vector, the tsetse fly.

Tsetse fly control techniques such as insecticide-treated traps/targets, spraying of insecticides, destruction of tsetse habitat, releasing sterile male flies, and the wholesale slaughter of wild host animals have been employed over the past century (Hargrove, 2003). However, these efforts to control tsetse have often been hampered by poor identification of infested areas, reinvasion of tsetse into previously controlled regions, substantial costs associated with the means of control, and a lack of adaptive management practices (Hargrove, 2003; Messina et al., 2012; Williams et al., 1992). While widespread agreement exists that integrated vector control should play a major role in alleviating the tsetse burden in Africa, there is no consensus on how to carry out control campaigns, or even whether control is feasible (Peck and Bouyer, 2012).

With the advent of modern Remote Sensing (RS) and Geographic Information System (GIS) technology, came an improved ability to identify suitable tsetse habitat, and the capacity to develop spatiotemporal models. Although improved habitat and distribution maps help aiding tsetse control campaigns in answering where-and-when questions, they provide no information on population dynamics. A wide variety of tsetse population models exist, often taking the form of mathematical models of varying complexity (Jarry et al., 1996; Rogers, 1988). These models are often used to compare the effectiveness of one or more control methods, and help select a desirable management plan, but always in a non-spatial context. While these models have been helpful in giving broad generalizations, unfortunately, in many ways they have inadequately addressed key aspects of the fly's biology and ecology, particularly the spatiotemporal variability of its habitats (Peck and Bouyer, 2012).

The objective of this study was to develop a spatially explicit tsetse agent-based model (ABM) running on a matrix of dynamic remotely sensed habitat data. The model was expected to provide daily spatiotemporal information on tsetse populations, and be generalizable, provided proper parameterization, to various locales across East Africa. Tsetse biology including longevity, sex, reproduction interval, and moving capability was considered in the model. In addition, the model was purposefully designed to test the impact of various tsetse control techniques on population dynamics, with the hope of providing information relevant to future tsetse control efforts. This tsetse ABM was parameterized for Nguruman, Kenya. The broad goal of our study is to develop a tsetse fly control planning tool by simulating (1) livestock and human infected by tsetse and (2) tsetse fly control outcomes using different control scenarios. The model presented in this paper is only a

starting point for more completely describing the complex relationships among tsetse, livestock, people, and the environment.

2 Background

ABM is embedded within complex systems theory, treating objects in a system as independent entities, usually referred to as an “agent.” The agent relies on a combination of rules governing development, movement, interactions, and other life processes often culminating in death. Traditional population models usually assume environments are constant, treating the population as a whole characterized by birth rate, mortality rate, or growth rate, fitted with mathematical models. When compared to mathematical models, ABM often requires less empirical mathematics by setting movement rules and survival rates for individuals under different circumstances such as variable climate regimes, land use / cover scenarios, and predator / prey interactions, while maintaining model complexity due to the stochastic interactions among agents (Getz, 2013). ABM also offers flexibility by allowing the user to treat an individual or a group of individuals as agents, depending on preferred details and available knowledge. Moreover, ABM does not require a training dataset to fit experience mathematics functions, so relatively few data inputs are required to initialize the model, offering tsetse control efforts a more adaptive management tool when lacking of resources to carry out field surveys.

ABMs have been used to investigate a variety of research topics including traffic management, migration, disease transmission, demographic change, water resource management, and social network analysis (see the review of Matthews et al., 2007). Recently, a few studies have developed ABMs in an attempt to bridge the gap between the space-time habitat models, and the theoretical population models (Alderton et al., 2013; Muller et al., 2004). ABMs provide simple means for adding complexity to tsetse population models, by allowing the easy incorporation of spatial data with tsetse biological and ecological knowledge (Alderton et al., 2013). In an ABM, each agent is reactive, pro-active, social, and autonomous with movements not limited to a grid or a lumped space model (Muller et al., 2004). While ABMs have the ability to easily capture more biological complexities than simple analytic models (Peck and Bouyer, 2012), all of the tsetse ABMs to date have been developed only in theoretical environmental matrixes, with generalized results. For example, Muller et al. (2004) used an ABM to model the spread of Human African Trypanosomiasis (HAT). The model simulated a scenario with several villages, forests, and cocoa plantations in a virtual place assuming tsetse population was constant. Alderton et al. (2013) developed a two-host ABM, which simulates trypanosomiasis infection among humans and cattle in a spatially abstract terrain also without environment and tsetse dynamics.

3 The dynamic agent-based model

The ABM presented in this manuscript was developed upon the platform NetLogo (Wilensky, 1999), using a GIS extension to integrate remotely sensed habitat data. More details of the tsetse population dynamic ABM are described in the following sections in

accordance with the ABM protocol firstly proposed by Grimm et al. (2006) then revised by Grimm et al. (2010).

3.1 Purpose

The purpose of the model is (1) to identify the temporal and spatial distribution, and population dynamics of tsetse flies in a diurnally dynamic environment, and (2) to assess various methods used in tsetse controls, including insecticide spraying, wild host culling, sterile male insect releases, and land use/cover modification.

3.2 Entities, state variables, and scales

Agents/individuals—The ABM is an individual level model, comprising four types of agents: tsetse flies (adults), tsetse pupae (juveniles), wild animals (representing hosts), and patches (habitats). They are characterized by the state variables listed in Fig. 1, which also shows relationships among agents.

Tsetse (genus *Glossina*) are generally subdivided, based on physiology and ecology, into three subgenus groups: (1) *morsitans* –savanna flies, (2) *palpalis* – riverine flies, and (3) *fuscus* – forest flies. The *morsitans* group is the predominate subgenus in Kenya broadly and Nguruman specifically, and hereafter, “tsetse” refers to the *morsitans* subgenus. Female (*Tsetse fly: Sex*) tsetse flies produce tsetse pupae after a specified period (*Tsetse fly: age*) if they are fed (*Tsetse fly: Bite*), mated (*Tsetse fly: Mated*), inseminated (*Tsetse fly: Inseminated*), and survive days without food (*Tsetse fly: Starvation days*) and dry period (*Tsetse fly: Desiccation days*). Female tsetse flies typically mate only once, a few days after emergence from pupa, and remain fertile for life (Knight, 1971). Female tsetse flies mating with sterile males (*Tsetse fly: Sterile*) cannot be inseminated to produce viable pupae. Tsetse flies can move (*Tsetse fly: Travel distance*) within a given range every day. Tsetse pupae develop into tsetse flies in a specified period (*Tsetse pupa: Age*) if they are not exposed to an unsuitable environment too long (*Tsetse pupa: Desiccation days*).

Given the considerable variety of hosts and uncertainty regarding their movements, the life cycles of the *Wild animals* are not simulated. Instead, certain numbers of *Wild animals* are distributed randomly within the study area every day regardless of suitability.

Spatial units—For the purposes of this manuscript, a known tsetse belt in Nguruman, Kenya was used. Nguruman is located in southern Kenya, along the Tanzanian border (Fig. 2). It covers 7,152 km², with 82% of grasslands, 6% of savannas, 4% field agriculture and very low density built environments, 4% of water, 2% of forest, and 2% of shrublands (Fig. 9).

Grid cells, with 250 m × 250 m spatial resolution, are the smallest spatial units of the model and treated as agents (*Patches*). Other agents, *i.e.* *Tsetse flies*, *Tsetse pupae*, and *Wild animals* live on *Patches*. Their locations on the grids are defined by the *Position* attribute. The smallest moving unit is one grid cell. The movement of *Tsetse flies* and *Wild animals* is controlled by changing the position attributes of the agents. *Tsetse flies* directly jump to objective grids such as grids with *Wild animals* or suitable grids. The following “Submodels” Section has more details on agent movements.

Environment—The *Patches* are classified as suitable or unsuitable for tsetse flies and tsetse pupae, based on land use/cover (*Patch: Land use/cover*), temperature (*Patch: Maximum temperature* and *Patch: Minimum temperature*), and humidity (*Patch: NDVI*), all of which are daily changed GIS data (input data). One time step of the model represents one day in reality.

Collectives—The *Wild animals* generally represent all the hosts including wild animals, cattle, and human beings. Each tsetse fly agent and tsetse pupa agent represents five tsetse flies and five tsetse pupae, respectively. The aggregation unit was set for tsetse flies and pupae to reduce total agent number in the model and improve computation speed. Tsetse flies are grouped into females and males.

3.3 Process overview and scheduling

The model runs daily over four stages (Fig. 3). First, at the beginning of a day, the *Patch* suitability is determined based on available remotely sensed data. Second, *Tsetse pupae* are “born” by female *Tsetse flies* after a fixed amount of time post insemination (*Tsetse fly: Inseminated*). Subsequent pupae are produced at a regular interval, based on the amount of time elapsed since the last pupa was born, with specific *Tsetse pupae* growth and hatch rates. *Wild animals* are randomly distributed. Third, *Tsetse flies* move to *Patches* with *Wild animals* to feed on. After feeding, male and unmated female *Tsetse flies* then search for mates. At the end of a daily time step, each *Tsetse fly* will attempt to return to a suitable *Patch*. However, a *Tsetse fly* is not allowed to exceed a maximum travel distance. Therefore, if it has traveled too far in search of food or a mate, it is not allowed to travel to a suitable *Patch*. Finally, a *Tsetse fly* can die from starvation, desiccation, or aging, with the age of each fly (*Tsetse fly: Age*) increased by one after each daily time step.

3.4 Design concepts

Basic principles—The ABM is based on tsetse fly life cycle and environmental change. In the model, the mortality rate of tsetse is dependent on (1) environmental change, (2) food source (wild animals), and (3) the individual longevity (1–3 months) set by the model randomly. Every day, tsetse flies look for food and mating opportunities, while avoiding unsuitable environments within their movement capability (800 m/day). We assume female tsetse flies mate only once during their lifetimes. Sterile male tsetse flies can effectively prevent fertilization in females. Female tsetse flies lay eggs continually after the first-born.

Emergence, adaptation, objective, learning, and prediction—The agents don’t have any adaptive trait.

Sensing—A *Tsetse fly* can sense the existence of the *Wild animals* in a radius range and move to the closest location where there is at least one *Wild animal*. When looking for food, the *Tsetse fly* can sense the tsetse fly density of the objective *Patch* and avoid the location where the density reaches the maximum criteria. A *Tsetse fly* can sense the *Patch* suitability and tries to come back to a suitable location after searching for food. A female *Tsetse fly* can sense the male within its reachable range and successfully mate with it.

Interaction—The environmental agents (*Patches*) define suitable habitats of *Tsetse flies* and *Tsetse pupae*. If a *Tsetse fly* cannot find food (*Wild animals*) within certain days (*Tsetse fly: starvation days*), it dies. If a *Tsetse fly* or *Tsetse pupa* stays in unsuitable *Patches* long enough (*Tsetse fly: desiccation days* and *Tsetse pupae: desiccation days*, respectively), it dies.

Stochasticity—The initial locations of *Tsetse flies*, *Tsetse pupae*, and *Wild animals* are random. The pupa hatch times are randomly set between 3 – 5 weeks. The tsetse longevities are randomly set between 1 – 3 months. The genders of the new-born tsetse flies are random. A tsetse fly randomly moves to a location within its reachable range when searching for food when no food is available at the current location. When a tsetse comes back after searching for food, it randomly comes to a suitable *Patch* within its reachable range. The wild animals randomly distribute at each time step.

Collectives—Female flies produce offspring while males cannot. No other behavior of higher level agent groups is simulated.

Observation—We compared the tsetse distribution map (Fig. 4) with the tsetse distribution map provided by Dr. Joseph Maitima of Ecodym Africa. The expert empirical knowledge map generally agreed with the map produced by the model with default parameters.

The insecticide spraying effect is simulated by setting certain percentage of *Tsetse flies* and *Tsetse pupae* to “die.” When the environmental carrying capacity (defined by *Wild animals* and *Patches*) hasn’t changed, the tsetse fly and pupa populations are expected to recover over time. Using the same method, wild host culling is simulated by setting a certain amount of *Wild animals* to “die.” The decrease of *Wild animals* (food sources for tsetse flies) causes *Tsetse fly* and *Tsetse pupa* populations decrease. By introducing sterile tsetse males in the system, *Tsetse pupa* population is expected to decrease due to failure of offspring viability and increased food source competition due to the additional adult sterile males. Agriculture and built-up land covers are not suitable for tsetse flies. Therefore, the expansion of those lands potentially decreases *Tsetse fly* and *Tsetse pupa* populations due to habitat shrinkage and fragmentation. None of the simulated tsetse control scenarios were empirically tested by field data.

3.5 Inputs

The model uses spatial data (Normalized Difference Vegetation Index, minimum temperature, maximum temperature, and land use/cover, Table 1) as input to provide daily environmental conditions. Please see the following “Submodels” Section: “Environment suitability and change,” for more details of the input data.

3.6 Initialization

At initialization, the NDVI (as a proxy of humidity and soil moisture), maximum temperature, minimum temperature, and land use/cover are loaded as attributes of the *Patch* agent. The suitable habitats for tsetse flies and pupae are defined by those attributes.

Initially, 60,000 *Tsetse flies* and 40,000 *Tsetse pupae* were randomly set within the suitable *Patches*. The tsetse population numbers were estimated based on the stable numbers after a three-year-run. The initial numbers of tsetse flies and pupae are not important, but the process is required to reach stable populations. Tsetse fly food sources included wild animals, livestock, and human beings, populations and locations of which were unknown in Nguruman. The *Wild animal* in the model served as a proxy for tsetse food sources and its number was estimated to be 7,700 based on a study near the Maasai Mara National Reserve, southwest of Kenya, about 100 km west of Nguruman (Butt et al., 2009). *Wild animals* are distributed randomly over the study zone. The biology parameters set for the tsetse fly are listed in Table 2 and based on existing literature.

3.7 Submodels

Environment suitability and environmental change (*Patch procedure*)—*Patches* are displayed as grids, using the NetLogo GIS extension developed by Eric Russell (<http://ccl.northwestern.edu/netlogo/faq.html>, last accessed on Aug. 4th, 2014). Four environmental variables, land use/cover, moisture, minimum temperature, and maximum temperature are used to classify a *Patch* as suitable or unsuitable for tsetse flies and pupae (DeVisser et al. 2010). Suitable land cover types include forest, shrubland, savanna, and wetland (Cecchi et al., 2008; Leak, 1999). The NDVI data from the Moderate Resolution Imaging Spectroradiometer (MODIS - MYD13Q1) is a proxy for moisture, with NDVI values higher than 0.39 being classified as suitable tsetse habitat (Williams et al., 1994). Long term minimum and maximum temperature regression models based on elevation are respectively proxies for daily minimum and maximum air temperature in the study area (Lin et al., 2012). The suitable temperature of tsetse flies and pupae ranges from 10 °C and 40 °C (Torr and Hargrove, 1999).

The ABM was designed to run at daily time step intervals. Ideally the environmental data used would have the same temporal characteristics as the model. However, this is currently not possible given data availability and completeness. The MODIS land use/cover data are only produced annually. The MODIS 16-day composite NDVI product was used to avoid the data gaps presenting in the daily product. The temperature is held constant since the temperature seasonal variations are small at the study area. We have tried the MODIS daily land surface temperature (LST) product as the temperature input data. However, our previous study demonstrated that we could not simply use LST to replace air temperature at very fine spatial and temporal scales as a complicated relationship exists between them after comparing weather station data and LST (Lin et al., 2012). Considering the small seasonal variation at the study area as measured by our weather stations, it is more reliable to use mean temperature calculated by the local regression model (with elevation as predictor) than LST (Lin et al., 2012). Daily air temperature interpolated from weather station data (given significant station densities) is suggested for areas with high seasonal variability. The model runs presented here used data from 2011 and looped those data to assess model performance. In other words, in this study we assumed that only NDVI / moisture conditions changed every 16 days. Table 1 shows more details of these input data.

Grows and hatches (*Tsetse pupae* procedure)—The pupa age (*Tsetse pupa: age*) increase one day at each time step. In 21 – 35 days (3 – 5 weeks), a *Tsetse pupa* hatches and a new *Tsetse fly* (Leak, 1999). At the same time, the longevity of the new fly is set randomly between 30 – 60 days (1 – 3 months) (Leak, 1999). The days exposed to desiccation and starvation are set at zero for new tsetse flies. The genders of emergent tsetse flies are randomly set. For the tsetse females, the states of mated, insemination, and parturition are initialized as false. For the tsetse males, the sterile states are set as false.

Randomly distributed (*Wild animal* procedure)—The *Wild animals* are distributed randomly on suitable *Patches* at each time step using the NetLogo “one-of patches” command. The suitable *Patches* are forest, shrublands, Savannas, grasslands, or wetlands where tsetse fly population is less than 2, 200 tsetse/km² (Mihok et al., 1992).

Goes out for food (*Tsetse fly* procedure)—There are two factors affecting tsetse flies’ success in looking for food. (1) *Wild animals* (food) must be within a reachable distance, i.e., 800 m for tsetse flies (Vale et al., 1984). (2) When too many flies (number > 2, 200 tsetse/km²) are collocated, *Tsetse flies* have to move to another *Patch* to find food, since *Wild animals* leave (Mihok et al., 1992). In the model, *Tsetse flies* always go the closest patch to eat. If a tsetse fly has moved its maximum daily flying distance (i.e., 800 m) and cannot find food, then it is not fed at the end of the day and stays randomly in a *Patch* within the radius of its maximum flying distance.

Copulates (*Tsetse fly* procedure)—The insemination status of tsetse females are set as “true” if there is one or more males within the maximum fly distance (i.e., 800 m). If a female is not fed (it has traveled its maximum flying distance for food), the copulation will not happen. After insemination, each female fly lays a single larva every 10 days (Wall and Langley, 1993).

Goes back to suitable habitats (*Tsetse fly* procedure)—When *Tsetse flies* are looking for food, they go to any *Patch* where there is (are) *Wild animal(s)*, regardless of the environment suitability of the *Patches*. After feeding, *Tsetse flies* try to return to suitable *Patches* if the current *Patch* is not suitable. The maximum fly distance for a day is 800 m. So if a *Tsetse fly* has gone too far away for food, it is not able to come back and has to stay in the unsuitable *Patch*.

Grows and dies (*Tsetse fly* and *Tsetse Pupa* procedure)—If a *Tsetse fly* or *Tsetse pupa* stays in climatologically unsuitable patches for more than 3 days, it dies from desiccation (Leak, 1999). If a *Tsetse fly* cannot find food for more than 7 days, it dies from starvation (Leak, 1999). The *Tsetse fly* also dies when it reaches its randomly set lifespan. When it is time for parturition (birth gap = 18 days for the first egg laying, 10 days for the 2nd and latter ones) (Leak, 1999), the female tsetse fly is viviparous and gives birth to a single larva (Knight 1971).

4 Results

4.1 Tsetse fly distribution

Tsetse fly distributions were dependent on environmental suitability and habitat connectivity. Tsetse flies were distributed all over suitable areas at the beginning (Fig. 4 a); however, they only appeared at the large connected areas (Fig. 4 b). Tsetse flies died out in small suitable areas, even if they were suitable all the time over a year (Fig. 4 c). The area of the southwestern suitable patches was large and served as a source population, which provided dispersal population for island patches.

Generally, about 50% of suitable areas were occupied by tsetse flies over a year (Fig. 5). The tsetse fly habitat occupation rate increased in dry seasons when suitable habitats shrunk. The maximum occupied rate is about 65%. In the wet seasons when suitable habitats expanded, the occupied rate could be as low as 30%.

Tsetse fly population varied substantially over time, with high values (around 58, 000) in wet seasons and low values (around 42 thousands) in dry seasons (Fig. 11). Restricted spatial distributions and lower population totals around Sept. 18th (day 260) provided the best timing to eliminate tsetse flies. The population and distribution area of flies in dry seasons decrease substantially compared to the wet seasons.

4.2 Slaughter of wild animals

Tsetse fly distributions and populations were sensitive to the density of wild animals (Fig. 6). When the density of wild animals decreased, tsetse flies living in small fragments could not survive travelling longer distances for food, resulting in greater chances of being exposed to unsuitable environmental conditions. The population of the tsetse flies also decreased with wild animal density ($y = 8.4415x - 10087$, $R^2 = 0.9986$, where y is tsetse fly population and x is wild animal population) (Fig. 6). When wild animal population decreased from 7, 700 to 1, 401 (19.35% of the initial population), tsetse flies became extinct in the study area (Fig. 6f).

4.3 Aerial spraying

Tsetse fly mating efficiency is high (Wall and Langley, 1993). Assuming tsetse flies could always find mates within the daily flying capability (800 m/d), it was only a matter of time that tsetse population recovered after part of population was randomly killed by aerial insecticide spraying. For example, the tsetse fly population could recover after about 6 months if 50% of flies and pupae were killed. It took about 15 months, 29 months, and 31 months, respectively, if 85%, 99%, and 99.9% of initial tsetse flies and pupae were killed (Fig. 7). When 99.9% of the tsetse flies were killed leaving 300 flies (males and females), the density of tsetse flies within occupied area was very low (1.9 males and females/km²).

4.4 Releases of irradiated males

The Sterile Insect Technique (SIT) widely promoted requires a great number of irradiated flies to produce significant effects (Fig. 8). Releasing 5, 000 sterile males to a community with 55, 000 flies, the population decreased by around 5, 000 after three months, then

recovered after another three months. Releasing substantial amount (50, 000) sterile males, the population decreased from 55, 000 to 23, 000, also recovering after another three months.

4.5 Agricultural expansion

Tsetse flies rarely frequent intensive agricultural areas or built environments, expansion of which makes tsetse habitats shrink and disconnected. When unsuitable agriculture or built-up expanded by 30%, 50% and 70% (Fig. 9), tsetse fly populations decreased by 5%, 9%, and 12%, respectively (Fig. 10). It is important to note that agricultural lands and the human built environment only accounted for about 4% of the study area. In higher human residency areas, higher tsetse population drops are expected.

4.6 Model parameter sensitivity

All of the model parameters in Table 2, except for the initial number of the agents (*i.e.*, tsetse flies, tsetse pupae, and wild animals), were tested for sensitivities. The model sensitivities were quantified by increasing and decreasing one of the parameters by 30%, while holding all other parameters at the default values listed in Table 2, and measuring the changes in tsetse fly and tsetse pupa populations. For each parameter sensitivity test, the model was first looped for five years using the default values to ensure a stable population, and then run for another three years with the $\pm 30\%$ parameter value being tested. The population results of the last year was compared with multiple (46) default runs with parameters listed in Table 2. The default runs were summarized as mean and standard deviation (SD) (Fig. 11, Fig. 12). The SD of the 46 runs with default parameters indicated the randomness of the model.

The state variables can be grouped into (1) population growth rate related, (2) environmental carrying capacity related, and (3) connectivity related. Group (1) includes birth gap, reproduction age, hatch time, longevity, desiccation days, and starvation days. Group (2) includes maximum density. Group (3) includes maximum movement distance. The tsetse fly ABM model was not sensitive to the environment capacity, with tsetse fly and pupa populations fluctuating generally within the range of one standard deviation. Instead, the tsetse populations were sensitive to the variables related to population growth rate, *i.e.*, tsetse fly longevity, and pupa hatch time (tsetse pupa longevity). When the longevity was increased by 30%, the fly population increased by 14%, while pupa population increased by 13%. When the longevity was decreased by 30%, the fly population decreased by 30% as well, while the pupa population decreased by 27%. The model was not sensitive to the other growth rate variables possibly due to low values: starvation days (7 days), desiccation days (3 days), reproduce age (18 days), and birth gap (10 days), compared to longevity (30–90 days) and hatch time (21–35 days). It was interesting that the model was not sensitive to the environmental carrying capacity defined by the maximum density. The environmental capability might be compensated by the mobility of flies, which moved to margin habitats when reaching the maximum density at a patch. The maximum density only changed the carrying capacity of the location with high tsetse fly population. It should be noticed that if the environmental capacity changed for the whole system, not just one location, total population would change. For example, when the randomly distributed wild animal density

decreased, the tsetse fly population also decreased (Fig. 6). Tsetse flies always move to a new habitat when the previous habitat reaches its maximum capacity. Therefore, the tsetse population depends on population growth rate and movement rate. We did not see populations sensitive to the maximum movement distance. Explanation for that might be the 16-day composited NDVI data that controlled the habitat change allowed long enough time for tsetse to move from one place to another place.

5 Discussion

5.1 Tsetse control planning tools

Traditional statistical tsetse species distribution models depend on presence/absence data as training data to predict distributions. By implementing spatial-temporal autocorrelation methods Sedda et al. (2014) have predicted tsetse dynamic using field survey data. However, obtaining the necessary data can often be difficult, time consuming, costly, and given our resources, was not practical in our study area. Historical tsetse distribution data, such as the widely used survey maps produced by Ford and Katondo (1977), may seem to be an acceptable alternative to collecting presence/absence data, but the available historical data on tsetse are very likely inaccurate, over generalized, or significantly out of date (Moore and Messina, 2010; Williams et al., 1994). Using historical data to map tsetse distributions inevitably produces significant uncertainties and has likely been a serious impediment to recent control efforts. Compared to statistical methods, niche models, like the Tsetse Ecological Distribution (TED) model (DeVisser et al., 2010), are free from the limitation of requiring extensive field training data. TED uses satellite data to track changes in the tsetse “fundamental niche” (suitable habitat), and tsetse movement rates to model the flies “realized niche.” Our model has improved the “realized niche” to “realized population” by considering individual tsetse fly life cycle, behaviors (*e.g.*, mating, looking for food, and escaping from unsuitable habitats), and interactions with hosts and other tsetse flies. The “Tsetse Plan” (the non-expert version), “Tsetse Muse” (the expert version), and “HAT-trick” (the combination of Tsetse Plan and Tsetse Muse) are tsetse control planning tools published online (<http://www.tsetse.org>, last accessed on April 24, 2015). In the Tsetse Muse program the tsetse population is density-dependent and simulated by a life table (Vale and Torr, 2005). The lumped population models used in the program can simulate population changes in a specific area (“fundamental niche”) using empirical fitted growth and death rates, but they ignore heterogeneity and temporal dynamics of the biotic/abiotic environment. This could result in unrealistic simulations when the environment heterogeneity is high. For example, using classic predator-prey models, as long as there are wild animals in the study area, tsetse flies will not be extinct. That is the conclusion of Hargrove (2003), saying wild animal selective hunting level is never sufficient to remove tsetse hosts and eradicate tsetse flies. However, our ABM simulation showed that even when some hosts remained in the ecosystem, non-consequent locations of hosts and tsetse flies could still cause tsetse flies to die out (Fig. 9). That is the gap between “fundamental niche” and “realized population.” The tsetse dynamic ABM model provides not only information on “when” and “where” but also how many tsetse flies at the location and the moment. Moreover, our model has produced finer spatial distribution data and increased the accuracy, in particular by removing some habitat fragments from tsetse distribution areas (Fig. 4). Those fragments are fundamental

niches or realized niches predicted by previous models, but actually may not be occupied by tsetse flies when more complex situations such as food sources are included. Tsetse fly is a K -strategist (instead of r -strategist) species with low reproduction rate. Therefore, it is of particular importance to include tsetse moving capability in the model since they cannot increase their populations quickly as suitable habitat becomes available. The tsetse only occupied about 50% of “fundamental niche” in our simulation (Fig. 5).

A more accurate tsetse distribution map derived in the ABM model potentially decreases costs in tsetse fly control. A case study in Kenya indicated that when replacing the “fundamental niche” map with a spatially-temporally dynamic “realized niche” map derived by the TED model (DeVisser et al., 2010), around 20 million dollars could be saved in a nationwide tsetse fly control campaign by only targeting tsetse flies at specific locations during dry seasons instead of all suitable areas along a year (McCord et al., 2012). The tsetse populations during dry seasons are remarkably spatially constrained compared to the wet seasons (Fig. 11). We believe that tsetse control would be even more cost-efficient when replacing the “realized niche” map with the “realized population” map derived from the ABM model.

The dynamic tsetse ABM presented here is a process-based model. Empirical statistical models are limited to the situations tied to the collection of training data. The process-based models are more generalizable than the empirical ones. The tsetse model presented here only requires spatial data (*i.e.*, NDVI, temperature, and land use/cover) as input data, which are freely available online. The model can be applied in a new area when those data are prepared and the host (wild animal) numbers are estimated. The initial populations of tsetse flies and tsetse pupae are not important since equilibrium populations can be reached after setting tsetse flies everywhere.

5.2 Limitations and future perspectives

We presented only simple control scenarios, which are arguably unrealistic. For instance, areal insecticide spraying may be applied several times during a single season instead of once. Several techniques may be combined as is often the case with SIT (sterile insect technique) applications. Instead of providing definitive information of possible schedules and combinations, we show the effects of single applications of each control technique to make the results as clear as possible. For a tsetse control campaign, more information such as cost and resources available should be included to provide more useful information for stakeholders (Vale and Torr, 2005). Other tsetse control techniques such as insecticide-treated cattle and fly trapping are not included here, but the model can be easily updated with those functions.

The tsetse population in the model depends on the environment defined by the input data: NDVI, DEM, and land use/cover. The accuracy of the output is limited by the quality of the input data. Fine scale temperature temporal change has been ignored in this study due to lack of reliable proxy. Future research exploring the relationship of tsetse population scale responses to the land surface temperature (LST, not air temperature) would make the ample remote sensing based LST very useful for any tsetse fundamental niche model.

Wild animals, cattle, and human beings are hosts for tsetse flies. We simulated movements of pastoralist and cattle using decision making rules from field surveys and cattle tracking data in the literature. However, at the moment we lack the knowledge to simulate wild animal agents including unknown numbers and species with unknown movement patterns. Without more comprehensive movement patterns for different animal hosts, we were not confident using anything other than a generic random distribution. Thus, we simply used the agent (*Wild animal*) to generally represent all the hosts. Some cattle and pastoralist movement patterns have been studied (e.g., Butt, 2010; Guo et al., 2009; Turner et al., 2000) but it is still difficult to set local rules for these hosts. Further field work is required to improve the host simulations. While not included in this version, Human African Trypanosomiasis (HAT) could also be analyzed within the ABM if the epidemiological rules of trypanosomiasis (Hethcote, 2000; Lloyd-Smith et al., 2009; Rogers and Packer, 1993) were translated for the model.

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Appendix A. Codes and sample data

The model codes and sample data associated with this article can be found in the online version at doi:10.1016/j.ecolmodel.XXXXXX.

Highlights

1. Tsetse fly distribution was predicted without present/absence survey data.
2. The distribution included both spatial and temporal dynamics.
3. We simulated the outcomes of common methods used in tsetse fly control.

Fig. 1.
Model agents and their relationships

Fig. 2. Study area with digital elevation map (DEM) data. The inset map on the top-left indicates location of the study zone within Kenya.

Fig. 3.
Model schedule

Fig. 4.

Tsetse distribution and environmental suitability. a) Tsetse flies (black dots, one dot = 5 flies) were set everywhere in suitable areas (green patches). b) At the end of a simulation year, tsetse flies were mostly present only in the large suitable areas. c) Scaled suitability, where black indicates zero days of suitability, and white indicates 365 days of suitability within a year. Red rectangles indicate example areas without tsetse even when 100% suitable during a year. One red dot presents one wild animal. One-year simulation result.

Fig. 5. Area occupied by tsetse flies. One pixel = 250*250 m². One-year simulation result.

Fig. 6.

Tsetse fly (black dot, one dot = 5 flies) distribution depends on wild animal (red dot, one dot = one wild animal) density. The figures show tsetse distribution after one-year simulations. Wild animal populations are (a) 100 % (i.e., 7,700), (b) 50% (i.e., 3,795), (c) 25% (i.e., 1,918), (d) 22.5% (i.e., 1,736), (e) 20.25% (i.e., 1,558), and (f) 19.35% (i.e., 1,401). Tsetse fly populations are (a) 53,675, (b) 22,140, (c) 6,105, (d) 3,940, (e) 1,675, and (f) zero. The green patches are suitable areas for tsetse flies. There is no tsetse fly in the figure overlap parts of a, b, c, d, and e.

Fig. 7.

Tsetse fly population recovers after praying insecticide. Four mortality rates (i.e., 50%, 85%, 99%, and 99.9%) as insecticide effects are simulated. The populations are single-run results, not mean values of multiple runs.

Fig. 8. Tsetse fly and pupa population changes for release of irradiated sterile males. The populations are single-run results, not mean values of multiple runs.

Fig. 9. Land use/cover change scenarios. (a) Land use/cover of 2011; (b), (c), and (d) is land use/cover with agriculture and built-up expanding 30%, 50%, and 70% above the 2011 level, respectively.

Fig. 10. Tsetse population changes for agriculture and built-up expansion. The populations are single-run results, not mean values of multiple runs.

Fig. 11.

Tsetse fly (adult) population sensitivities to $\pm 30\%$ of model parameter value changes. Mean and standard deviation (SD) (black lines) were calculated from 46 default runs as baselines.

Fig. 12.

Tsetse pupa (juvenile) population sensitivities to $\pm 30\%$ of parameter value changes. Mean and standard deviation (SD) (black lines) were calculated from 46 default runs as baselines.

Table 1**Input data**

Data name	Data source	Note
NDVI (Normalized Difference Vegetation Index)	Vegetation Indices 16-Day L3 Global 250m (MYD13Q1); http://reverb.echo.nasa.gov	Data in 2011 were used in every year cycle.
Maximum temperature (T_{max})	Global Multi-resolution Terrain Elevation Data 2010(GMTED2010), 250 m; http://eros.usgs.gov	$T_{max} = 33.915 - 0.004 \times \text{Elevation}$ (Lin et al., 2012)
Minimum temperature (T_{min})	Same as above	$T_{min} = 24.292 - 0.007 \times \text{Elevation}$ (Lin et al., 2012)
Land use/cover	Land Cover Type Yearly L3 Global 500 m SIN Grid (MCD12Q1); http://reverb.echo.nasa.gov	Resample to 250 m

Table 2

Model parameters

Variable	Value	Reference [*]
Initial tsetse number	12, 000	Estimated
Initial pupa number	8, 000	Estimated
Initial wild animal number	7, 700	Estimated
Maximum tsetse movement distance	800 m/day	(Vale et al., 1984)
Tsetse starvation days	7 days	(Leak, 1999)
Tsetse desiccation days	3 days	(Leak, 1999)
Pupae desiccation days	3 days	(Leak, 1999)
Reproduce age	18 days	(Leak, 1999)
Birth gap	10 days	(Wall and Langley, 1993)
Maximum tsetse density	2, 200 tsetse/km ²	(Mihok et al., 1992)
Pupa hatch time	3–5 weeks	(Leak, 1999)
Tsetse fly longevity	1 – 3 months	(Leak, 1999)

^{*} The values are initialized and adjusted per the reference cited.