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Économie du contrôle des trypanosomoses africaines animales sous les changements climatiques

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Abstract

African animal trypanosomiasis (AAT), transmitted by the tsetse fly, is a climate sensitive animal disease that is a major obstacle to sustainable development of livestock husbandry and agriculture in sub-Saharan Africa. To address this problem, the African Union set up in 2000, the Pan-African Tsetse and Trypanosomosis Eradication Campaign (PATTEC) to implement extensive campaigns of tsetse eradication across the continent and overcome this disease. In order to optimize these campaigns, we propose in this thesis two contributions. The first is an understanding of the risk of AAT and the second is an improvement of ex-ante economic analysis of these projects. Therefore, we first developed a spatial risk analysis of trypanosomosis risk induced by climate and environment in order to guide the eradication campaign in the Niayes area in Senegal. This model, compared to existing models, enabled complete tsetse eradication while using fewer resources such as traps and labor. Moreover, this risk analysis was refined in Burkina-Faso and Ghana to take into account seasonal climate variability. Finally, these risks models developed in this thesis were used in a bio-economic model that combined also climate change projections and the results of a participatory workshop with herders in the Niayes area. This economic analysis showed that taking into account or not climate change projections has a great influence on the potential benefits of tsetse eradication. In the Niayes campaign, the model showed that the potential benefits were overestimated although the project is still profitable. This analysis also highlighted another important result, in tsetse-free area cleared by the project, farmers innovated and replaced their herds of trypanotolerant cattle by more productive but trypanosusceptible herds, while reducing herd sizes. Therefore, we can conclude that in the context of the eradication campaign in Niayes, reducing the risk of AAT could help to mitigate climate change by limiting the gases from cattle farming and could also allow the livestock system to adapt to anticipated global changes such as fodder shortage.

Keywords: Risk of African animal trypanosomiasis, Climate change mitigation, Cost-Benefit.

Résumé

La trypanosomose africaine animale (TAA), transmise par la mouche tsé-tsé, est une maladie animale sensible au climat qui est un obstacle majeur au développement durable de l'élevage bovin et de l'agriculture en Afrique subsaharienne. Pour faire face à ce problème, l'Union africaine crée en 2000, la *Pan-African Tsetse and Trypanosomosis Eradication Campaign* (PATTEC) afin de mettre en œuvre des vastes campagnes d'éradication de glossines à l'échelle du continent pour venir à bout de cette maladie. Dans le but d'optimiser ces campagnes, nous proposons dans cette thèse deux contributions. La première, est une meilleure analyse du risque de TAA et la seconde, est une amélioration des analyses économiques ex-ante de ces projets. Dans cette optique, nous avons développé une première analyse spatiale du risque trypanosomien induit par le climat et l'environnement afin de mieux guider la campagne d'éradication dans la zone des Niayes au Sénégal. Ce modèle, comparativement aux modèles existants, a permis une éradication rapide des glossines tout en utilisant moins de ressources. De plus, cette analyse de risque a été affinée au Burkina-Faso et au Ghana afin de prendre en compte la variabilité climatique saisonnière. Finalement, toujours dans le cadre du projet d'éradication des Niayes, et en s'appuyant sur les modèles de risques développés dans cette thèse, un modèle bio-économique qui intègre des projections climatiques et les résultats d'un atelier participatif avec des éleveurs a été développé. Il ressort de cette analyse économique que la prise en compte ou non des projections climatiques a une grande influence sur les bénéfices potentiels de l'éradication des glossines. Dans le projet des Niayes, le modèle montre que les bénéfices du programme auraient été surestimés même si le projet reste rentable. Cette analyse met aussi en relief un autre résultat important : dans les zones libérées du risque par le projet, les éleveurs innovent et remplacent leurs troupeaux d'animaux trypanotolérants par des troupeaux d'animaux plus productif mais trypanosensibles, tout en réduisant la taille des troupeaux. On peut donc conclure que dans le cadre du projet d'éradication des Niayes au Sénégal, réduire le risque de TAA permet d'atténuer les changements climatiques en limitant les gaz issus de l'élevage bovin et pourrait également leur permettre une meilleure adaptabilité aux changements anticipés, comme une réduction du disponible fourrager naturel.

Mot-clés : Risque de trypanosomose africaine animale, Atténuation du changement climatique, analyse coût-bénéfice.

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List of abbreviations

AAT: African Animal Trypanosomosis

AU: African Union

AW-IPM: Area-Wide Integrated Pest Management

BCS: Body Condition Score

CIRDES: Centre International de Recherche-Développement sur l’Elevage en zone Subhumide

DDT: Dichlorodiphényltrichloroéthane

FAO: Food and Agriculture Organization of the United Nations

GDP: Gross Domestic Product

HAT: Human African Trypanosomosis

ILCA: International Livestock Center for Africa

ILRAD: International Laboratory Research on Animal Disease

ILRI: International Livestock Research Institute

ISRA: Institut Senegalais de Recherche Agricole

ITC: Insecticide-Treated Cattle

ITT: Insecticide-Treated Target

OIE: World Organization for Animal Health

PATTEC: Pan African Tsetse and Trypanosomiasis Eradication Campaign

PCR: Polymerase Chain Reaction

PCV: Packed Cell Volume

USD: US Dollars

SAT: Sequential Aerial Treatment

SIT: Sterile Insect Technique

Forewords

This thesis is submitted to fulfill the degree of doctorate in climate change economics at the University of Dakar. This research is funded by the West African Science Center for Climate Change and Adapted Land Use (WASCAL) program.

The topic of this thesis is about the economics of the control of climate-sensitive livestock disease: African animal trypanosomosis. This topic is particular in the sense that during the past 3 years of research, it required a thorough understanding of a complex epidemiology system and how to integrate this system into a general economic model. This integration of biological process and the development of a “bio-economic” model was required to capture the impact of climate change on the control of African animal trypanosomosis.

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Chapter 1: Introduction

1.1. Introduction

Sub Saharan African (SSA) countries are the least developed countries in the world and hunger and poverty are widespread, especially among the rural populations. In Africa, population from rural areas relies mostly on agriculture and livestock husbandry for their livelihood. Livestock is a source of protein (meat and milk), draught power and manure for improving crop production. In addition to the global climatic change which compromises crop production in the SSA but also has an impact on the vector-borne animal disease such as African animal trypanosomosis. It is a parasitic disease caused by species of flagellate protozoa belonging to the genus *Trypanosoma* which inhabit the blood plasma and various body tissues and fluids. These parasites are found in many animals but seem to be pathogenic only for mammals, including man. This disease causes important loss in animal production and can due to its epidemiology, it is highly sensible to climate change.

African animal trypanosomosis is transmitted by tsetse fly and remains one of the major constraint to the development of agriculture in 10 million km^2 within 38 African countries (Alsan, 2015). Agriculture is the most important sector in Africa with 32% percent of gross domestic product (GDP) and 65% of the continent labor’s force with a 35% contribution of the livestock sector to its growth (Group, 2012). However, the impact of AAT on livestock production can be reduced by the use of various control techniques and options. The most commonly used option are the use trypanocidal drugs and the introduction of trypanotolerant cattle breeds. Besides these control methods, one way to reduce the transmission rates is to control the vector of AAT: tsetse fly. The control of tsetse fly has seen a lot of innovation during the last century with methods such as such the use of insecticide-treated cattle (ITC), insecticide-treated trap (ITT), ground or aerial insecticide spraying, the sterile insect technique (SIT) or just by reducing the risk of exposure through changes in livestock management (Holt et al., 2016).

In order to coordinate efforts to fight AAT at the continental level and because of transboundary nature of this disease, Africa Union, at the summit held in Lome, Togo in July 2000, created the Pan-African tsetse and trypanosome eradication campaign (PATTEC).

PATTEC was given the task to initiate and coordinates large scale tsetse and trypanosomosis control throughout the continent. Even though this objective represents an important challenge that would require extensive resources, and whether the availability of fund to achieve this goal is questioned, the last decade has seen renewed interest in the research and development of new control options for AAT. Therefore, many governments and philanthropists have made funding available for this purpose. However, despite this recent rise in fund, the reality is that a lot of people of the communities afflicted by AAT still have insufficient resources available for its control and these communities are not always reached by control programs (Alsan, 2015; Holt et al., 2016).

Moreover, besides the availability of funding and willingness of various stakeholders to tackle this important issue, the technical aspect surrounding the techniques used to eradicate tsetse fly must be improved. Indeed, the feasibility of area-wide integrated pest management operations must be based on sound analysis of the study area, the risk of AAT and the agricultural potential once the area will be cleared from tsetse fly. However, when the suppression or the eradication of the vector is not feasible, livestock owner must live in an area with varying risk (Bouyer et al., 2006). Therefore, even when eradication is not an option, stakeholders must be informed about AAT risk and its variation. However, AAT risk maps and surveillance based tool are still lacking.

This thesis was therefore carried out to understand, using data from various the case of one eradication campaign and data from other control projects in West Africa, how eradication campaign can be optimized and how economic analysis of tsetse control can be refined to take better decision. It is expected that the results could inform priority setting and the development of tailored recommendations for AAT control strategies in the continent.

1.2. Objective of the thesis

This thesis seek to fill two gaps, one in the analysis of African animal trypanosomosis risk and second gap in the economic analysis of African animal trypanosomosis control by integrating climate change simulation, in order to better plan future control of AAT.

1.2.1. Research questions

The goal of this thesis is then to enhance our understanding of the risk of AAT and the economics of trypanosomosis control in a changing climate. To achieve this aim, we will combine statistical analysis, spatial epidemiology and economics analysis in order to develop spatial, spatio-temporal risks models and a bio-economic model that can capture the complexity of the disease system evaluated in order to achieve more optimal control. Having these two goals as prime objectives, the research questions we seek to answer are the following:

1. How environment and climate affect African animal trypanosomosis risk?
2. How to evaluate the risk of African animal trypanosomosis under climate change?
3. How the design of refined risk analysis of AAT can optimize control operation?
4. What is the impact of climate change on the economics of African animal trypanosomosis control?

1.2.2. Research objectives

Answering these questions, required us to split the main objective in three main parts:

1. Evaluate the risk of African animal trypanosomosis to optimize eradication campaigns
2. Analyze how climate and environment affect the risk of African animal trypanosomosis in space and time in order to inform stakeholder on AAT risk when eradication is not an option
3. Analyze the impact of climate change on the economics of the control African animal trypanosomosis

1.2.3. Research hypotheses

The following hypotheses will be tested:

1. Control operation and eradication campaign in particular can be optimized by fined-grained ex-ante risk analysis

2. Climate and specially temperature related variables has an important impact on the risk of AAT and Space-time risk index can be developed on this basis

3. Climate change impact the risk of AAT and thus affect the economic analysis of eradication campaigns

1.3. Description of the study area

1.3.1. The Niayes area, Senegal

Figure 1: The Niayes area, Senegal (source: Google Map)

The study area had a total surface of 7,150 km², located in the Niayes region of Senegal (14.1° to 15.3° N and 16.6° to 17.5° W). At the time of the study, it is the target of an eradication campaign against an isolated *G. p. gambiensis* population. The climate is hot and dry from April to June, whereas the rainy season occurs from July to October and the cold dry season from November to March.

The area is characterized by high population density and marked intra-regional disparities, with an average density is 193 hab/km^2. The population density in the Niayes area is the result of natural growth combined with inter-regional migration from the North, South, and from the Sahelian hinterland towards the coast. These migratory flows have increased since the mid-1970s, resulting in rapid urbanization.

In 1998, the population of the four regions of Dakar, Thiès, Louga and Saint-Louis was 3.6 million, this number rose to 7.3 million in 2015 which is approximately 50% of the population of the whole country. Therefore, with such density, the natural resources and land in particular of the Niayes are under high and constant pressure. This phenomenon is even more pronounced as rural areas are increasingly engulfed by densely populated urban sprawl, and the opportunities offered by urban markets encourage more intensive forms of agriculture. This has led to the emergence of progressively inter-related urban and industrial development (Touré and Seck, 2005).

Furthermore, particular meteorological and ecological characteristics of this area provide great potential for agricultural development in general and animal production (cattle, donkeys, horses, small ruminants, pigs and poultry) in particular. However, in 2004 the dairy farms of the peri-urban area of Dakar produced less than 6,000 L of milk per day. In 2005, intensified livestock production systems with exotic breeds such as Holstein, Montbéliarde, Jersey, Girolando, and cross-breeds between these breeds and local cattle were only found on 1% of the farms. Mean daily milk production was still limited to 6.9 L (s.d. 3.0 L) despite much higher genetic potential of these exotic breeds and the use of large amounts of inputs (food concentrates, drugs, etc). From 1984 to 1993 these farms received government support that included training, animal health care and feed ingredients. Despite this support, farmers were still disorganized in 2005 in terms of milk distribution and inputs. In 2008, a project called "La Grande Offensive Agricole pour la Nourriture et l'Abondance (GOANA) (http://www.gouv.sn/IMG/article_PDF/article_777.pdf) was launched which included a component of artificial insemination of local breeds with exotic dairy breeds and by December 2011, more than 91,000 cattle had been inseminated. In view of its proximity to the Atlantic Ocean, the Niayes area is a particular eco-region that is more resilient to climate change as compared to other regions in Senegal e.g. the area only experienced a reduction of 150 mm in annual precipitation the last 20 years compared to 200 mm of precipitation in the rest of Senegal. Unfortunately, this microclimate also favours the presence of *Glossina palpalis gambiensis* Vanderplank, a riverine tsetse species. Tsetse flies (Diptera: Glossinidae) are the vectors of human African trypanosomosis (HAT) and African animal trypanosomosis (AAT), the former a major neglected human tropical disease, and the latter considered among the greatest constraints to improved livestock production in sub-Saharan Africa. Most domestic animals are susceptible to AAT which was until recently still highly prevalent in the Niayes area. It was a major pathological problem especially for cattle crossed with exotic breeds and Gobra zebus which are very susceptible to trypanosome. The sustainable removal of the vector, the tsetse fly, would be the most efficient way of managing AAT.

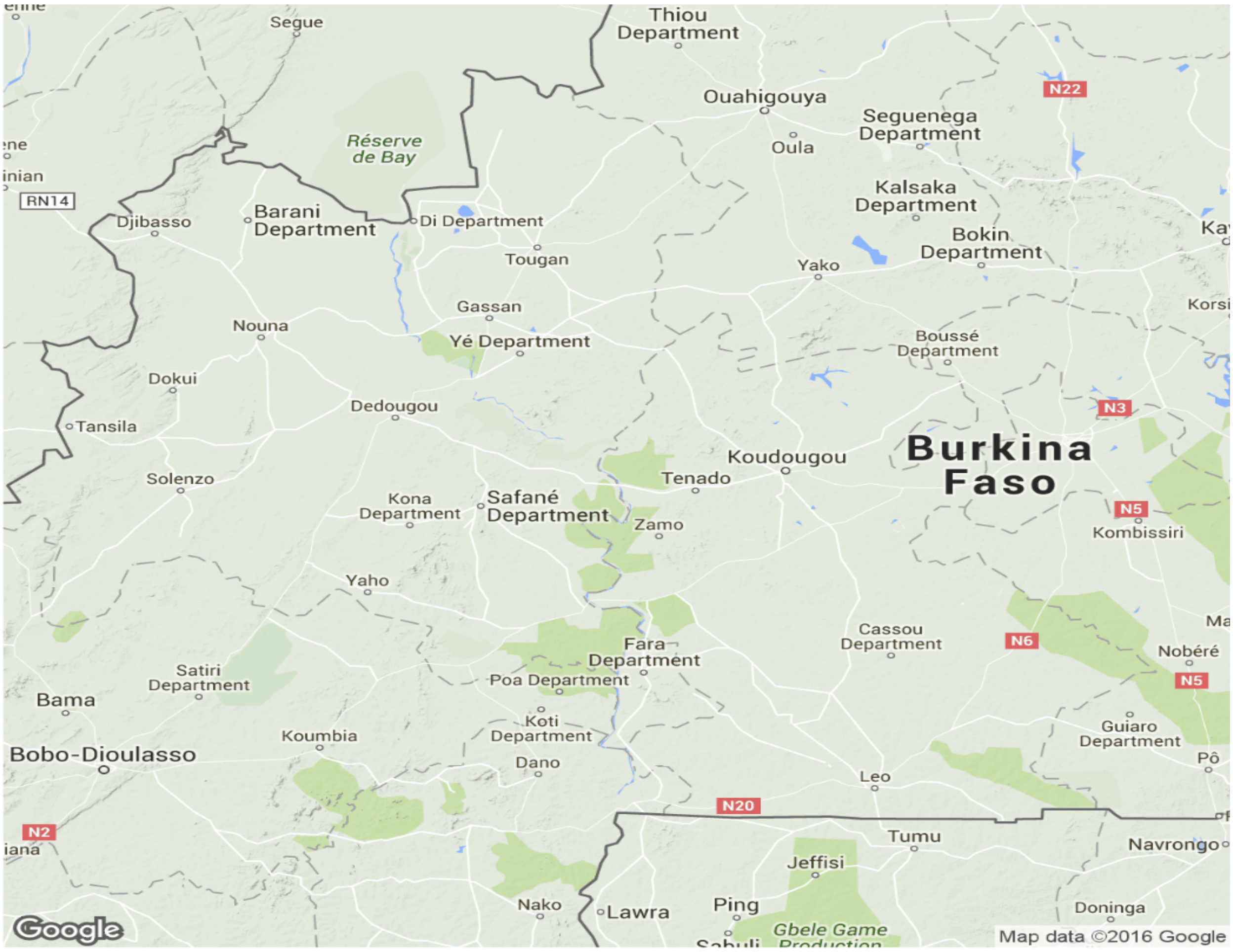

Figure 2: Southern Burkina Faso and Northern Ghana (source: Google Map)

1.3.2. The Southern Burkina Faso and Northern Ghana

The study area in south-western Burkina Faso and north-western Ghana is located between latitude 9º23' – 15º5'N and longitude 0º29' - 5º31' W. The area is approximately 372,000 km^2, and the main river is the Mouhoun/Black Volta. Mean monthly temperatures vary between a minimum of 18°C and a maximum of 36°C and annual precipitation between 250 and 1,170mm. The study area is constituted of Sudano-Guinean savanna in the south, Sudanian savanna in the central part and Sahelian savanna in the north.

In the upper-west region of Ghana and Southern Burkina Faso, the human density is low compared to the rest of the areas their respective countries and the major economic activity is agriculture and livestock husbandry. There are three main breeds of cattle: the West African Shorthorn (WASH), Zebu and Sanga. The WASH is the most common breed of cattle raised in the area because of its high trypanotolerance as compared to the other two breeds (Mahama et al., 2004). These animals are mostly herded by Fulani immigrants, acting as paid employees. The husbandry system is sedentary with communal grazing along rivers, shuttling from settlements to the main peririparian grazing areas, usually located in a radius of 2–5 km. The practice of transhumance is also occasionally encountered in the area (Mahama et al., 2004).

1.4. Outline and organization of the thesis

This thesis is structured in 5 chapters, this chapter, the first, gave the context and introduced the primary issues. The study area was described and the objectives, research questions and hypotheses were elaborated.

In Chapter 2, we described African animal trypanosomosis as a disease problem in livestock production in the continent. We presented the epidemiology of the disease system and the option to control this disease and a brief literature review on the economics of AAT control.

This chapter help to facilitate the economic and statistical analysis by providing the biological and technical parameters required to pursue such analysis.

Chapter 3 were mostly about the research design and methodology. It is divided in 3 parts, one part for each objectives to describe how we design our research to answer each research questions.

In chapter 4, was presented the results and discussed them based on the literature. We followed the same structure as chapter 3 and divided it in three part, each part for a research question.

Finally, in the conclusion, we presented a summary of the results, we discussed the policy implications from this research and we proposed potential directions in which this research can be extended.

Chapter 2: African animal trypanosomosis and its control: a literature review

In West Africa, millions of agropastoral households rely on livestock as their primary source of income. However, most of these populations are at risk of livestock diseases which represent one of the most serious threats for livestock production. Trypanosomosis, transmitted by tsetse flies, remains the most important pathological constraint to livestock production and intensification in the 10,000 km2 infested by these vectors, including the sub-humid area of West-Africa (Van den Bossche et al., 2010). Tsetse flies also known as glossina, referred as ”Africa’s bane” by Nash (1969), are responsible for the transmission of trypanosomes which cause African Animal Trypanosomosis (AAT) in livestock. Many veterinary and agricultural experts consider AAT as the single greatest health constraint to increased livestock production and intensification in sub-Saharan Africa (Vreysen et al., 2012).

2.1. Epidemiology of African animal trypanosomosis

The epidemiology of African animal trypanosomosis is complex and is determined by various factors among which the most important are tsetse flies, the parasite and the hosts and reservoir (Moore et al., 2012; Rogers and Randolph, 1988). Of major importance are firstly the diet composition of the tsetse, then the distribution and density of the tsetse and the hosts and finally the prevalence of trypanosomal infections in tsetse and in the host (Rogers and Randolph, 1988). This complex system can be described through the interaction with the pathogen, the vector, the host, and the climate and environment.

2.1.1 The pathogen: the trypanosome

African Animal trypanosomosis (AAT) is a parasitic infection caused by an extracellular flagellate protozoa from the genus Trypanosoma. Trypanosomes belong either to the Salivaria or Stercoraria groups. The Stercoraria trypanosomes are excreted in the faeces of blood sucking insect vectors like triatome bugs. The African pathogenic trypanosomes affecting human or livestock belong to the Salivaria group. Trypanosomes are unicellular protozoan parasites of the phylum Sarcomastigophora, order Kinetoplastida, family Trypanosomatidae, and genus Trypanosoma (Vaughan and Gull, 2003). The Trypanosoma brucei complex, one of the most important species of trypanosomes, is grouped into three morphological identical subspecies: *T. brucei brucei, T. b. rhodesiense*, and *T. b gambiense*.

Among these three sub-types, only *T. b. brucei* is pathogenic to cattle, the other subspecies cause acute sleeping sickness in East Africa and chronic sleeping sickness in West Africa. *T. congolense, T. vivax* and, to a lesser extent *T. b. brucei*, are the major pathogenic species of African cattle (Morrison et al., 1981). *T. congolense* is considered the most important cause of AAT in East Africa, and *T. vivax* in West Africa (Stephen and others, 1986, p. 198). In particular, In AAT, *T. congolense* from the savanna type is the most pathogenic and is responsible for acute infection and death of diseased animal. Trypanosomes are able to infect a wide variety of domestic hosts and more than 30 species in the wild. However, mixed infections that involve two or three species are frequent in areas of medium to high tsetse challenge (Taylor and Authié, 2004). *T. vivax and T. b. brucei* have spread beyond the tsetse fly belt by transmission through mechanical vectors such tabanides and some other insects.

In cattle, the pathogenesis of AAT is usually dominated by three characteristics: anaemia, tissue lesions and immune suppression. Anemia is a complex phenomenon to track down in cattle and other mammal hosts. Although haemolysins are released by trypanosomes, intravascular haemolysis is not a prominent feature, and anaemia is rather attributed to erythrophagocytosis by cells of the mononuclear phagocytic system in the spleen, bone marrow, lungs and lymph nodes. These cells are stimulated by the formation of complexes between immunoglobulin specific for trypanosomes and antigen or complement attached to red cells (Mehlhorn, 2001). Three phases of anemia usually occurs, the acute form, the chronic form and the recovery form (Anosa and others, 1988, p. 19). Pathology in tissues is associated with the ability of the parasites to invade extra vascular spaces and organs. Whereas *T. congolense* remains confined to the vascular system, *T. b. brucei* is distributed in both the circulation and in the tissues; *T. vivax* although primarily a vascular parasite, has also been found in extravascular locations.

2.1.2 The vector: glossina

Tsetse flies also known as glossina are the cyclical vector of African Animal trypanosomosis (AAT). They are only found in Africa, they organized into one genus, *Glossina*, and there is 31 species of tsetse flies that have been identified. Tsetse flies are historically classified into three groups, based on their ecology, behavior and morphology (Newstead and others, 1924). They are the biological and/or mechanical vector of trypanosomes and constitute a constant threat to humans and livestock over much of sub-Saharan Africa (Gooding et al., 2004). However, even if all species are potential cyclical vectors of AAT, only a few of them transmit human sleeping sickness. The palpalis group (subgenus Nemorhina) is found in the riverine galleries of West and Central Africa but can extend into savanna regions between river systems; G. palpalis and G. tachinoides are important AAT vectors in this group. In West Africa and particularly in our study area, two species from this group are of interest: *Glossina palpalis gambiensis* and *Glossina tachinoides*. They are riverine species occurring in narrow thickets along river banks (Sudanese ecotype), constituted by short mimosa pigra and morelia senegalensis, the swampy forests of mitragyna inermis, and riparian vegetation (hydrographic networks of dry and wet savannas (Guinean and Sudano-Guinean ecotypes) (Bouyer, 2006). In particular, *G. p. gambiensis* live in the riparian vegetation types Guinea and mangroves of the savanna zone, while *G.tachinoides* live in riparian Sudanese cords with maximum densities border region

Tsetse feed exclusively on blood, they are holometaboulos insects. Tsetse fly have an unusual reproducible cycle compared to other insects. The female mate juste once and give birth to full-grown larvae which rapidly pupate in the soil. When the tsetse flies suck blood, development of trypanosomes in them depends on the species of Trypanosoma. In fact, *T. vivax* only colonizes the proboscis, *T. congolense* and *T. simiae* the midgut and the proboscis, whereas *T. b. gambiense*, *T. b. rhodesiense* and *T. b. brucei* develop in different regions of the intestine. The metacyclic infectious forms are found in the salivary glands of the tsetse fly.

Taking into account their longevity, mobility and feeding frequency, tsetse fly is a highly efficient vector of AAT, but the low rate of population growth has an important implication for vector control: a small increases in mortality rate can result in population decline and even extinction (Hargrove and others, 2003).

The tsetse fly is very sensitive to environmental conditions and they are highly thermosensitive in particular. Their movement and dispersal is influenced by their density in the area and how fragmented the environment is (J. Bouyer et al., 2009). Tsetse fly cannot survive in areas that are too hot, too dry, or too cold. Therefore, there is a particular environmental niche when they can live and reproduce and thus adapted to environment with low climatic variability (Bouyer, 2006, p. 200).

2.1.3. The hosts

Tsetse fly feed on various hosts. In the wildfile, mammals and certains type reptile are usually preferred. In particular, warthog, buffalo or the monitor lizard are considered as natural hosts of tsetse and they usually display a tolerance to trypanosome infections. Therefore, they also serve as reservoir for both AAT and HAT (Taylor and Authié, 2004).

In AAT epidemiology, beside the role of Wildlife as reservoir, there is a large interest on how tsetse affects domestic animal and livestock in particular. In cattle the pathogenesis was well documented.

In West Africa, *Trypanosoma vivax* infections are the most common and zebu (Bos indicus) are very sensitive (Itard and Frézil, 2003). The incubation period may be short (about a week). Parasitaemia is persistent and strong in primary infection. In the acute form, lethality is important and occurs within 2 to 3 weeks after the onset of symptoms. The chronic form develops over two to three months with a high fever (40-41 °C), a progressive wasting up to cachexia, asthenia, quilted coat, tearing, mucous blades due to anemia, and enlarged lymph nodes prescapular and precrural. Dyspnea and tachycardia are observed during the febrile episodes. In sensitive cattle breeds when the disease is untreated, it can lead animal death from hypothermia (Itard and Frézil, 2003).

T. congolense is the most pathogenic species for cattle (Itard and Frézil, 2003). Zebu are also the most sensitive, Métis between zebu and bull and usually develop a chronic form of the disease while the bull purebred have good resistance to disease. The incubation period lasts about fifteen days. Fever manifest itself in more or less important febrile (fever over frequently 40 °C).Cattle affected are low, prostrate (with head down); they have a slimming evolving towards cachexia, adentis, anemia that can be severe, tearing and sunken eyes, a nose hair falling and sclerosis. In the most severe form, the subject shows sign of anorexia, diarrhea and with difficulties to move. Few weeks after, if the animal do not recover, he can die from hypothermia.

The *T. brucei* infection usually manifests as a chronic form with slow installation of the following symptoms: intermittent febrile seizures, nasal and ocular discharge, digestive disorders, progressive anemia, dives hairs then fall. The terminal phase is characterized by paralysis. The disease can last up to two years. In conclusion AAT is usually a herd problem affecting all demographic parameters and productivity.

2.1.4. Climate and environment

Climate may strongly influence temporal and spatial distribution of vectors and vector-borne diseases (Gage et al., 2008; Rogers and Randolph, 2006). According to (IPCC, 2007) climate change is expected to impact significantly vector-borne diseases distribution and pattern. In trypanosomoses, changes in climatic factors can impact on i) survival and reproduction rates of the vectors, thus influence their distribution and abundance, ii) intensity of activity of the vectors (esp. biting rate), and iii) cycle, survival and reproduction rates of the trypanosomes (Van den Bossche et al., 2010). A recent model has predicted a large-range expansion of sleeping sickness in East and South Africa, caused mainly by a shift of up to 60 per cent of its geographical extent. The model also predicts an increase of 46–77 million additional people at risk of exposure by 2090, depending on the climatic scenario used. The model used is a classical epidemiological SEIR (susceptible, exposed, infected and recovered) compartmental model including humans, animals and vectors (Moore et al., 2012). This change is mainly anticipated from predicted changes in global temperatures impacting on the following entomological and epidemiological parameters: total tsetse population size, natural death rate of tsetse, parasite maturation rate in tsetse and tsetse biting rate.

Besides climate, the influence of the environment in the epidemiology of AAT have been highlighted several times and its role has been highlighted in order to understand the variability in AAT risk (de La Rocque et al., 2001).

The droughts in West Africa during the early 1980’s and the ensuing migration of people towards the south (resulting in the destruction of vegetation and fauna) have degraded the habitat of several tsetse species and caused a reduction in their density. Indeed, the distribution of *G. tachinoides* has now receded to the intermediate zone between the forest and the savanna in Cote d'Ivoire and *G. morsitans submorsitans* and *G. tachinoides* are now seldom in the "W" park in Niger and Burkina Faso. Thus, with continued demographic pressure and ever widening human impacts on the environment, the further retreat of some tsetse species and reduction in the wildlife reservoir has already been observed and affected the distribution of tsetse flies (Clair, 1988; Katondo, 1984).

2.2. Control of African animal trypanosomosis

Each of the available methods for tsetse and trypanosomosis control has its own specific limitations. The choice of the control method to be applied will depend on many aspects. The most important are the targeted zone, the impact on the environment, the tsetse species targeted, the possibility of isolation of treated areas, the economic impact, the possibilities of land use after control and the available funding at the moment of the operations and for the future. Based on control operation throughout the continent, the most widely used method to control trypanosomosis are used of drugs and the use insecticides to control tsetse fly, they are usually the first options before any other method can be applied (Allsopp, 2001).

In West Africa, the recommended strategy for controlling the disease has been an integrated approach combining vector suppression in epidemiological hot spots and disease management at the herd level through the strategic use of trypanocides combined with the keeping of local trypanotolerant breeds (Jérémy Bouyer et al., 2013a). However, trypanocidal drug treatment used alone without any integration with other control methods remains the principal disease control method applied by livestock owners.

The control of AAT is based on essentially three strategies (Allsopp, 2001; Bouyer, 2006):

- Parasite control in the host
- Trypanotolerant breed
- Vector control

2.2.1. Parasite control in the host

Curative or preventive trypanocidal drugs are used to maintain susceptible livestock in trypanosomosis enzootic area. So far, the protection of livestock by immunization is not possible and there is no vaccine in development.

This control technique is mostly based on the curative and prophylactic use of trypanocidal drugs. Trypanocidal drugs are one of the most widely used methods applied by farmers and herders to control trypanosomosis in Africa (Leak, 1999, p. 199; McDermott and Coleman, 2001). The use of such drugs are usually either therapeutic or prophylactic purpose and sometimes both way are combined. The use of preventive drugs can help to prevent susceptible animals from contracting the disease for a period of two to four months. Furthermore, there are very few trypanocidal drugs available and efficient for curative purpose.

The high adoption rate of this method of control can be tracked down to the cheap price of the main molecule which is around a 1 USD per treatment (Affognon, 2007). In West Africa, only two molecules are used to tackle the disease, namely diminazene and isometamidium. They are often the first drugs tried by farmers when their cattle develop (any) symptoms of the disease (Geerts et al., 2001). It has been estimated that about 35 million doses of trypanocides are administered each year to an approximately 45 - 60 million cattle at risk of trypanosomosis (Geerts et al., 1998; Holmes and Torr, 1988).

There are still millions of herders that based their control strategies on the exclusive use of trypanocides which is associated to a high risk of diffusion of resistant strains of trypanosomes even though strategies based on combined vector control and trypanocides treatments are promoted by stakeholders (Affognon, 2007; Jérémy Bouyer et al., 2013a; Geerts et al., 2001).

The misuse of drugs in West Africa was pointed out of one of the main reason for poor production in cattle and increase in the risk of drug resistance in livestock (Clausen et al., 2010). Indeed, in some areas, despite the common knowledge among herders that there is low AAT risk, the use of drugs is high and persistent.

Although there is a continuous demand for trypanocides by livestock keepers, the African market of trypanocides estimated at about USD 30 million, is not considered sufficient to justify investment by large pharmaceutical companies. Indeed, the development and licensing of new animal trypanocides cost was estimated to USD 800 million (DiMasi et al., 2003).

This strategy of trypanocidal drugs use can be optimized. One way to reduce the risk of drug resistance is to link the use based on the magnitude and the seasonality of the tsetse challenge, trypanosomosis risk, and the degree of livestock susceptibility to trypanosomosis. Furthermore, used properly, trypanocidal drugs can improve animal health and welfare. It allows for a higher levels of production and can safeguard the livestock. (Affognon, 2009).

In conclusion, trypanocidal drugs treatment will probably remain the mainstay of control of African animal trypanosomosis for the coming years, and the development of resistance to the small number of available compounds would still generally be a cause of considerable concern (Affognon, 2007; Geerts et al., 1998).

2.2.2. Trypanotolerant breed

Trypanotolerance is the capacity of an animal to reduce and control the development of the parasites causing animal trypanosomosis and to limit their negative effects (Itty et al., 1993; Murray et al., 1988). Therefore, the introduction and use of such animal in place of susceptible livestock can considered as a way to produce under AAT risk. Trypanotolerance of some livestock species allows some breeds to survive, reproduce and remain productive under high trypanosomes risk. This knowledge was recognized and exploited by farmers for a long time. In Africa, the number of estimated of trypanotolerant cattle are estimated to 12 million, which is approximately 5% of the total cattle population, with the largest population in West Africa (Agyemang, 2005). The distributions of cattle breed in West Africa indicates that they originated from African bull, Asian zebu and taurine from the Middle East which was established by human migrations, climatic variations and particularly by the health risk (Freeman et al., 2004; Hanotte et al., 2002). In fact, a large body of literature showed that there is a strong correlation between the distribution of trypanotolerant breeds and animal trypanosomosis risk (Freeman et al., 2004; Seck et al., 2010; Taylor and Authié, 2004).

Trypanotolerant cattle, because of their small size, trypanotolerant livestock are perceived as less productive than other breed (Holmes, 1997). Their suitability as draught animals is also disputed. This statement about their productivity was nuanced by some research carried under the umbrella of the International Livestock Research Institute (ILRI). They demonstrated that in some areas where the tsetse challenge was low or zero, the productivity of trypanotolerant breeds (N'dama and the West African shorthorn) was similar to that of the physically larger trypanosusceptible Zebu breed (Trail et al., 1993). They are however, not very popular with many livestock owners in view of their small size, low milk and meat productivity and lack of strength to provide adequate draught power (Holmes, 1997). In fact, despite their advantages in risky areas, wherever Zebu can be raised they displace the trypanotolerant breeds. However, we can note that crossing trypanotolerant cattle with Zebus is widely practiced by farmers when it is possible.

2.2.3. Vector control

Vector control is a strategy of control based on the idea that the cyclical vector of AAT can be contained, eliminated or even in certain case eradicated. In theory, it is the most desirable way to control AAT (Bouyer et al., 2010).

Several strategies have been used in the past to control tsetse flies. The first series of vector control strategies in the beginning of 20th century was based on the destruction of the habitat and wild host of tsetse. Between the early 1940’s and early 1970’s, the number of animal killed per km^2 could go up to 16 (Jahnke, 1974). These types of invasive methods lead to some ethical and ecological problem since the destruction of the environment and animals is not acceptable anymore.

Since then, other approaches have been developed and there has been a lot of innovation the in development of new technologies to control tsetse and trypanosomosis (Leak, 1999, p. 199). Based on the tsetse challenge, scale of the control project, some of these methods were more effective than others. For example, biological control using predators or pathogens has had little success so far (Van der Vloedt and Klassen, 1991).

On the other hand, a technique such as the sterile insect technique (SIT) has shown some interesting results. SIT is a technique that relies on production of large numbers of the target insect in specialized production centers, the sterilization of the males (or sometimes both sexes), and the sustained and systematic release of the sterile males over the target area in numbers large enough in relation to the wild male population to out-compete them for wild females (Vreysen et al., 2012). Based on reproduction cycle of tsetse flies, mating of sterile insects with virgin, native female insects, results in no offspring.

The SIT is non-intrusive to the environment, has no known adverse effects on non-target organisms, is species specific and can easily be integrated with other biological control methods (Vreysen et al., 2012). However, the sterile insect technique is only effective when the target population density is low, it requires detailed knowledge on the biology and ecology of the target pest, and the insect should be amenable to mass-rearing. In particular, in the case of tsetse flies, their low reproductive rates make the rearing of large numbers challenging. In addition, we can also note that the SIT requires efficient release and monitoring methods, which have to be applied on an area-wide basis (Vreysen, 2005). Despite the advance in this method, some fundamental questions remains about the feasibility, appropriateness and cost-benefit of this method (Rogers and Randolph, 2002; Shaw et al., 2015).

The SIT was used on Zanzibar, a small island with little risk of reinvasion and eradication was declared in 1997 and trypanosomosis has not recurred since then (Vreysen et al., 2014, 2000). The PATTEC at the Africa Union (AU) promote the use of SIT as an environmental friendly option to control tsetse and trypanosomosis.

One of the most important form of tsetse control has been the use of insecticides. Ground and aerial spraying of residual insecticide on tsetse sites was widely used following the introduction of cheap persistent insecticides such as DDT, endosulfan dieldrin. More recently, campaigns have used less toxic synthetic pyrethroid insecticides. The most successful example of the widespread use of persistent insecticides resulted in the elimination of a population of 3 species of Glossina from 200,000 km^2 of savanna area in northern Nigeria. This project had conducted between 1955 and 1978, the campaign mainly used ground spraying. Five operational spraying teams (each team consisting of 350 staff) cleared tsetse from on average 8000 km^2 each dry season. The entire campaign consumed 745 metric tons of DDT and dieldrin to achieve this goal. This campaign was the most successful ever undertaken and was very well organized (Jordan and others, 1986).

This method has also been modified and used in community-managed campaigns for localized AAT control. Indeed, new techniques such as the use of pyrethroid footbath on the domestic hosts or the use synthetic pyrethroid insecticides to impregnate traps and screens are currently employed in West Africa (Jérémy Bouyer et al., 2013a; J. Bouyer et al., 2007).

The major drawback to the sustainability of this kind of approach is that it requires the active participation of the whole community. Therefore, the approach requires some incentives, in particular economic incentives in order to be accepted by farmers as compared to alternative such as the use of curative or prophylactic drugs or trypanotolerant livestock (Jérémy Bouyer et al., 2013a; Kamuanga, 2003). Among other issue with this technique we can highlight the fact that it is labor intensive, requires a close supervision and detailed planning. We can also add that it can be potentially dangerous for the environment, the animals and the operators.

Finally, for more than 50 years, there is still an ongoing effort to control tsetse control throughout Africa. Many vector control programs were not able to deliver the promise of tsetse-free area, with the risk of re-infestation by immigrating flies being important. Some studies have even shown that less than 2% of the tsetse habitat at the continent level has been cleared (Budd and Britain, 1999). However, some recent eradication campaign have shifted paradigm toward more innovative approaches. Indeed, the eradication campaign in Senegal based on area-wide integrated pest control framework is a good example of such approach. The main characteristic of this new paradigm is the use of research output to feed to control operation on the ground with tools ranging from mathematical modeling, economic analysis and participatory sociology (Bouyer et al., 2014a; J. Bouyer et al., 2015; Dicko et al., 2014b).

2.3. Mapping the risk of African animal trypanosomosis for tsetse control

2.3.1 Species distribution model for area-wide eradication campaign

The Pan African Tsetse and Trypanosomosis Eradication Campaign (PATTEC) is a political initiative started since 2001 that calls for intensified efforts to reduce the tsetse and trypanosomosis problem (Kabayo, 2002). As part of this global effort, the Government of Senegal embarked in 2007 on a tsetse eradication campaign in a 1,000 km^2 target area of the Niayes region, neighboring the capital Dakar. In this area, the limits of the distribution of the tsetse target populations were assessed using a stratified entomological sampling frame based on remote sensing indicators (Bouyer et al., 2010) *Glossina palpalis gambiensis* Vanderplank and it was responsible for the cyclical transmission of three trypanosome species, i.e. *Trypanosoma vivax*, *T. congolense* and *T. brucei brucei* listed in order of importance (Seck et al., 2010), the high prevalence of animal trypanosomosis (serological prevalence of 28.7% for *T. vivax*) hampered peri-urban intensification of cattle production (particularly dairy cattle). A population genetics study demonstrated that the *G. p. gambiensis* population of the Niayes was completely isolated from the main tsetse belt in the south-eastern part of Senegal (Solano et al., 2010) *G. p. gambiensis* population in the Niayes which prompted the

Government of Senegal to select an eradication strategy using area-wide integrated pest management (AW-IPM) principles (Vreysen et al., 2012).

The successful implementation of an AW-IPM strategy requires a thorough understanding of the ecology of the target population, particularly its spatial distribution: a study which was undertaken in the Niayes from 2007 to 2011 prior to the start of the operational eradication efforts. The selected strategy integrates insecticide treated targets (ITT) and cattle (ITC) with the release of sterile insects (SIT). As the habitat of *G. p. gambiensis* is very fragmented (Bouyer et al., 2010), the targeting of suitable habitats for deployment of the ITT is crucial to optimize cost efficiency (Kagbadouno et al., 2011) but also to enable the selection of appropriate sites for deployment of the monitoring traps to assess the impact of the control campaign. Although the initial entomological sampling was well developed and efficiently implemented in the target area (Bouyer et al., 2010), we deem the development and use of species distribution models to be very beneficial in this regard.

Several scientists have tried to model the distribution of tsetse populations to inform stakeholders on the risk of African animal trypanosomosis. Rogers and Randolph showed that the abundance and mortality of tsetse were negatively correlated with temperature-related indicators derived from meteorological satellites (Rogers and Randolph, 1991). Images from advanced very high resolution radiometers (AVHRRs) that are on-board satellites of the National Oceanic and Atmospheric Administration, and in particular the normalized difference vegetation index (NDVI), a measure of the photosynthetic activity of vegetation, were used to predict the distribution of *Glossina morsitans* and *G. pallidipes* in Kenya and Tanzania with a predictive power of around 80% (percentage of correctly classified sites) (Rogers and Randolph, 1993). The same methodology using satellite-derived data (NDVI, ground temperature, and rainfall) subjected to temporal Fourier analysis was applied to eight species of tsetse flies in West Africa with an average predictive power of 82% (Rogers et al., 1996). Discriminant analysis and logistic regression were used to produce probability maps of presence at a spatial resolution of 8 km and indicated that thermal data played a more important role in predicting tsetse presence than vegetation indices. This methodology is the basis of the maps still used by the Food and Agriculture Organization of the United Nations (Robinson et al., 1997).

Robinson et al. proposed a methodology based on a sequence of discriminant analysis, maximum-likelihood image classification, and principal component analysis of AVHRR data (1.1-km resolution) to determine the distribution of four species of tsetse in southern Africa (Robinson et al., 1997). The remotely sensed variables were the NDVI, soil temperature, and elevation, and predictive powers up to 92% were obtained for some species. Hendrickx et al. used unsupervised classifications of AVHRR (8-km resolution) and METEOSAT (5-km resolution) satellites to develop distribution and abundance maps of tsetse (Hendrickx et al., 1999). More recently, vegetation units at different spatial resolutions of a land cover classification system (resolution of 1 km) were used to map suitable habitats of several tsetse species in Africa. However, the correlation between tsetse presence and vegetation classes/units was low for the Palpalis group (47%) (Cecchi et al., 2008). Fragmentation analyses were also used to map tsetse densities in Burkina Faso and Zambia (Ducheyne et al., 2009; Guerrini et al., 2008).

2.3.2. Mapping the risk when eradication is not an option

In recent years, the habitat of tsetse fly vector (genus *Glossina*) has undergone significant modifications due to demographic and climatic pressures. Landscape fragmentation is progressively reducing the geographic distribution and densities of tsetse, and is also affecting the epidemiology of the disease by reducing host, vector and parasite diversities (Van den Bossche et al., 2010). In Burkina Faso and Ghana, climatic and human factors, such as cattle keeping and crop-farming, have altered the riverine landscapes over the last decades, leading to a fragmentation of gallery forests (Guerrini et al., 2008). Two tsetse species remain in most of this region, namely *Glossina palpalis gambiensis* Vanderplank and *Glossina tachinoides* Westwood (Diptera: Glossinidae). Their presence and densities heavily depend on the climate, the ecotype of riverine vegetation and its degree of disturbance (Bouyer et al., 2005).

In Burkina Faso, several studies have investigated the impact of fragmentation on tsetse distribution and densities (Bouyer et al., 2005), as well as on population structure and dispersal (Jeremy Bouyer et al., 2007; Koné et al., 2010). A longitudinal survey investigated seasonal dynamics of tsetse and mechanical vectors of trypanosomoses in landscapes at various levels of fragmentation (Koné et al., 2010). Environmental factors, namely temperature and relative humidity, appeared to structure tsetse distribution and densities and thus the risk of AAT. Indeed, previous studies has shown that average maximum temperature was highly correlated to the tsetse infectious rates (Jérémy Bouyer et al., 2013b). A spatio-temporal model of tsetse apparent densities was also developed in a few sites along the Mouhoun river, where a longitudinal monitoring of the parasitological status of cattle was conducted (Sedda et al., 2010). Finally, two recent national eradication initiatives with a regional dimension were undertaken in south-western Burkina-Faso and north-western Ghana under the umbrella of the Pan African Tsetse and Trypanosomosis Eradication Campaign (PATTEC), within which extensive baseline data on vector distributions and disease prevalence were generated (Adam et al., 2012; Sow et al., 2013). The feasability of the eradication in these areas required a degree of isolation and other characteristics. Nonetheless, millions of herders still live with the risk of AAT and try to manage the risk on their daily activity. Therefore, it is possible to develop information based risk management tools than can help stakeholders to implement risk mitigation strategies based on sound and objective quantitative analysis.

EIR is a simplified index derived from vectorial capacity, which is directly correlated to the rate of transmission (R0) of a vectorial disease (Tran et al., 2005). This index does not give the prevalence in cattle, but the risk for cattle that would enter a given area to become infected from a bite by cyclical vectors. A number of authors have demonstrated previously that EIR (or tsetse challenge) is well correlated to the incidence of trypanosomosis in animals (Claxton et al., 1992; Rawlings et al., 1991; Rogers, 1985; Snow et al., 1996).

By building on the above body of information, there is a need to map AAT risk by developing a spatiotemporal statistical model of the entomological inoculation rate (EIR).

However, this risk index was never mapped in space and time and linked to climatic variables. Mapping the EIR can help designing some future climate risk management mechanisms to control AAT. In particular, early warning system and potential index based insurance can be built using the output of this spatiotemporal modeling of AAT risk.

2.4. Economic impact of African animal trypanosomosis and its control

2.4.1 Economic impact of African animal trypanosomosis

The economic impact of African animal trypanosomosis has been the subject of a large body of work by economists. An estimated 45 to 60 million cattle and tens of millions of small ruminants are at risk from trypanosomosis, among which about three million cattle die each year due to AAT (Gilbert et al., 1999). Direct annual production losses in cattle are estimated at USD 600–1200 million (Hursey and Slingenbergh, 1995).

Estimates of the overall annual lost potential in livestock and crop production have been as high as USD 4750 million (Budd and Britain, 1999). (Mortelmans, 1984) pointed out that three to four times more livestock could be carried if trypanosomosis was absent in some tsetse infested region of Africa. Direct costs due to AAT involve decreased livestock productivity (mortality, fertility, milk yield, ability to work as traction animals) to which can be added expenditure on controlling the disease (Shaw et al., 2015; Shaw, 2003). Moreover, tsetse impedes the integration of crop farming and livestock keeping, which is required to develop sustainable agricultural systems (Feldmann and Hendrichs, 1995). In Sub-Saharan Africa, the availability of productive livestock would be required to significantly improve agriculture and is considered a prerequisite to alleviate hunger, food insecurity and poverty. The presence of tsetse and trypanosomosis can therefore rightfully be considered one of the major root causes of hunger and poverty in Sub-Saharan Africa. This is best illustrated by the correlation and overlap between the 36 tsetse-infested countries and 34 heavily indebted poor countries in Africa (Feldmann et al., 2005). The presence of tsetse flies and animal trypanosomosis in much of Sub-Saharan Africa is thus a major influence on the agricultural systems since large areas are unsuitable for livestock production due to presence of tsetse flies. A recent study demonstrated that the presence of tsetse fly in the continent, historically and profoundly shaped human settlement on the continent and was a major barrier to agricultural development of an important part of the continent (Alsan, 2015).

2.4.2. On the economics of trypanosomosis control

If it is well accepted that epidemiological analysis has a deep impact on the control of animal disease, the impact of economic analysis in this debate is relatively recent. Indeed, the economics of animal disease control and prevention is relatively young compared to other branch of economics. However, in many reviews, the role and importance of quantitative method in economics in order to better inform decision maker in tsetse and trypanosomosis control operation has been demonstrated (Bennett, 1992). Because of the economic importance of AAT and the burden of this disease on agriculture in particular, a large amount of literature has been devoted to the economics analysis of control options. Most of this literature was based on cost-benefit analysis.

Cost-benefit analysis (CBA), in a context of a disease control project, is the examination of a decision in terms of its costs and benefits. From a theoretical perspective, it identifies choice that increase welfare but from a utilitarian perspective. In practice, in a CBA, the projects which make a positive profit at shadow prices are accepted projects.

The first major economic analysis of trypanosomosis and tsetse control was undertaken in Uganda and evaluated the use insecticide, this analysis shows that spraying insecticide was more effective than the widely used game and environment destruction (Jahnke and others, 1976). It was an important step in trypanosomosis control because it shows that, from an economic standpoint and beside the ethical problem of game destruction, other control options are more effective and profitable. It was one of the first economic analysis that used cost-benefit analysis in order to compare control option. Since then, in Africa, several studies have followed.

In the early 1980’s in West Africa, the economic impact of AAT on the productivity of four breeds of cattle were investigated in Cote d’Ivoire (Camus, 1981). In his analysis he concluded that the direct loss due to AAT in Northern Cote d’Ivoire were estimated to around 200,000 USD.

In Nigeria, around the same time period, a comparative analysis of control method were compared and evaluated with similar conclusions (Putt et al., 1980).

A cost-benefit analysis was also carried in Burkina Faso and Cote d’Ivoire in order to compare the effectiveness of various control options such as sterile insect techniques (SIT), sequential aerial spraying techniques (SAT) and impregnated traps (Brandl, 1988). In this evaluation, based on a demographic herd module, it was shown that the profitability of SIT was the lowest as compared to other control methods. From this analysis, it was also highlighted that scale and levels of tsetse and trypanosomosis challenge was the main factors affecting the viability of the analysis.

However, since this analysis, major development have been made in SIT control method and recent analysis has shown the profitability of such techniques in area-wide control paradigm. In fact, in Zanzibar the productivity of the agriculture after the clearance of the area was impressive (Vreysen et al., 2014). Indeed, the income for farming increase by 30% few years after the eradication campaign, with a milk production that nearly triples. In the Niayes area of Senegal, an economic analysis showed that the profitability of the SIT method with a benefit around USD 2800 per km^2 in a horizon of 30 years (Bouyer et al., 2014a). Finally, in East Africa, elimination of tsetse flies using various techniques including the SIT has shown better benefit cost ratio than continuous control based on insecticide or drugs (Shaw et al., 2015).

The use of trypanotolerant cattle were also investigated from an economics perspective and especially the profitability of trypanotolerant ranching. The first major analysis throughout the continent was carried out by the International Livestock Center for Africa (ILCA) (Itty and others, 1992). A dynamic bio-economic model combined with a cattle herd simulation was used to project the economic performance, meat and milk production (Itty, 1995). From this series of evaluations, it was shown that introduction of trypanotolerant through import was not necessarily the best option (Itty et al., 1993).

The use of trypanocidal drugs and the problem of drugs resistance was analyzed by economists recently in West Africa. The role of time and risk preferences was assessed through the use of experimental economics methods (Liebenehm and Waibel, 2012). The impact and economics of livestock husbandry under the problem of drugs resistance was also analyzed using households survey and econometric (Affognon, 2007).

Finally, some analysis has also investigated the return on research and the design of a vaccine to control AAT. (Kristjanson, 1999) developed one of the first of model that computed the potential benefit from developing a hypothetical vaccine to control AAT. They developed one of the few analyses that shows the benefit from controlling AAT at the continent level. In this study, they combined an economic surplus model to a geographical information system and a herd simulation model. They concluded that the potential benefit from meat and milk production only from controlling AAT amounts to 700 million USD each year. This amount was underestimated since manure and traction was not added into the benefit. On the cost side, a yearly amount of 1340 million USD. They finally estimated at 33% the internal rate of returns from a research project on vaccine for AAT.

In the Niayes area around Dakar, a cost-benefit analysis was conducted (Bouyer et al., 2014b) Three main cattle farming systems were identified: a traditional system using trypanotolerant cattle and two ‘‘improved’’ systems using more productive cattle breeds focusing on milk and meat production. In improved farming systems herd size was 45% lower and annual cattle sales were EUR 250 (s.d. 513) per head as compared to EUR 74 (s.d. 38) per head in traditional farming systems (1023). Tsetse distribution significantly impacted the occurrence of these farming systems ($p = 0.001$), with 34% (s.d. 4%) and 6% (s.d. 4%) of improved systems in the tsetse-free and tsetse-infested areas, respectively. The potential increases of cattle sales as a result of tsetse elimination considering two scenarios, i.e. a conservative scenario with a 2% annual replacement rate from traditional to improved systems after elimination, and a more realistic scenario with an increased replacement rate of 10% five years after elimination. The final annual increase of cattle sales was estimated at EUR 2800/km^2 for a total cost of the elimination campaign reaching EUR 6400/km^2.

Chapter 3 : Research design and methodology

3.1. A spatial model to optimize tsetse eradication campaign

The use of species distribution models to optimize vector or pest control is quite novel. The existing tsetse distribution models were critical for a better understanding of tsetse distribution and AAT epidemiology but their spatial resolution was not sufficient to guide an eradication process. In this paper, we used higher resolution images and recent advances in species distribution modeling methods to improve the prediction accuracy. Predictive models, and more specifically machine learning methods were used to model the distribution of *G. p. gambiensis* (Guisan and Thuiller, 2005). Model choice has an impact on the final output and also depends on available data. In this study, both presence and absence data were available, which is uncommon with respect to tsetse data. Therefore, following (Brotons et al., 2004), we used both data sets. Understanding how predictions from presence-absence models relate to predictions from presence-only models is important because presence data are more reliable than absence data.

The goal of this analysis is to show how we selected among two competing approaches of species-distribution modeling based on a large and accurate set of presence/absence data and how we used the best results to optimize the eradication campaign in the Niayes of Senegal.

3.1.1 Site description

The study area had a total surface of 7,150 km², located in the Niayes region of Senegal (14.1° to 15.3° N and 16.6° to 17.5° W). At the time of the study, it is the target of an eradication campaign against an isolated *G. p. gambiensis* population (Bouyer et al., 2010) (Fig. 4). The climate is hot and dry from April to June, whereas the rainy season occurs from July to October and the cold dry season from November to March.

3.1.2. Input data

3.1.2.1. Entomological data

A cross-sectional survey was implemented from December 2007 to March 2008 (dry season), to collect baseline data for the eradication campaign using 683 unbaited Vavoua traps

(Bouyer et al., 2010).Traps were removed as soon as a tsetse fly was caught (minimum one day). In the absence of capture, the traps were retrieved after a maximum of 42 days.

To homogenize data quality and avoid pseudo replication (data points in the same pixel), the dataset was simplified in two ways. Firstly, the study area was rasterized into square pixels with a 250-m resolution to match the model predictors.

For the presence data, all trap positions located within the same pixel were aggregated and concentrated in the pixel center. Presence data were observed in 68 pixels, from 91 presence points (Fig. 3).

For the absence data, all trap positions located within a buffer of 500 m around a presence point were removed (to account for tsetse dispersal capacity). Furthermore, we removed absence pixels with $p > 0.01$ that the flies were present despite absence of trapping, using the model described by (Barclay and Hargrove, 2005). From the initial 592 absence data, 333 were finally retained, 56 of which were used in the validation dataset. Therefore, the training data set was composed of 68 presence and 269 absence data.

3.1.2.2. Entomological data used for validation

Trap data were collected independently from the training dataset from April 2009 to February 2013 during different surveys (tsetse dispersal and competitiveness studies, longitudinal monitoring of the demographic structure of tsetse populations, etc.). This dataset included 92 presence and 64 absence data. It was processed as described above; resulting in a dataset of 64 presences and 1 absence data (trapping times were not long enough to ascertain tsetse absence). A subset of 56 absence data was extracted from the 333 absence data described above.

A second validation dataset was created using 182 aerial photos taken from a gyrocopter, at altitude ranging from 100 to 300 m. The environment identified from these pictures was subsequently categorized as suitable or unsuitable for tsetse habitat by one of the co-authors (JB) (Bouyer et al., 2010). Picture coordinates were corrected using Google Earth to take the angle and deviation from the ground into account. Overall, 23 suitable and 159 unsuitable habitats were identified, thereafter called “expert-based habitats” (Fig S1).

3.1.2.3 Environmental data

Climatic and environmental data were derived from time series of the Moderate Resolution Image Spectroradiometer available from the National Aeronautics and Space Administration (NASA: MODIS, version V005). Composite daily and nightly land surface temperature (DLST and NLST: MOD11A2, 8-day averages), middle infra-red (MIR: MOD13Q1, 16-day averages) and the normalized difference vegetation index (NDVI: MOD13Q1, 16-day averages) were selected for the analysis (Rogers et al., 1996). The spatial resolution of pixels was 250 × 250 m for all data except for the land surface temperature (LST) products (1 km × 1 km). Data were projected into universal transverse mercator-projected coordinate system 28N/WGS84. LST data were resampled to match the finest spatial resolution of 250 × 250 m, using the nearest-neighbor method (Neteler, 2010). Summary statistics of environmental to use it for modeling purpose (average, minimal and maximal values, range, and standard deviation) were calculated for the period 2007–2009.

A supervised classification of the vegetation was achieved using Landsat 5 Thematic Mapper (TM) satellite images with a spatial resolution of 30 m x 30 m. Four cloud-free and haze-free satellite images were used from October 2009, April 2010, June 2010, and December 2010 to take into account the seasonal dynamics of these habitats, named “forests” in this document.

3.1.3. Models

3.1.3.1 Niche exploration using Ecological Niche Factor Analysis

The relationship between occurrence of tsetse and environment data was explored with multidimensional exploratory analysis. For this purpose, we used the Ecological Factor Niche Analysis (ENFA) (Hirzel et al., 2002) which is a presence-only multidimensional method based on the concept of ecological niche (Hutchinson, 1957). Ecological niche factor analysis (ENFA) was thus used to characterize the habitat of *Glossina palpalis gambiensis* in the target area. It is a variant of factor analysis used to explore and model species ecological niches. The environmental space actually used by the species is compared with the available environmental space using two indicators: marginality and specialization (Hirzel et al., 2002). Marginality is a measure of central position. It captures the dimension in the ecological space in which the average conditions where the species lives differ from the global conditions. A large marginality value implies that the conditions where the species is found are far from the global environmental conditions. In contrast, specialization measures the spread and use of the ecological space along dimensions of niche use. The higher this value, the narrower the space used by the species. Consequently, the species niche can be summarized by an index for marginality and another for specialization, represented on a factor map within the biplot framework (Gabriel, 1971).

3.1.3.2. Predictive modeling using MaxEnt and regularized logistic regression

A MaxEnt model was used to model presence-only data (Phillips et al., 2006). MaxEnt is a machine learning model that fits a species distribution by contrasting the environmental condition where the species is present to the global environment characterized by some generated pseudo-absence data, also called the background. This model, which is one of the most widely used to model species distributions, is a machine-learning method based on maximum entropy. Absence data are replaced with so-called background data, which are a random sample of the available environment. MaxEnt fits a penalized maximum likelihood model to avoid overfitting (L1 penalization). The logistic output from MaxEnt is a habitat suitability index rescaled to range from 0 to 1. Recently, the equivalence between MaxEnt and an infinitely-weighted logistic regression was also pointed out (Fithian and Hastie, 2012).

Presence-absence data on the other hand, were modeled using a regularized logistic regression to avoid overfitting with respect to model parameters. There are various approaches to regularization for least square methods in statistical learning. The most widely used are the ridge regression and the lasso. Ridge regression bounds the regression coefficients space by adding the L2 norm (root square of the sum of squares values) of the coefficients to the residual sum of squares whereas the lasso is a penalized least square method that shrinks the coefficient space by imposing an L1 penalty (sum of absolute values) on the regression coefficients. The elastic net framework used in this analysis is a compromise that combines ridge regression (L2 penalization) and the lasso (L1 penalization) for more flexibility in model selection (Zou and Hastie, 2005). This model was chosen because of its flexibility and capacity to penalize complex models (Friedman et al., 2010).

For each model (MaxEnt and regularized logistic regression), we used a linear and quadratic combination of environmental variables. In a similar way that marginality and specificity account for tendency and spread in an ENFA, linear combination accounts for centrality and habitat preference, and quadratic transformations of the features reflect species tolerance to that dimension.

For each model, variable selection was done automatically through the use of optimal regularization parameters. These optimal parameters were obtained using a 10-fold cross-validation on the training set. We finally selected sub-models (associated with specific regularization parameters) with the highest predictive performance as assessed by the capped binomial deviance indicator. For the regularized logistic regression model, specific tuning parameters (regularization coefficients) were obtained using a double cross-validation (one for each of the two regularization coefficients). For MaxEnt, the beta multipliers that account for the magnitude of the regularization coefficient of each variable were obtained through a 10-fold cross-validation. The final models were replicated 50 times to estimate non-parametric confidence intervals for performance metrics, marginal curves, and so forth.

Finally, MaxEnt and regularized logistic regression was used to predict habitat suitability. Approximately 10,000 pixels were sampled from the environmental variables (background) to calibrate the model for the MaxEnt model. Because of the small sample size for presence data (56 points), only linear and quadratic transformations of these variables were used.

3.1.3.3. Model performance and comparison

Model performance and comparison were assessed using the two validation sets (Elith et al., 2006). Model performance metrics were computed for each predictive model (Liu et al., 2005).The metrics used were the area under the receiver operating curve (ROC), called area under curve (AUC) (DeLong et al., 1988). The area under the receiver operating curve (ROC) ranges from 0 to 1. A score of 1 indicates a perfect discrimination, whereas a score of 0.5 characterizes a random model. This statistic does not depend on the threshold. Moreover, optimal thresholds were computed to maximize the following metrics: the percentage of consonants correct (PCC); the specificity (Sp), that is, the probability of a negative result given that the individual is negative (probability of true negative); and the sensitivity (Se), that is, the probability of having a positive result given that the individual is positive (probability of true positive). The ROC curve is a graphical representation of Se against false positives (1-Sp).

Furthermore, the regularized gain which indicates how good the MaxEnt model fits the data, compared with a uniform distribution, was also used. The exponential of regularized gain measures how many times the likelihood of the MaxEnt model is higher compared with this random uniform distribution. This metric was used to compare variables and their contribution to the goodness of the MaxEnt model.

Marginal response curves were also computed to assess the relationship between the predicted suitability index and a given environmental data. These curves were obtained by varying this variable while keeping all others at their average value.

Finally, predicted values from regularized logistic regression and MaxEnt models were compared using Spearman’s rank correlation coefficient.

3.1.3.4. Impact of control operations

We used a generalized linear mixed model (Laird and Ware, 1982) to measure the impact of the suppression on tsetse apparent densities. The response data was tsetse counts in the traps. Time (measured in weeks), treatment (suppression or not) and the block (1 or 2) and some interactions were used as fixed effects whereas the trap locations were used as random effects. The generalized linear mixed model was fit by maximum likelihood using a Poisson distribution. A log link was used for the response variable (tsetse catches), and the observations were weighted with the inverse of trapping duration. Simpler models, as well as models without weighted observations, were compared with the complete model using the corrected Akaike information criterion (AICc) (Burnham and Anderson, 2003). The best model was considered as the one with the lowest AICc.

The probability that eradication was effective in block 1 was estimated using the same model used to clean the absence dataset (Barclay and Hargrove, 2005), considering that at least a couple of flies was necessary to maintain the population.

3.2. A spatio-temporal model for African animal trypanosomosis risk

In recent years, the habitat of tsetse fly vector (genus *Glossina*) has undergone significant modifications due to demographic and climatic pressures. Landscape fragmentation is progressively reducing the geographic distribution and densities of tsetse, and is also affecting the epidemiology of the disease by reducing host, vector and parasite diversities (Van den Bossche et al., 2010). In Burkina Faso and Ghana, climatic and human factors, such as cattle keeping and crop-farming, have altered the riverine landscapes over the last decades, leading to a fragmentation of gallery forests (Guerrini et al., 2008). Two tsetse species remain in most of this region, namely *Glossina palpalis gambiensis* Vanderplank and *Glossina tachinoides* Westwood (Diptera: Glossinidae). Their presence and densities heavily depend on the ecotype of riverine vegetation and its degree of disturbance (Bouyer et al., 2005).

In Burkina Faso, several studies have investigated the impact of fragmentation on tsetse distribution and densities (Bouyer et al., 2005), as well as on population structure and dispersal (Jeremy Bouyer et al., 2007; Koné et al., 2010). A longitudinal survey investigated seasonal dynamics of tsetse and mechanical vectors of trypanosomoses in landscapes at various levels of fragmentation (Koné et al., 2010). Environmental factors, namely temperature and relative humidity, appeared to structure tsetse distribution and densities quite differently to those of most species of mechanical vectors.

A spatiotemporal model of tsetse apparent densities was also developed in a few sites along the Mouhoun river, where a longitudinal monitoring of the parasitological status of cattle wasconducted (Sedda et al., 2010). Finally, two recent national eradication initiatives with a regional dimension were undertaken in south-western Burkina-Faso and north-western Ghana under the umbrella of the Pan African Tsetse and Trypanosomosis Eradication Campaign (PATTEC), within which extensive baseline data on vector distributions and disease prevalence were generated (Adam et al., 2012; Sow et al., 2013).

By building on the above body of information, the present analysis focuses on AAT risk assessment by developing a spatiotemporal statistical model of the entomological inoculation rate (EIR). EIR is a simplified index derived from vectorial capacity, which is directly correlated to the rate of transmission (R0) of a vectorial disease (Tran et al., 2005). This index does not give the prevalence in cattle, but the risk for cattle that would enter a given area to become infected from a bite by cyclical vectors. Since we used cattle parasites only to calculate and model the infection rate in tsetse, the risk that we map here is specific to cattle. The use of a simplified index presents the benefit to avoid the multiplication of uncertainties for each parameter that finally reduces the predicting power of such an index (Dye, 1992). A number of authors have demonstrated previously that EIR (or tsetse challenge) is well correlated to the incidence of trypanosomosis in animals (Claxton et al., 1992; Rawlings et al., 1991; Rogers, 1985; Snow et al., 1996). This is the first time however that this risk index is mapped in space and time and linked to climatic variables. This index will help designing some future climate risk management mechanisms to control AAT. In particular, early warning system and potential index based insurance can be built using the output of this spatiotemporal modeling of AAT risk.

3.2.1. Site description

The study area in south-western Burkina Faso and north-western Ghana is located between latitude 9º23' – 15º5'N and longitude 0º29' - 5º31' W. The area is approximately 372,000 km^2, and the main river is the Mouhoun/Black Volta. Mean monthly temperatures vary between a minimum of 18°C and a maximum of 36°C and annual precipitation between 250 and 1,170mm. The study area is constituted of Sudano-Guinean savanna in the south, Sudanian savanna in the central part and Sahelian savanna in the north (Aubréville, 1950).

3.2.2. Input data

3.2.2.1. Entomological data

In Burkina Faso, tsetse eradication efforts, targeting the northern part of the Mouhoun river basin started in 2008 (http://www.pattec.bf). In Ghana, the eradication project started in 2010 (Sow et al., 2013). During the feasibility studies of these projects, baseline entomological surveys were carried out and generated an important amount of data, such as tsetse apparent density and their trypanosome infection rates. Biconical traps were used in all surveys (Challier and Laveissière, 1973).

In Burkina Faso, for the PATTEC baseline survey, all traps were set for three days (Sow et al., 2013) and they were deployed following a grid-based approach, within grid cells of 10x10 km (Leak et al., 2008). Within each grid cell, 13 traps were set in the most suitable sites, in particular along the rivers and riparian thickets.

We also used longitudinal data on tsetse densities and infection rates originating from a longitudinal survey conducted in Burkina Faso. In this survey, 13 traps were spaced by 100m and set along three sections of the Mouhoun River. Traps were kept in place for three days a month, for total duration of 18 months in 2006 and 2007 (Dayo et al., 2010).

The last dataset from Burkina Faso are from a recent study in the southern part of the country where entomological surveys were conducted in Moussodougou and Folonzo (Rayaisse et al., 2015). In these surveys, 25 traps were deployed in each site for 5 days during the rainy and dry seasons 2011-2012.

In the PATTEC baseline entomological survey done in Ghana, traps were deployed every 200m for 24h along the main rivers in dry seasons of 2008 and 2009 (Sow et al., 2013).

In addition to this entomological data from Burkina Faso and Ghana, 25 biconical traps were set in Kalofo, in northern Côte d’Ivoire. This survey was conducted during the dry and rainy seasons 2012 (Djohan et al., 2015a). The space between each trap was 200m along a transect and they were set for 5 days and collected daily (Djohan et al., 2015b).

Finally, in Mali, we used data from a PATTEC baseline entomological survey conducted in 2000-2002 for the habitat suitability model only. In this study, traps were set every 1km for 24h along the rivers (Djiteye, personal communication, and data in S7 supplementary file).

Figures S1and S2 present the entomological data used in the models that are also provided as supplementary materials (data in S7 & S8 supplementary files).

3.2.2.2. Parasitological and serological data

Data on bovine trypanosomosis originated from various sources and studies. In particular, the parasitological and serological statuses and the packed cell volume (PCV) of surveyed bovineswereassembled. PCV is the proportion of red cells in the blood; it allows measuring the level of anemia in cattle. We used a threshold of 25% below which the animal was considered anemic (Bellier and Cordonnier, 2010). Anemia is one of the main symptoms of AAT and it is considered to be correlated with most cattle productivity parameters (Itard and Frézil, 2003). In addition to data on trypanosomosis and anemia (PCV), information on sex, breed, and age of animals was also available. Three sources were used to generate the final dataset.

The first source is a cross-sectional survey carried out in the Boucle du Mouhoun region in Burkina Faso: 47 villages were selected and 2,650 cattle were sampled between September 2007 and November 2007. The study and experimental design have been previously described (Adam et al., 2012).

The second dataset is from a longitudinal survey conducted in southern Burkina Faso. Six villages were sampled and a total of 363 cattle were monitored every four weeks between June 2003 and June 2005 (Dayo et al., 2010).

The last survey was performed between February 2008 and March 2008 in the Upper West Region of Ghana. In this cross-sectional study, the area was divided into 180 grid cells of 10x10 km and 36 cells were randomly selected. In each cell, 50 cattle were sampled giving a total of 1,800 cattle for the whole area (Sow et al., 2013).

For all the above surveys, blood samples were obtained from each animal and the level of parasitaemia was scored using to the phase contrast buffy coat technique (Paris et al., 1982). For the serological status, antibodies against *Trypanosomavivax, T. congolense* and *T. brucei* were detected using the antibodyenzyme-linked immunosorbent assay (ELISA) (Desquesnes et al., 2001). Finally, the PCV, ameasure of anaemia, was recorded after centrifugation of blood samples. Figure S3 presents the location of the sampled herds and their serological prevalence. Data are provided in S9 supplementary file.

3.2.2.3. Environmental data

For the present study, a series of remote sensing data at high spatial and temporal resolution was used to assess the spatio-temporal risk of AAT (Fig. 1, Table 1). Firstly, Moderate-resolution Imaging Spectroradiometer (MODIS) data from the Terra and Aqua satellites were downloaded (http://e4ftl01.cr.usgs.gov/MOLT for Terra and http://e4ftl01.cr.usgs.gov/MOLA for Aqua). Daytime (DLST) and night-time land surface temperature (NLST) were extracted from MOD11A2/MYD11A2 temperature and emissivity MODIS products. DLST and NLST are used as proxies for both soil and air temperature, which play an important role in the epidemiology of AAT.

Both DLST and NLST data have a temporal resolution of eight days for each satellite (same composite daily data patched for both Terra and Aqua) and a spatial resolution of 1km. Low quality pixels were removed using the accompanying quality assessment layer and outliers were filtered using a variant of the boxplot algorithm (Neteler, 2010). The cleaned time series of DLST and NLST data was finally averaged monthly.

Monthly vegetation indices at 1km spatial resolution and monthly temporal resolution (MOD13A3/MYD13A3) were also downloaded and processed using a quality assessment layer. In particular, the Normalized Difference Vegetation Index (NDVI) and Middle Infrared (MIR) reflectance were selected to describe the vegetation condition in the study area.

Finally, a time series of dekadal gridded (11km spatial resolution) precipitation data product from FEWS-NET called Rainfall Estimator version 2 (RFE2) (Novella and Thiaw, 2013) were downloaded, downscaled (using bilinear downscaling) to match MODIS-based covariates spatial resolution (1km) and temporal resolution (monthly cumulated precipitation). We thus ended up with 11 years of monthly environmental variables (DLST, NLST, NDVI, MIR, and RFE) for the period up to December 2013. However, the resulting dataset were still missing a few values due to cloud contamination, failure of some satellite instruments, and the data pre-processing scheme used (filtering of outliers and low quality pixels). Therefore, a spatiotemporal spectral analysis was used to fill the gaps. In particular, multivariate singular spectrum analysis was used because of its ability to capture the spatiotemporal dependence in the data and its excellent performance in comparison to other gap-filling routines when using similar spatiotemporal data (Kondrashov and Ghil, 2006). In addition to these time series of remote sensing data, a digital elevation model (DEM) from the Shuttle Radar Topography Mission (SRTM) was used. The SRTM product at 1km spatial resolution was acquired through the CGIAR-CSI GeoPortal (http://srtm.csi.cgiar.org/). Lastly, a recently enhanced FAO cattle density layer was used (Robinson et al., 2014). This layer matches fairly recent statistics (2006 FAOstat data) and is characterized by a spatial resolution of 1km. This data was downloaded from the FAO Geonetwork website (http://www.fao.org/geonetwork/).

3.2.3. Models

The main goal of the modeling exercise was to estimate the EIR in the study area using climatic and environmental data. EIR represents the number of infectious bites a host receives during a given period.

EIR, which is also known as tsetse challenge, is one of the most widely used and effective indicators of risk for tsetse-borne trypanosomosis (Rogers, 1985).

The indicator is well known and widely used by malariologists to measure the intensity of malaria transmission (Smith et al., 2005). Some efforts have been recently made to map EIR for malaria using similar spatiotemporal entomological data (Rumisha et al., 2014).

EIR is calculated as the product of tsetse apparent density and trypanosome infection rates of tsetse. For a location s at a time t, we thus have:

$$EIR_{s,t} = ADT_{s,t} \times IR_{s,t}$$

(ADT and IR are the apparent density per trap and infection rates respectively).

For this study, the statistical models were fitted separately for each one of the two layers constituting the EIR. This was necessary because the input data used originate from various sources, and in particular, infection rates were not available for all samples. In order to maximize the use of all available data, we decided to compute separately the apparent density and infection rates, rather than fitting a single model for the observed EIR. For the rest of this analysis, the following components of the EIR were then considered:

- Tsetse habitat suitability.
- Tsetse apparent density per trap.
- Trypanosome infection rates in tsetse.

The first layer, habitat suitability, is not part of the mathematical definition of EIR, but it is always implied that we measure the risk of transmission where the vector occurs. Consequently, we first analyzed the habitat of the main tsetse vectors of AAT in the study area (i.e. *G. p. gambiensis* and *G. tachinoides*) before estimating and predicting EIR where the vectors can survive and transmit AAT.

3.2.3.1. Tsetse habitat suitability

The first layer needed to map the risk index is the habitat suitability. We used this layer to determine the area where the vector of the disease can survive (the ecological niche). A statistical analysis of the habitat was carried out using correlative species distribution models. Occurrence data from already described entomological surveys were used as input. Characterization of the environment in the study area relied on the 11-year average, minimum, maximum, range and standard deviation of each spatiotemporal layer (DLST, NLST, NDVI, MIR, RFE), with the DEM added to the set of summarized variables.

The methodology used to predict tsetse habitat suitability is based on the framework developed in the Niayes areas (Senegal) using the Maximum Entropy model (MaxEnt)

(Dicko et al., 2014b). MaxEnt is one of the most widely-used species distribution models. It is a machine learning method based on the information theory concept of maximum entropy (Elith et al., 2006). MaxEnt fits a species distribution by contrasting the environmental condition where the species is present to the global environment characterized by some generated pseudo-absence data, also called the background. The logistic output from MaxEnt is a suitability index that ranges between 0 (least suitable habitat) and 1 (most suitable habitat). It therefore gives us a quantitative indicator of the habitat preferences of the two tsetse species in the study area.

Moreover, to account for the sampling bias present in the entomological data, a gaussian kernel based grid that gives more weight to more densely sampled areas was constructed (Fig. S4).

In order to build this grid, a smoothing parameter is needed. Five parameters corresponding to the range of maximal dispersal distance of tsetse fly were used (2, 4, 6, 8, 10km) (J Bouyer et al., 2009) to build five bias grids for the MaxEnt models (Phillips et al., 2006; Phillips and Dudik, 2008).Model complexity in the MaxEnt framework can be controlled using the beta regularization parameter. Five parameters (1, 1.5, 2, 3, 4) were used to fit a model for each parameter. Finally, we ended up with five regularization parameters and five bias grid (one for each smoothing parameter), resulting in twenty five models. Multi-model inference was then made using model averaging weighted by the AICc (Burnham and Anderson, 2003; Warren and Seifert, 2011).

A model was fitted for each species and we created binary maps by setting the thresholds for presence that maximize the True Skill Score (TSS = sensitivity + specificity). These thresholds were 0.33 and 0.30 for *G. p. gambiensis* and *G. tachinoides* respectively. The final layer of tsetse habitat suitability for both species was obtained by combining the two previous layers: a pixel was considered as tsetse infested when it was infested by at least one species.

3.2.3.1. Tsetse apparent density

The second layer of the risk index is the dynamic of the apparent density of tsetse flies, as measured using biconical traps, considered here as substitution hosts. The number of tsetse caught per trap per day is thus considered to be correlated to the relative density of tsetse to hosts. We predicted tsetse apparent density per trap (ADT) at a monthly temporal resolution and a spatial resolution of 1km^2 using spatiotemporal statistical model fitted against the monthly temperature (DLST), vegetation (NDVI) and the DEM. A negative binomial model with spatial random effects was used. Negative binomial models can be seen as an extension of the classical Poisson regression to account for over-dispersion in count data.

Covariates were chosen on the basis of the available literature on tsetse population dynamics and ecology (Rogers and Randolph, 1986). In particular, thermal- and vegetation-related covariates impact on tsetse population dynamics through their direct effects on demographic parameters (birth, mortality, etc.).Moreover, because of the sampling bias and clustering of the observations in such entomological data, a spatial random effect using the Matern correlation structure was used (Cressie and Cassie, 1993). The correlation structure was further altered to account for the temporal effects and thus resulted in a fully spatiotemporal correlation structure. Finally, model selection and, in particular, the optimal temporal lag between environmental data and tsetse apparent density was carried out by means of a likelihood-based information criterion (corrected Akaike information criterion, AICc) (Burnham and Anderson, 2003). Each specie was modeled separately and the final layer of tsetse apparent density was obtained by summing the fitted apparent densities of both *G. p. gambiensis* and *G. tachinoides*.

3.2.3.2. Trypanosome infection rates in tsetse

The infection rate of tsetse flies represents the third and last layer in our risk index. A fly was considered infected if any major trypanosome species was detected (*Trypanosomavivax*, *T. congolense* and *T. brucei*). The infection rate was modeled irrespective of tsetse species, unlike the two other models, since previous studies in the area indicated that the two species have similar infection rates (Jérémy Bouyer et al., 2013b). It was also analyzed in the flexible framework of a generalized linear mixed model. In particular, the infection rates were investigated using a logistic regression with a random effect on the trapping site to account for spatial heterogeneity in the data. We considered temperature and host density as the main factors that influence trypanosome infection in tsetse in our study area (Jérémy Bouyer et al., 2013b). Consequently, the model was fitted using DLST and cattle density as principal covariates and a sinusoidal function of the month when the infection status was recorded was added to the regression to account for seasonality. We also tested the same spatiotemporal correlation structure used for apparent density, which did not improve the model and was thus discarded for the sake of simplicity.

3.2.3.3. Validation and combination of the models

For the tsetse distribution models, we used the area under the ROC curve (AUC), the specificity and the sensitivity to assess the accuracy of the fitted models. For the apparent density model, we kept one tenth of the trapping sites for each species as testing sets and we computed the percentage of variance explained by the predicted values for each models. Finally, the infection rates model was validated by computing the McFadden pseudo-R^2 (Long, 1997).

The expected apparent density of tsetse (ADT) was multiplied by the tsetse infection rates (IR) and projected into the suitable habitat (HS) to estimate the EIR (tsetse challenge). In order to have an external validation of the index and to assess its ability to predict the relationship between EIR and bovine trypanosomosis, sero-prevalence, parasitological prevalence and percentage of clinical cases were explored for various temporal (1 to 4 months) and spatial (3 to 10km around the cattle pens) lags. It must be noted that positivity to the ELISA test corresponds either to active infections or cured, past infections. Antibodies detected with this method persist for three to five months for *T. vivax* (Dia and Desquesnes, 2007), and about two to four months for *T. brucei* (Jancloes et al., 2014; Lowe et al., 2011). Low level of haematocrit (PCV) combined with the results of the serological status was also used as a proxy of bovine trypanosomosis: an ill animal was thus defined as a sero-positive animal with a PCV below 25%.

3.3. The economics of African animal trypanosomosis control under climate change

In 2005, the Senegalese Government joined the PATTEC initiative, starting a tsetse control campaign that aimed at the elimination (elimination is here considered as local eradication) of *G. p. gambiensis* from the Niayes area.

The program is implemented by the Government of Senegal (Direction of Veterinary Services (DSV) and the Senegal Institute for Agricultural Research (ISRA)) and technically and financially supported by the International Atomic Energy Agency (IAEA), the Food and

Agriculture Organization of the United Nations (FAO), the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), and the USA through the Peaceful Uses Initiative (PUI) (www.fao.org/news/story/en/item/211898/icode/). During the feasibility study of this project the limits of the *G. p. gambiensis* distribution were determined to be within a 1,000 km^2 area (Bouyer et al., 2010) and it was demonstrated that this population was completely isolated from the main tsetse belt in the south-eastern part of Senegal (Solano et al., 2010). Therefore, the Government of Senegal selected a strategy of elimination following area-wide integrated pest management (AW-IPM) principles to create a sustainable zone free of *G. p. gambiensis* in the Niayes. The strategy combined insecticide-treated targets and cattle for initial fly suppression with the aerial release of sterile male flies as the final elimination component. The study area was divided in four operational blocks that are being treated sequentially. At the time of writing, more than approximately 60.20% of the project area was already cleared of *G. p. gambiensis* (no capture of wild flies during 18 months in the monitoring traps) and the apparent density of the fly population had been reduced with 99% in an additional 40% the remaining part of the project zone. This project constitutes a major governmental intervention that will have a great positive impact on the Niayes agro-ecosystem.

Three main cattle farming systems were identified: a traditional system using trypanotolerant cattle and two ‘‘improved’’ systems using more productive cattle breeds focusing on milk and meat production. In improved farming systems herd size was 45% lower and annual cattle sales were EUR 250 (s.d. 513) per head as compared to EUR 74 (s.d. 38) per head in traditional farming systems (1023). Tsetse distribution significantly impacted the occurrence of these farming systems ($p = 0.001$), with 34% (s.d. 4%) and 6% (s.d. 4%) of improved systems in the tsetse-free and tsetse-infested areas, respectively. We calculated the potential increases of cattle sales as a result of tsetse elimination considering two scenarios, i.e. a conservative scenario with a 2% annual replacement rate from traditional to improved systems after elimination, and a more realistic scenario with an increased replacement rate of 10% five years after elimination. The final annual increase of cattle sales was estimated at EUR 2800/km^2 for a total cost of the elimination campaign reaching EUR 6400/km^2.

The aim of this paper is to provide an insight on how to do an economic evaluation of tsetse and trypanosomosis control program taking into account climate change. The eradication campaign in the Niayes area will serve as example.

The potential benefits from the removal of bovine trypanosomosis (equivalent to reducing the physical and financial losses due to the disease) were calculated by first using a spatial micro-simulation model based on a socioeconomic survey of herder in the study area conducted in 2010 (Bouyer et al. 2014). This model was combined to scenarios developed during a participatory workshop with herder used to project the cattle population numbers in a series of spatially defined production systems in the study area over a 30-year study period using "with trypanosomosis risk" production parameters. Then, the output from the spatial micro-simulation model, in terms of milk, meat, and offtake was calculated and prices applied to estimate income year by year. The same procedure to calculate income was then repeated using the "without trypanosomosis risk" scenario. The “with” and “without” trypanosomosis were assessed by using the prediction of *G. gambiensis* presence in the study area (Dicko et al., 2014b). Finally, the difference between the two income streams gives the potential benefits from the disease absence.

For costs, the present analysis follows the framework developed in (Bouyer et al., 2014a) since the area and project are is the same. We then compared the potential benefits from removing the disease to the cost of the project with or without taking into account the impact of global climate change on tsetse distribution and thus trypanosomosis risk.

3.3.1. Input data

3.3.1.1. Socioeconomic survey

A socioeconomic survey was performed during the feasibility phase of the elimination project, 50% of the livestock farmer (in 2010), which represent 513 herders, were georeferenced and a subset of these farmers (192) were then sampled using a stratified sampling based on the herd size. The data were collected between July and November 2010 and information on households characteristics, livestock demographic parameters and productivity. Data on farming activities and sales of livestock products were also collected. More details can be found on (Bouyer et al., 2014a).

A second socioeconomic survey was organised for the purpose of this study from May to July 2015 in the first block of the eradication area, where eradication is effective since 2012 (Dicko et al., 2014b). The same zoo-technical questionnaire than in 2010 was used, plus some innovation indicators depicted from a qualitative study of the farmers socio-technical networks (cross-analysis of ten study cases) (F. Bouyer et al., 2015). The survey involved 63 farmers, from which 23 were the same than the ones surveyed in 2010. We used the same categories of farming systems as described before to calculate mutation rate (Bouyer et al., 2014a) : trypanotolerant system when the percentage of trypanotolerant cattle (Djakoré breed) was upon 70%, improved meat farming system when the percentage of Gobra cattle was upon 70%, and improved milk farming system for the remaining farmers.

Finally, a focus group and a participatory workshop were organized in July 2015 to confirm the socio-technical dynamics previously described in the qualitative study and to better define the innovation trajectorie (F. Bouyer et al., 2015).

3.3.1.2. Cattle data

Cattle population densities was provided by the Gridded Livestock of the World project (Robinson et al., 2014). The modeled global distribution of cattle was adjusted to match the FAOSTAT national census for the year 2006 at a spatial resolution of 1km.

3.3.1.3. Environmental layers and global climate models

In order to map the risk of bovine trypanosomosis and understand how climate change would affect the risk of AAT, a series of remote sensing data at high spatial and temporal resolution was used. Two types of data were used: climatic and environmental data. Most of the climatic data and vegetation indices were derived from the Moderate-resolution Imaging Spectroradiometer (MODIS). Data from the Terra and Aqua satellites were downloaded (http://e4ftl01.cr.usgs.gov/MOLT for Terra and http://e4ftl01.cr.usgs.gov/MOLA for Aqua) and processed.

The thermal data which play an important role in the epidemiology of AAT was acquired and extracted by using Daytime and Nightime land surface temperature from MODIS temperature and emissivity product MOD11A2/MYD11A2.

Monthly vegetation indices at 1km spatial resolution and monthly temporal resolution (MOD13A3/MYD13A3) were also downloaded and processed. In particular, the Normalized Difference Vegetation Index (NDVI) was selected to describe the vegetation vigor in the study area. Furthermore, a supervised classification of the vegetation was also achieved using Landsat 5 Thematic Mapper satellite images with a spatial resolution of 30 × 30 m. Four cloud-free and haze-free satellite images were used, from October 2009, April 2010, June 2010, and December 2010, to take into account the seasonal dynamics of these habitats, they were aggregated to match the spatial resolution of 1km.

Finally, in order to model the impact of climate change on the risk of bovine trypanosomosis, two global climate circulation models from the Intergovernmental Panel on Climate Change (IPCC) fifth report were used:. The CSIRO Mk 3.6 and MIROC5 global circulation model. The considered scenarios considered correspond to a radiative forcing (the change in energy in the atmosphere due to GHG) that stabilized at 8.5 W/m^2 (RCP 8.5) by the end of the century. The choice of a concentration pathway (RCP) of 8.5 corresponds to a high greenhouse gas emission pathway. This pathway was compared to a baseline ("no-change") scenario when the climate remained stable without any change. For each model, simulations were run until 2050. Finally, the Delta method was used to downscale the climate change data, in order for the grid to match the spatial resolution of grid use in the analysis (1km). For each climatic variable, (mostly temperature and precipitation) and climate model (CSIRO, MIROC) we thus have an estimate of the projection of each due to climate change. To simplify the analysis, we kept all vegetation related variables such as NDVI were kept static. The global climate models were obtained from CCAFS web portal (http://ccafs-climate.org/data/).

For the rest of the analysis, the spatiotemporal MODIS grids were summarized for modeling purpose. For each climate scenarios and the baseline, a set of summarized climatic and environmental variable was generated.

3.3.2. Models

3.3.2.1. Impact of climate change on bovine trypanosomosis risk

The analysis of climate change impact on the risk of bovine trypanosomosis was done using disease mapping techniques. The risk was assessed by mapping the habitat suitability of the disease vector in the study area using correlative approaches. We then used a suitability threshold (corresponding to a sensitivity of 96%), to consider that a given pixel as tsetse infested, and the cattle herds located at less than 2km from such a pixel were considered as exposed to the trypanosomosis risk (Dicko et al., 2015; Seck et al., 2010).

The methodology used to predict tsetse habitat suitability is based on the framework developed in the Niayes areas (Dicko et al., 2014b) and further refined in Burkina Faso in a recent analysis using the Maximum Entropy model (MaxEnt) (Dicko et al., 2015). MaxEnt is one of the most widely-used species distribution models. It is a statistical learning method based on the theoretical concept of maximum entropy. MaxEnt fits a species distribution by contrasting the environmental conditions where the species is present to the global environment characterized by some generated pseudo-absence data, also called the background. The output from MaxEnt is a suitability index that ranges between 0 (suitable habitat) and 1 (unsuitable habitat). It therefore gives us a quantitative indicator of the habitat preferences of the species in the study area. Moreover, to account for the sampling bias present in the entomological data, a Gaussian kernel based grid that gives more weight to more densely sampled areas was constructed. In order to build this grid, a smoothing parameter is needed. Five parameters corresponding to the range of maximal dispersal distance of tsetse fly were used (1, 3, 5, 7) to build 4 bias grids for the MaxEnt models. The bias grids were used to sample pseudo-absence from surveyed area. In addition to the generation of pseudo-absence, we also accounted for model complexity in the modeling process. In the MaxEnt framework, it can be controlled using the beta regularization parameter. Entomological data were randomly split in two sets, a training set (75% of the total data) and a testing set for further processing. Seven beta regularization parameters (1, 1.5, 2, 2.5, 3, 3.5, 4) were then used to fit a model on the training set, one model for each parameter. Finally, we ended up with nine regularization parameters and five bias grids (one for each smoothing parameter), resulting in thirty-five models. The final model was an average of the thirty-five built models. *G. p. gambiensis* distribution was finally created through a binary maps by applying a threshold to the suitability index corresponding to a sensitivity of 96% on the testing set.

Finally, the evolution of the habitat suitability index (risk) were made by projecting the validated model on each set of climate model linked co-variates. In particular, the response curves of climatic variable were used for such projection.

3.3.2.2. Spatial micro-simulation of herders

Following the protocol laid out by in the Niayes area (Bouyer et al., 2014a), 50% of herders of the Niayes area were surveyed for their analysis. For this analysis, we thus decided to simulate the rest of the herders of the study area using micro-simulation methods and by exploiting the socio-economic survey (table 3), the risk map and cattle density layer. A static spatial micro-simulation model was used as a tool to simulate an alternative to small area estimation because of the capacity of this method to integrate the results of various sources of data (census, participatory approach, etc.) on the evolution of the livestock system without trypanosomosis. An important scenario considered in this analysis and elicited from participatory workshop (F. Bouyer et al., 2015), is the replacement rate of traditional cattle system (Diakore) to improved system (Exotic or Gobra) at a 10% rate, five years after the elimination. The simulation model was run 100 times, in order to analyse the variability of the different output and get an idea of how sensitive the model is.

3.3.2.3. Economic evaluation of the eradication campaign

A partial analysis was used to lay out the economic evaluation of the project and was applied using a benefit-cost analysis. The principles of benefit-cost analysis is to discount the benefit and cost attributable to a project over time and then compare the two discounted values (Shaw, 2003). The monetary assessment of the benefits and costs of the benefit-cost analysis was based on the calculation of the Net Present Values (NPV) and the benefit-cost ratios (BCR).

Six scenarios were considered for the analysis, the two climate change scenarios, a scenario without climate change and for each of these scenarios we considered the baseline (no control) and the control case (eradication campaign). The decision was made by comparing the present value of benefits to present values of all costs. Furthermore, a time horizon of 30 years and a discount rate of 10% which is quite common for such project (Bouyer et al., 2014a; Shaw et al., 2015) was used. This relatively high discount rate was selected as reflecting both the higher returns expected from investments in the livestock sector and the economic growth rates and real interest rates in the study region (Shaw et al., 2015).

For the cost, it is important to point out that at the time of writing, the elimination project that started in 2007 is still running and is expected to finish by 2017. We therefore have the real observed cost until October 2015 and anticipated expenditures until January 2017. However, to have results comparable with (Bouyer et al., 2014a), we used observed expenditures until December 2013 and anticipated costs for the rest of the period.

Chapter 4: Research findings and discussion

4.1. A spatial model to optimize tsetse eradication campaign

4.1.1 Research findings

4.1.1.1. Ecological niche of the species based on the ENFA

All the variables associated with forest habitats and mean NDVI were highly correlated with presence of *G. p. gambiensis* (Fig. 3). Conversely, night and day Land Surface Temperature (LST) ranges, and maximum Middle InfraRed (MIR) were negatively correlated with presence of *G. p. gambiensis*. High values of these variables corresponded to lower vegetation cover, reducing the buffering of macroclimatic conditions by the vegetation.

Standard deviations of MIR, NDVI, day and night LST had high values on the specialization axis, while the environmental envelop for *G. p. gambiensis* was very narrow on this axis. This suggested that these satellite derived parameters captured important environmental features for the species, for which variations were poorly tolerated.

4.1.1.2. Predictive models outputs

Regularized logistic regression and MaxEnt presented similar ROC (Receiver Operating Characteristic) curves using the presence/absence validation dataset, with Areas Under Curve (AUC) of 0.89 and 0.92, respectively (Fig. 4). Their predictions were highly correlated (Fig. S1, $r = 0.68$, $p < 0.01$ and fig. 3). MaxEnt presented a slightly better sensitivity using 0.5 as a threshold for presence, or the threshold allowing the best Percentage of Correctly Classified (PCC) index, and a better specificity when the threshold was set to enable a sensitivity of 0.96 (Table 1). Using the expert-based landscape classification derived from aerial photography, MaxEnt predicted suitable habitats better than the regularized logistic regression (AUC = 0.79 and 0.58, Fig. 4).

Regularized training gain (likelihood based measure of model quality) of the MaxEnt habitat suitability model is presented in Fig. S2. The MaxEnt models are presented using a single predictor, or all of the predictors except for the one of interest. The mean area of forest was the predictor giving the best gain when used alone, followed by the mean NDVI and the maximum forest area. These three predictors were highly correlated with each other along the ENFA marginality axis (Fig. 3). Moreover, LST night standard deviation had the highest negative effect on the gain (even if it was still very limited) when it was removed: thus, it contained specific information not accounted for by other predictors. The negative effect on the gain was the most prominent (6%) when all Landsat-related predictors (average, minimum, maximum, and standard deviation of forest areas) were removed.

Marginal response curves for the different predictors (Fig. S3) showed that the percentage of the area covered by forest was positively correlated with habitat suitability, with a sharp increase after 5% of forests and a plateau after 20%. With respect to average LST day, habitat suitability was stable between 20 and 35°C, and then sharply decreased: while average LST day was not low enough in the study area to limit presence of *G. p. gambiensis*, high temperatures were unsuitable. The correlation between minimum LST day and habitat suitability was bell shaped with a maximum between 20 and 25°C. This could be related to the buffering effect of dense tree cover on temperature drops at night. Indeed, night temperature drops faster in open environments than in the forest. Habitat suitability dropped sharply with minimum temperatures exceeding 25°C. The correlation between mean NDVI and habitat suitability was a sigmoid curve that increased sharply after 0.2. Regarding NDVI range, a plateau of habitat suitability was observed until 0.5 and sharply decreased after this threshold, thus illustrating the importance of perennial tree vegetation for this tsetse species. The relationship with habitat suitability was similar for MIR standard deviation, related to the strong negative correlation between NDVI and MIR.

4.1.1.2. Use of the MaxEnt predictions in the tsetse eradication project

Before the availability of the MaxEnt model in the Senegal project, operational choices such as selection of trap sites were taken using a vegetation classification obtained from a LandSat 7 ETM+ image of April 2001. Suitable habitat for *G. p. gambiensis* was mapped from this classification with high sensitivity but low specificity (Bouyer et al., 2010). The availability of the MaxEnt predictions was used in four ways to optimize the implementation of the eradication effort.

Firstly, boundaries of the target eradication area, shown as grey grids in figures 4 and 5, were validated by the model. All the new suitable habitat areas identified by the MaxEnt model within a range of 5 km around sites where wild *G. p. gambiensis* had been trapped (at any occasion) were already included in the control strategy (see discussion). The target area was subdivided in 4 operational blocks, which are being sequentially addressed during the operational program (fig. 4). Each block was subjected to a 1-year tsetse-density reduction phase, followed by an 18-month eradication period using the sterile insect technique (SIT).

Secondly, the spatial distribution of the monitoring traps deployed since January 2012 in block 1 and since October 2012 in block 2 was modified through relocating 22 of the 97 monitoring traps (23%) to more suitable sites according to habitat suitability as predicted by the MaxEnt model (fig. S4). In block 3, where monitoring has not started yet at the time of writing, the monitoring trap sites will also be deployed in sites that have a high (predicted) suitability value as indicated by the model.

Thirdly, 1,347 insecticide-impregnated traps used for tsetse-density reduction were deployed in block 2 according to predictions of MaxEnt during the period December 2012 - February 2013, from which 661 were renewed during the period January - February 2014. The total surface area covered by block 2 is close to 500 km^2 but it contains only 80.6 km^2 of predicted suitable habitat, thus giving a final trap density of 16.7 traps / km^2 of suitable habitat (Fig. 6).

Fourthly, predicted suitable habitats were also used to optimize aerial releases of sterile male *G. p. gambiensis*. Polygons with similar surface areas of suitable patches were identified (RL1 and RL2 in block 1 for example, fig. 4) and the density of released sterile males adjusted proportionally to the area of suitable habitat in these polygons (0.24 and 0.11 flies per ha in RL1 and RL2 respectively).

4.1.1.3. Optimization of tsetse eradication by the model

In the first block, the apparent density of *G. p. gambiensis* dropped from an average of 0.42 (s.d 0.39) flies/trap/day before control, to an average of 0.04 (s.d. 0.11) flies/trap/day and 0.003 (s.d. 0.01) flies/trap/day during the suppression and eradication phases respectively (fig. 5). In the second block, the apparent density dropped from an average of 1.24 (s.d. 1.23) flies/trap/day before control, to an average of 0.005 (s.d. 0.017) flies/trap/day during the suppression phase.

Apparent fly density in block 2 was higher than in block 1 (GLMM, p= 0.009, Supplementary information 2) before the start of the suppression, which initially sharply reduced tsetse densities (p = 0.001). This effect was limited in time (6 months) and tsetse density remained stable and even increased with time thereafter ($p < 10^{-3}$), although remaining at a very low level (<0.04 fly/trap/day), until the eradication phase started. The cumulated reduction of densities with time was higher in block 2 (reduction of 99.6%) than block 1 (reduction of 90.4%, $p < 10^{-3}$).

In block 1, the last wild fly was captured on 09 August 2012, ~6 months after the start of sterile male releases. It was an old female (more than 40 days old) in its fourth larviposition cycle, with an empty uterus and the next follicle was immature and small, indicating an abortion. This female showed a copulation scar and its spermatheca were 85% filled, indicating that its sterility was probably induced by a mate with one sterile male. From the beginning of the eradication phase in block 1 (16 March 2012) to the date corresponding to the last capture, only three other wild females could be dissected and had all indications of having mated with a sterile male. The average percentage of sterile males as a proportion of all catches was then 99.2% (s.d. 1.6%), corresponding to a sterile to wild male ratio of 130. The percentage of sterile males remained 100% thereafter (no wild fly captured for 78 weekly collections with 25 monitoring traps), corresponding to a very likely eradication (probability of not detecting potential remaining flies of 0.002 only).

4.1.2. Discussion

4.1.2.1. Ecological niche of G. p. gambiensis in the Niayes

Our analysis showed that the ecological niche of *G. p. gambiensis* in the Niayes area corresponded to permanent ligneous vegetation with a tree density sufficient to provide adequate shade, to buffer temperature and relative-hygrometry variations in comparison with macroclimatic conditions occurring in the surrounding open environments. Air temperature in dense tree vegetation in gallery forests can be 4°C lower as compared to the surroundings and relative humidity 15% higher. This habitat provides resting sites for *G. p. gambiensis* in contrast to the more open habitat into which they may disperse for short periods (some hours) in search for a blood meal, e.g. their hunting sites. Suitable *G. p. gambiensis* habitat may be seasonal because of the variations of macroclimatic conditions and of non-permanent vegetation.

The MaxEnt model confirmed that permanent dense tree vegetation was important for *G. p. gambiensis*, but also that the larger the area occupied by the flies during the rainy season (corresponding to their dispersal capacity), the more suitable this habitat appears to be for *G. p. gambiensis*. Evidence is provided by the positive correlation of the forest range to the ENFA marginality axis (fig. 1).

The data layers derived from Landsat images which have a higher spatial resolution (30m) than the MODIS data (250m), were important predictors of presence of *G. p. gambiensis*. This was expected given their ability to survive in very small vegetation patches in the Niayes (Bouyer et al., 2010).

4.1.2.1. Comparison of the regularized logistic regression and MaxEnt models

The nature of predictions differs between regularized logistic regression (probability) and MaxEnt (index). However, both predictions were highly correlated, as observed elsewhere (Gormley et al., 2011). Model quality-assessment metrics were similar using the presence / absence validation dataset. MaxEnt predicted suitable areas better than regularized logistic regression based on the expert-based landscape classification. Tsetse presence data are generally more meaningful than absence data, since all known traps have a very low efficiency with respect to trapping rates (as a percentage of available individuals) i.e. ≤ 1% per day per km^2 (Bouyer et al., 2010). Under other circumstances (trap efficiency unknown, different trap models or trapping protocols), trapping may generate false absence data. Using only presence data to assess habitat suitability has the advantage that data derived from different sources (e.g. compilation of published data) can be combined to inform control projects.

Moreover, MaxEnt prediction were important for the eradication program as all suitable habitat needed to be included in the monitoring and the target area, even if they were not infested at the time of sampling due to possible movement among the patches. In the Niayes area, *G. p. gambiensis* are never present in all suitable patches at the same time. Instead, they form a metapopulation with patches connected through dispersal (Peck, 2012).

4.1.2.2. Use of model predictions for optimization of the eradication project

To generate a binary presence/absence map to delimitate the infested area, we chose a threshold providing a high sensitivity (96%). Indeed, in the case of an eradication project, it is paramount to reduce false-negatives as much as possible, to avoid leaving tsetse-infested pockets not subjected to the control effort. Such areas can act as a source of reinvasion into previously cleared areas. During the entomological baseline data survey, the target area was divided into operational 5 x 5 km grid cells where at least one tsetse had been captured, plus a buffer zone consisting of the grid cells contiguous to these infested cells. This strategy was validated by the MaxEnt predictions using this sensitivity threshold and confirmed that the target area was spatially isolated from any other suitable area for *G. p. gambiensis*. The area selected for model predictions did not include the populations of northern Sine Saloum (Bouyer et al., 2010) because they represent a different ecotype, genetically isolated from the Niayes metapopulation. We however included the “small coast” area of Senegal, again to avoid leaving tsetse-infested pockets south to the target area (Solano et al., 2010).

Interestingly, the MaxEnt model predicted some suitable habitat north of the target area (fig. 3), which were infested by *G. p. gambiensis* in the 1970s and subjected to a control program using residual spraying of dieldrin and trapping (Bouyer et al., 2010) that were completely isolated from the main infested area by sand dunes. Actually, no *G. p. gambiensis* flies were captured in these sites despite intensive sampling for several months and using numerous traps (Bouyer et al., 2010), despite that these sites appeared fully suitable for this species based on phytosociological criteria.

The improvement provided by the MaxEnt model, in comparison to the maps of suitable habitats (forests) based on the supervised classification of Landsat ETM+ images, is mainly related to specificity: 0.43 with this classification vs. 0.57 with MaxEnt. Sensitivity was already 0.96 with the supervised classification. MaxEnt selected those permanent tree habitats where climatic conditions (particularly temperature) allowed tsetse survival. Even if MODIS data mainly provide information on the macroclimate, they also allow making inferences on tree cover (particularly using nightly LST) and therefore on the buffering effect of permanent vegetation on macroclimatic conditions. MaxEnt models thus allowed increasing the sensitivity of the monitoring system, since traps previously set in unsuitable habitats have been moved based on suitability predictions (fig. S4).

Regarding the suppression strategy, the use of the vegetation classification in block 1 (MaxEnt predictions were not available then) already represented a great improvement in comparison to previous tsetse control programs: 269 targets were set in block 1 from Dec. 2010 to Feb. 2011 using this classification (corresponding to 19.4 targets / km^2 of suitable habitat). They allowed a good suppression of the flies whereas in the absence of a model of suitable habitat, densities of 60 targets / km^2 were required in Guinea against the same sub-species: recently, on Fotoba island, 30 targets / km^2 could only reduce the apparent fly density with 62% (Kagbadouno et al., 2011). In block 2, MaxEnt further improved the results and a significantly higher reduction rate (99.6%) than in block 1 was obtained with a lower target density of 16.7 targets / km^2 of suitable habitat (and 2.7/km2 of the target area only). Considering a target cost of EUR 3 in our project and a deployment cost of EUR 6 per trap (J Bouyer et al., 2013).

Moreover, MaxEnt predictions allowed concentrating the release of sterile flies on suitable habitats in block 1: with only 16.5 (s.d. 7.0) sterile flies released weekly per km^2, a sterile to wild male ratio of 130 was obtained, inducing 100% sterility in females and thus driving the population to extinction. The minimal weekly release rate was set at 10 and 100 flies per km^2 of unsuitable and suitable habitat respectively. Initially, sterile males were released from the air using carton boxes dropped from a gyrocopter, but since February 2014, a more advanced automatic chilled adult release machine was used (Mubarqui Smart Release Machine, fig. 4) that can be parameterized on a daily basis considering these parameters and the amount of flies available at the emergence center (ISRA) (Bouyer and Lefrançois, 2014; Mubarqui et al., 2014), with a gyrocopter flying at a speed of 110 km/h. In the absence of the MaxEnt models, it would have been necessary to release at least 100 flies per km^2 everywhere in the target area (in Zanzibar, up to 300 flies per km^2 were even released in the forest section to eradicate *Glossina austeni* (Vreysen et al., 2000)). With a mean cost of 0.2 USD per pupa [including production costs at Centre International de Recherche-Développement sur l'Elevage en zone Subhumide (CIRDES), Burkina Faso and the Slovak Academy of Sciences (SAS) and USD 0.04 transport cost per pupa], this represents major savings of 590,000 USD for our project, taking into account that 70% of received pupae provide for operational sterile flies, when taking into account the emergence rate and mortality rate at the insectarium before release. Moreover, the total number of sterile male *G. p. gambiensis* pupae produced by the CIRDES, Burkina Faso and the SAS, Slovakia is currently limited to 25,000 pupae per week, and treating the full area would not have been possible without adjusting release densities to the availability of suitable habitat. *G. p. gambiensis* pupae produced by the CIRDES, Burkina Faso and the SAS, Slovakia is currently limited to 25,000 pupae per week, and treating the full area would not have been possible without adjusting release densities to the availability of suitable habitat.

The same methodology will be applied in the two remaining blocks following the rolling carpet approach: when eradication is started in a given block, suppression is started in the contiguous block to avoid any risk of re-invasion. Based on this strategy, the full target area is planned to be cleared from tsetse by end 2016. The same approach might be used to optimize any vector or insect pest control program, especially when eradication is the selected strategy (Vreysen et al., 2012).

4.2. A spatio-temporal model for African animal trypanosomosis risk

4.2.1. Research findings

4.2.1.1. Tsetse habitat suitability

NDVI-related covariates and cumulative rainfall estimates that describe health of vegetation (greenness relative density) and humidity were positively correlated with the presence of both *G. p. gambiensis* and *G. tachinoides,* whereas high values of temperature-related variables (DLST and NLST) lead to a low suitability index for both species. Figure S5 presents the variable contributions and response curves for the different variables. The most important variables for *G. p. gambiensis* were (in order on decreasing importance) minimum LST, minimum NDVI and mean LST whereas for *G. tachinoides, altitude, mean* LST and the standard deviation of NDVI were the most influential. The response curves showed that overall, the response of both species to the different environmental variables were similar in shape. Mean LST, mean MIR and altitude were negatively correlated to suitability whereas minimum NDVI was positively correlated to suitability. However, the response of *G. tachinoides to* minimum NDVI was clearly less pronounced than that of *G. p. gambiensis,* confirming that the former is more xerophylous.

Figure 2 shows that hydrological network is in general highly suitable, with a wider distribution for *G. tachinoides* than for *G. p. gambiensis*. Except for a small area in western Burkina Faso, the uncertainty in the prediction was low (S6 Fig.). The predictive power of each model was high with an average AUC of 0.95 (resp. 0.91) for *G. p. gambiensis* (resp. *G. tachinoides*) (Fig.3). The average sensitivity of the model for *G. tachinoides* (0.85) is higher than for *G. p. gambiensis* (0.76). The kappa statistic follows the same pattern, whereas average specificity for the habitat suitability model of *G. p. gambiensis* is higher (0.84) than that of the *G. tachinoides* one (0.80).

4.2.1.2. Tsetse apparent density

The abundance of *G. p.gambiensis* was positively correlated to DLST (Table 2, p=0.002), and the suitability index (p=0.02) and negatively correlated to NDVI (p=0.02). The abundance of *G. tachinoides* was not affected by DSLT (Table 2, p=0.22), whereas NDVI (p<0.01) and the suitability index (p<0.01) had a positive impact.Finally, percentage of variability explained by the covariates on a test dataset was high for *G. p. gambiensis* (94%) and moderate for *G. tachinoides* (39%).

4.2.1.3. Trypanosome infection rates in tsetse

High infection rates of tsetse were associated with high temperatures (table 3, OR=1.10, p< 0.01). However, a negative correlation with cattle density (domestic host) was observed in the study area (OR=0.97, p=0.03). The generalized linear mixed model captured the seasonality of infection rates in tsetse although with a low pseudo-R^2 of 11%.

4.2.1.4. Entomological inoculation rates and AAT seroprevalence

The computed EIR was high around rivers during all dry season and more widespread during the all rainy season between 2003 and 2013 (Fig. 11). Optimal spatiotemporal lag for the regression of serological prevalence against EIR was obtained for a time lag of one month and a radius of 5km, which was then kept for the predictions (lowest AICc, Table 4).

For the model of seropositivity, fitted at the animal level (cattle), we used the breed (zebu/taurin/cross) of the animal and its age as co-variables. EIR had an important positive impact on sero-positivity probability (OR=1.5, CI=1.3 – 1.7) with a positive marginal effect (Figure 12, Table 5). Observed serological prevalence aggregated at the village level showed a positive correlation with the predicted sero-prevalence (Fig 13, r^2=22%). Optimal spatiotemporal lag for the regression of parasitological prevalence against EIR was obtained for a time lag of one month but there was no difference between the three distances tested (table 4). For homogeneity with the serological prevalence model, we kept the 5km radius model.

EIR was also significantly associated to the parasitological status (Table 5, p=0.02) and marginally to the illness status at the individual level (Table 5, p=0.1). Older animals were also less probable to be positive to the buffy-coat test (p=0.02). Model quality and accuracy was assessed by comparing predicted disease metrics against observed metrics aggregated at the village level on a testing dataset (25% of all data). The model had a good level of accuracy with a correlation of 67% between the observed and predicted parasitological prevalence at the village level whereas predicted illness rate at the village level was not correlated to observed values (Fig. 13, r^2 = 2%).

4.2.2. Discussion

Overall, EIR allowed a good prediction of parasitological and serological status. Environmental parameters were shown to have an impact on both the apparent densities and infection rates of the two riverine species considered (*G. p. gambiensis* and *G. tachinoides*).Both species responded similarly to environmental parameters but with various intensities. The more important impact of minimum NDVI on *G. tachinoides* confirmed that this species is more xerophilous. From the spatial standpoint, the most visible and arguably predictable pattern is that AAT risk is linked to the river network, but, interestingly, a few river sections are much more risky than others, and as such they might offer priority targets for control efforts – as also previously proposed (Bouyer et al., 2006; de La Rocque et al., 2005; Guerrini and Bouyer, 2007). The spatiotemporal risk map of AAT presented in this study was generated and validated at a high spatial resolution and concerns a wide area. In this area, the exercise was made less challenging by the scarcity of wild fauna, leading to an endemic cycle where trypanosomes circulate mainly among livestock (Van den Bossche et al., 2010). This cycle leads to the selection of less virulent strains that can be controlled by the combined use of curative and preventive trypanocidal drugs (Jérémy Bouyer et al., 2013a; Van den Bossche and Delespaux, 2011).The prediction area still includes a zone where wild fauna is abundant, around the protected forest of Diéfoula, where cattle are not supposed to enter. Our model succeeded to predict a high EIR in this area and indeed, a herd that was monitored by (Dayo et al., 2010) in Ouangolodougou, very close to Folonzo, during 2 years, had a very high AAT incidence (up to 20% monthly). This incidence dataset was part of the validation process. Even if farmers are not supposed to enter the protected areas, they still do so in search of better grazing areas which leads to the contact between tsetse and cattle (Jérémy Bouyer et al., 2013a). In fact, our model probably underestimate the severity of the disease in this situation, since the strains of trypanosomes that are transmitted from wild fauna to cattle are more virulent (Van den Bossche et al., 2010).

Our analysis confirmed that higher temperatures lead to increased infection rates in tsetse. This has been attributed to increased physiological stress of tsetse associated to a higher sensitivity to infection by trypanosomes (Jérémy Bouyer et al., 2013b).

EIR was best at predicting sero-prevalence when a time lag of one month and a radius of 5km were used. The one month time lag is probably related to the time of seroconversion (Desquesnes, 1997, p. 199) but the best correlation with the smallest time lag tested show that the risk is quite variable in time and that our model succeeded in capturing this temporal pattern. The distance of 5km is generally considered as the ray of grazing of local sedentary herds (Koné et al., 2012), which were targeted as apriority during the various surveys. EIR is best associated to parasitological than sero-prevalence and illness status. Both parasitological and serological results can suffer from various biases. Serological diagnostic is far more sensitive than BCT and less affected by other factors like the use of trypanocide drugs, inter-recurrent diseases that may affect PCV or low parasitaemia due to trypanotolerance. On the other hand, antibodies can persist up to 13 months (Van den Bossche et al., 2000). Thus, the probability that the animals were sampled in the area where they were actually exposed to the risk during this period is lower, even if sedentary herds were selected, due to either commercial exchanges or to past movements of the herd not necessarily considered by the farmers at the time of sampling (Koné et al., 2012). In our study, the second category of bias is apparently more important than the former, explaining the better prediction of parasitological infection rates. Age was positively correlated to seropositivity but negatively correlated to the infection probability (Desquesnes et al., 1999; Van den Bossche and Rowlands, 2001), which confirms that older animals develop some immunity against trypanosomes and are able to control infections better (Paling et al., 1991). The unexpected results vis-à-vis breeds (lower seropositivity and illness in zebu than in trypanotolerant taurine cattle) might be due to confounding factors (Murray et al., 1984). For instance, zebu are mainly present in the northern part of the study area where EIR is lower, and farmers use trypanocides more readily on zebu than on trypanotolerant cattle. Moreover, our model does not account for parasite virulence which is higher in the vicinity of protected areas (Van den Bossche et al., 2010). Finally, trypanotolerant are generally raised under different breeding systems (F. Bouyer et al., 2015; Porter and others, 1992). The only way this is accounted for in our model is through the selection of the grazing range in the model predicting serological and parasitological infection in cattle. However, we used the same range for all the prediction area whereas it might differ a lot between sites with different farming systems.

The present analysis is a first step in a framework for an efficient risk management approach to control climate-sensitive diseases. The methodology described in this study is generic to be applied to mitigate the risk of other vector-borne diseases through an evidence-based design of climate service mechanisms. The development and use of climate services in public health has increased recently and continues to grow, especially in the context of a changing climate (Jancloes et al., 2014). More specifically, an optimal transfer of bovine trypanosomosis risk and incentives for disease control by livestock owners can be achieved through the design of index-based animal disease insurance (Dicko et al., 2014a).

This analysis has also consequences for Human African Trypanosomosis (HAT) commonly known as sleeping sickness. Indeed, it has been suggested that climate change is likely to impact the risk of HAT in Africa (Rayaisse et al., 2009). However, despite the advocacy for a One Health approach (Okello et al., 2014; Smith et al., 2015) to control such diseases, climate services to mitigate both the risk of HAT and AAT have not been designed yet. The model developed in this study can be scaled up across Africa (Cecchi et al., 2015) and might thus serve as the basis for a spatiotemporal model of sleeping sickness risk in Africa.

The approach developed in this study enjoys a degree of flexibility because modeling separately each component of the risk (EIR), state-of-the-art methodology for each compartment can be used. However, there are some caveats when using this "one layer - one model" approach; which are related to the increasing uncertainty at each step of the modeling process (Rumisha et al., 2014, p. 20). This uncertainty impacts on the estimated EIR directly. Therefore, further work is needed to develop a more robust approach to design spatiotemporal risk maps based on sparse entomological data and to evaluate these maps so that they can potentially serve as early warning systems (Chaves and Pascual, 2007).

Another important aspect to keep in mind regarding AAT risk is the role of mechanical transmission (Desquesnes et al., 2009). In fact, it has been suggested that, when tsetse population become sparser or disappear, other biting flies like Tabanides or Stomoxines could maintain AAT transmission, also through episodic epidemics similar to those observed in South America for *T. vivax*. This can constitute a potential bias in our model that accounts only for cyclical transmission. Indeed, Tabanides, which are very common in the study area, have been shown to transmit *T. vivax* at incidence rates as high as 63% (*Atylotusagrestis*) and 75% (*Atylotusfuscipes*) within 20 days, and *T. congolense* at a cumulative incidence rate of 25% (*A. agrestis*) in experimental conditions (Desquesnes et al., 2004).

4.3. The economics of African animal trypanosomosis control under climate change

4.3.1. Research findings

4.3.1.1. Socioeconomic surveys

Table 1 presents the synthetic figures derived from the socioeconomic surveys to calibrate the micro-simulation model.

The socioeconomic survey run in 2015 confirmed a reduction of herd sizes since 2010, and more importantly a decrease of the percentage of trypanotolerant cattle (fig. 1, $p<0.05$). Using the former criteria to describe farming systems, the 23 farmers included 22 trypanotolerant systems and 1 improved meat system in 2010 against 19 and 4 respectively in 2015. Considering that the eradication of tsetse occurred in 2012, this corresponds to a mutation rate of 4.8% over this period. Improved meat breeds (Gobra and Gouzerat) were thus preferred (significant increase of their relative frequencies in the herds, $p = 0.01$) to improved milk breeds (Holstein, Montbeliard, Jersey, Pakistanese) (no significant increase, $p = 0.75$).

The focus group and participatory workshop allowed to better define the previously established scenarios. According to the farmers, the mutation rate from trypanotolerant systems to improved ones will be 6% yearly, from which 60% will change to improved meat systems and 40% to improved milk systems (table 2). This assessment does not distinguish between transitions from one system to another from disappearance of existing farms and creation of new farms.

4.3.1.2. Impact of climate change on African animal trypanosomosis risk

The species distribution model was quite accurate (average AUC of 0.75). Environmental and the climatic variables (precipitation and temperature) response curves are presented in (figure 2).

The response curve of species suitability index against land surface temperature showed a decrease in suitability with higher temperature, with a steady decline after.

Precipitation, on the other hand, is positively correlated to *G. p. gambiensis* suitable environment. For the CSIRO climate model, the simulation showed a 95% decrease of suitable habitats of 95% by 2030 and for the same model by 2050 the Niayes area would likely be unsuitable for *G. p. gambiensis* to survive by 2050. A similar trend wais observed for the MIROC5 model, by 2030 with we will experience a loss 87% of suitable habitats by 2030 and 96% of habitat will be loss by 2050 (Fig 15). For both models, the projections showed that the Niayes area wouldill be mostly tsetse-free by 2050.

4.3.1.3. Evolution of the livestock systems from the microsimulation model

The main results of the microsimulation models was how the number of animal cattle in the Niayes area would be reduced because of the transition from trypanotolerant (Djakoré) to improved breeds. By 2040, in a mostly tsetse-free area, the number of Diakore in the Niayes area was less than the number of Exotic breed or Gobra. On average, in the CSIRO climate model, the rate at which the number of Diakore were replaced by improved breeds were higher than the same number for the MIROC scenario and the baseline scenario without climate change (Fig 16).

4.3.1.4. Economic evaluation of the eradication project

The average BCR of the eradication project using the baseline scenario was 2.40. For both the CSIRO and MIROC climate models the BCR was similar around 1.34. The average NPV for the CSIRO model was EUR 1.52 million and EUR 1.4 million for the MIROC climate model compared to the EUR 6.3 million of average NPV for the baseline model (Fig 17).

The total cost of the tsetse elimination project was estimated at EUR 6.4 million contributed by the Ministry of Livestock of the Government of Senegal (37%), the ISRA, the US Department of State (35%), the FAO and the IAEA (19%) and finally the CIRAD (9%) (Bouyer et al., 2014).

The field cost account for more than half of the total cost (60%) with an estimated cost EUR 3.9 million. This is mostly due to operational implementation of the insecticide-treated traps (ITT), insectide-treated cattle (ITC) and sterile insects techniques (SIT) on the field. In fact, 3600 impregnated traps were deployed for the ITT component, 25000 cattle for ITC component.

4.3.2. Discussion

Our simulations have showed that climate change are likely to substantially reduce trypanosomosis risk in the Niayes area, even in the absence of control. These changes in distribution are gradual and can be explained mainly by the increase in temperature, predicted in the area by climate models (based on tsetse suitability index reponse curves to thermal data).

The microsimulation models highlight a decrease in cattle number and a shift from traditional herder to modern farming with more productive animals. In this study, we did not account for all benefits. Therefore, laying out other benefits that might arise from the eradication project, like environmental benefits. Actually, since keeping less productive trypanotolerant cattle breeds (Diakore) would urge traditional farmers to increase their herd size which in turn increases the competition for land use and ends with a negative environmental impact of cattle through overgrazing. In the Niayes area of Senegal for example, it was estimated that eradicating tsetse would result in more than tripling cattle sales whereas the herd size will be reduced by 45%.

However, when we take took climate change into account for the Senegalese campaign, the Benefit-cost ratio move dropped from 2.39 on average to 1.4 for CSIRO and 1.33 for the MIROC climate models. A similar trend was observed when we analyze the results considering the NPV. We can thus conclude that in this case, economic analysis in the Niayes area ignoring climate change interaction with AAT risk, overestimated the net benefit from the project.

One of the aspects that need to be improved in our approach is the potential adaptation of tsetse to new environmental conditions. The ecological niche of *G. p. gambiensis* is already very much modified in the Niayes area where river have disappeared, urging the tsetse populations to adapt to man-made habitats (Bouyer et al., 2010; Dicko et al., 2014b) that are totally different from the gallery forests in which they live in the main tsetse belt, southern to the study area (Bouyer et al., 2005). Therefore, the projection of tsetse suitability index using climate scenarios can be improved to integrate such adaptive mechanism.

In the present study, we also distinguished only three types of farming systems (trypanotolerant, improved meat and improved milk) for the sake of simplicity. However, the trypanotolerant and improved meat systems are both composed of agro-pastoralists, with an ancestral culture of cattle breeding, and mixed crop livestock farmers whereas improved milk systems include mixed crop livestock farmers and specialized dairy farmers. This will in turn condition the probability of transition of herders from the trypanotolerant system to the two others. During the participatory workshop, the livestock farmers distinguished between the mixed strategy (milk and meat) of agro-pastoralists that are replacing the Djakoré trypanotolerant breed by the Gobra breed and the strategy of mixed crop livestock farmers that tend to replace the Djakoré breed by the Guzérat breed towards an intensive meat strategy. For zootechnicians, Gobra and Guzérat breeds are considered as meat breeds since the milk production of these breeds is below 1.5L per animal per day. However, for cultural reasons, milk has a great social importance for Fulani people even if they are classed within the improved meat category when considering herd composition (>70% Gobra).

The main input from the participatory workshop in building the scenarios is a qualitative confirmation of the mutation of trypanotolerant systems towards improved systems (or new installations), as well as the reduction of the number of farmers – and cattle heads- in the Niayes area. On the other side, the analysis of the herd structures between the two socio-economical surveys (2010 and 2015) allowed quantifying the mutation rates of trypanotolerant systems towards improved systems and confirmed that the mutation rates used in the models are coherent, even if they are higher than the ones observed in Zanzibar after tsetse eradication (~2% yearly) (Vreysen et al., 2014).

The participatory workshop also revealed that herders try to improve their productivity to survive in a very a competitive environment to improve their income. Their strategy depends on their objectives, including cultural objectives, and on decision making processes that are built collectively. Trypanosusceptible breeds are preferred in a context without trypanosomosis risk, and allow intensifying for meat, milk or mixed productions. The Gobra breed is very much appreciated by traditional Fulani herders that have cultural objectives (F. Bouyer et al., 2015). Even if the global climate change reduces the trypanosomosis risk until it will finally disappear, the tsetse eradication project provided a clear advantage in the run for innovation. Actually, in parallel to the massive investment of the Senegalese authorities in artificial insemination campaigns and in a credit access program for livestock breeding, the simultaneous elimination of the trypanosomosis risk will allow to increase the cost-effectiveness of these actions and to reinforce the ongoing intensification dynamics. In term of innovation, the pathway is always both uncertain and irreversible and a change in the timing of actions almost always leads to a change in the innovation pathway (Akrich et al., 2006). Considering the concurrence between agriculture and cattle farming in front of land pressure, this fast eradication of tsetse and thus trypanosomosis will probably represent a major asset for their better integration in the Niayes area.

The economic evaluation showed that the elimination campaign in the Niayes area is still a sound investment despite an overestimation. The figures (BCR, NPV) have indicated that the elimination of the *G. p. gambiensis* population from the Niayes will result in a major overall socio-economic benefits for the farmer community that is composed of several farming systems, more or less exposed to the disease. This analysis was mainly financial and it can be the starting point of a more refined economic that will seek to understand the impact of the project and its potential impact directly on herders utility.

A recent study conducted all along the northern tsetse belt of *G. p. gambiensis* in west Africa revealed the presence of other isolated populations in this region, that might be targeted by similar eradication programs in the future (J. Bouyer et al., 2015). If these new areas are selected for such eradication campaigns, it will be important to account for climate change when calculating their cost-effectiveness.

More generally, it becomes more and more important to account for the global climatic changes when estimating the cost-effectiveness of animal health interventions.

Figures

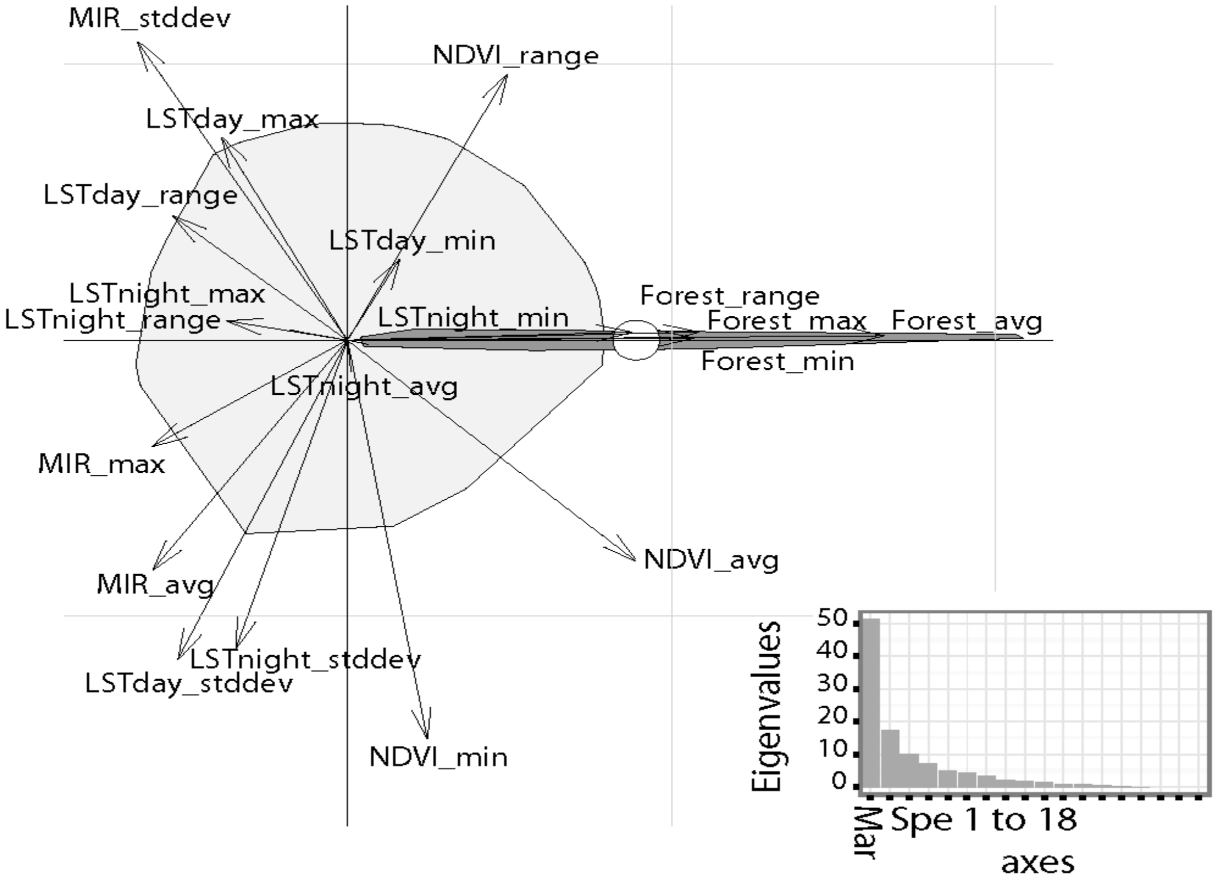

Figure 3: First plan of the Ecological Niche Factor Analysis (ENFA)

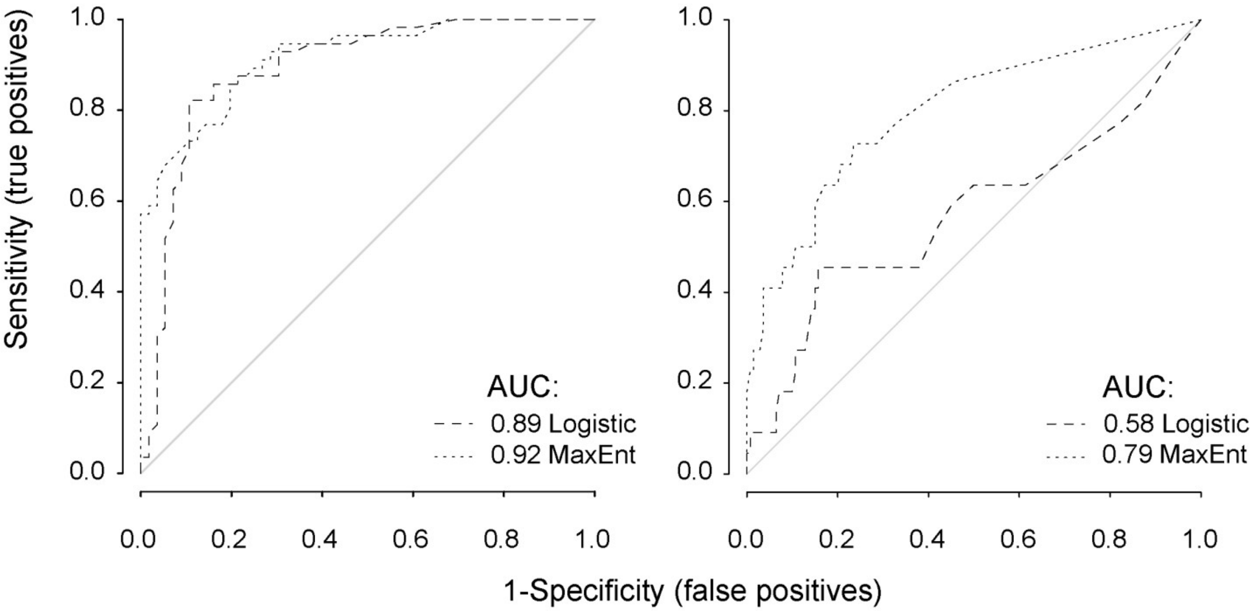

Figure 4: ROC curves and AUC of the regularized logistic regression and MaxEnt models

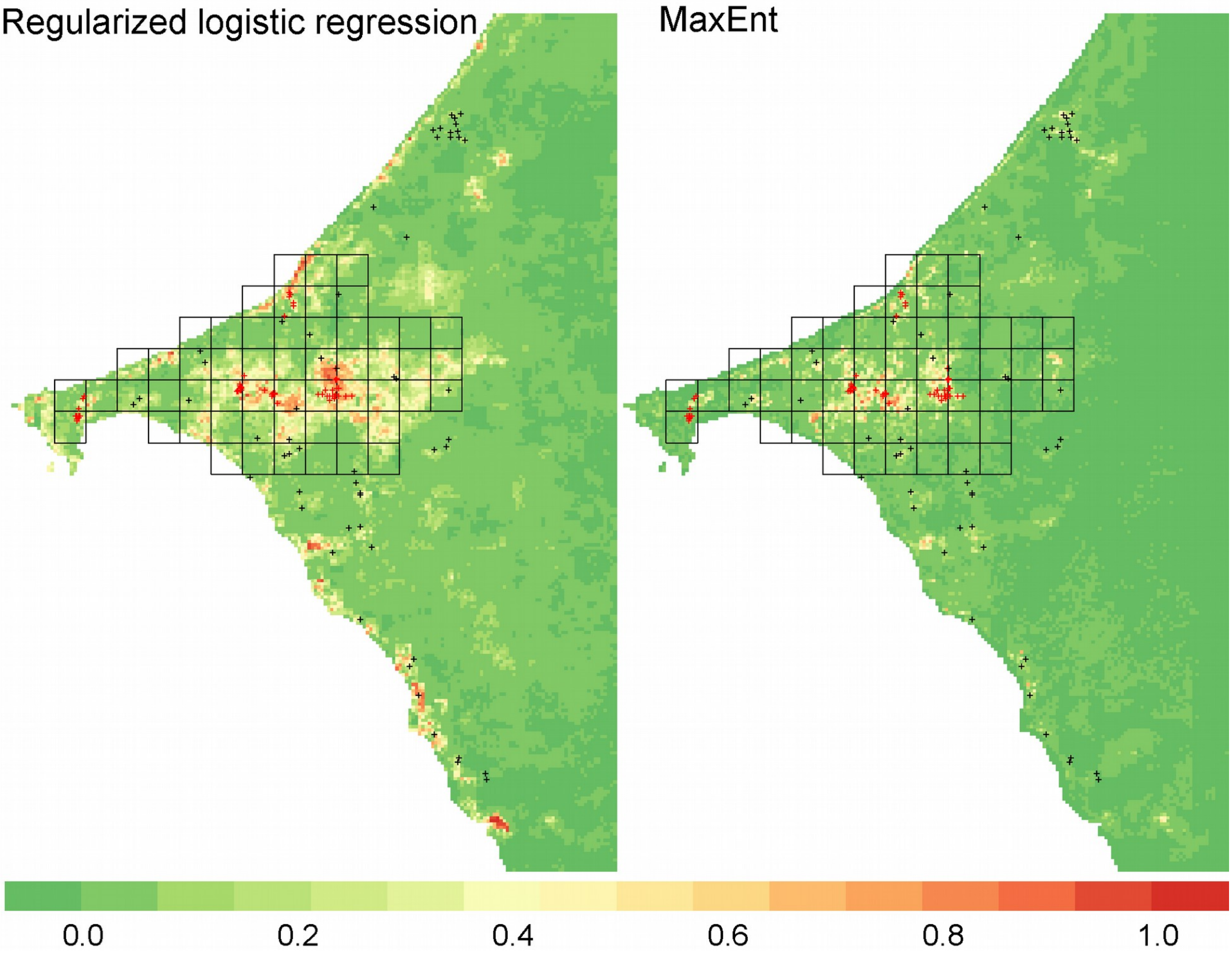

Figure 5: Predictions of the regularized logistic regression and MaxEnt models

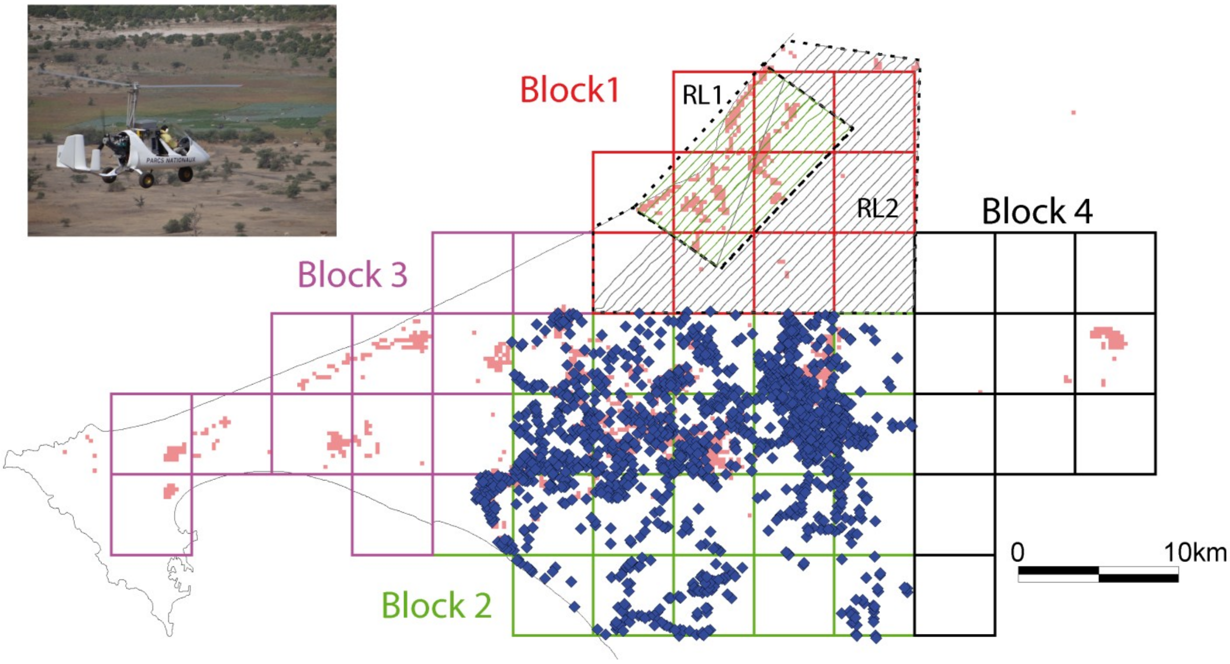

Figure 6: Optimization of the integrated control strategy using model predictions

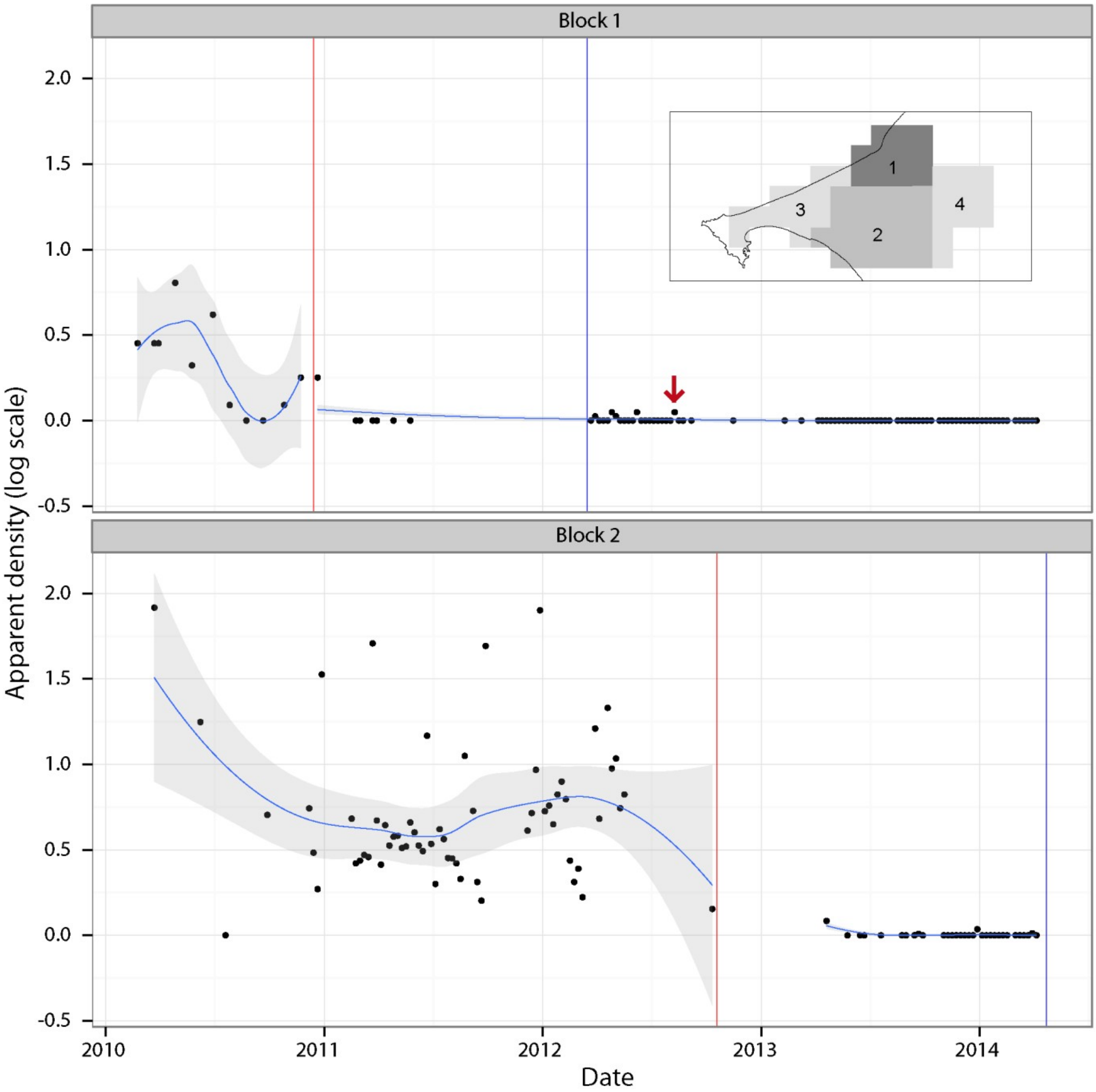

Figure 7: Impact of the control operations on tsetse apparent densities per trap per day

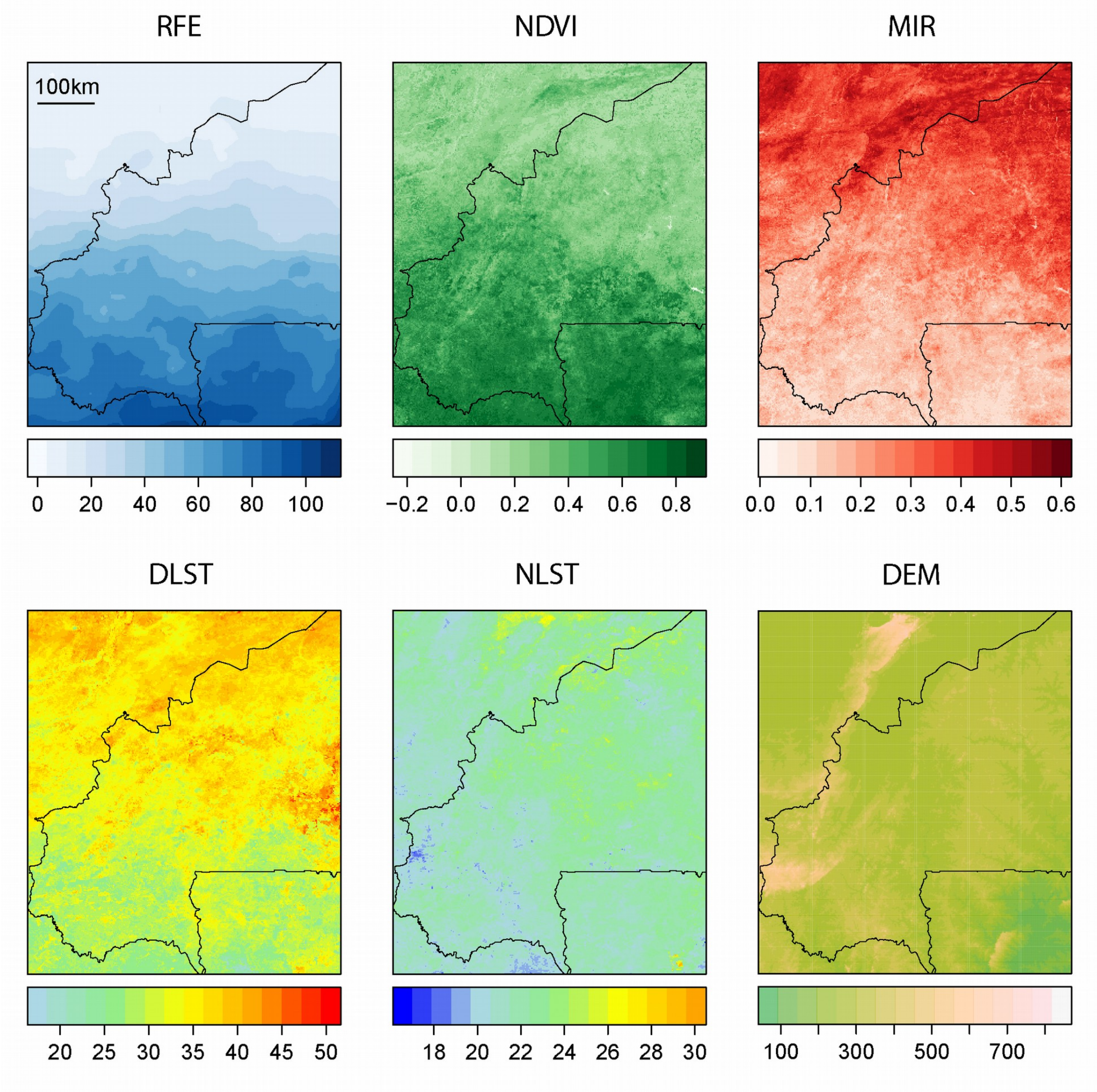

Figure 8: Remote sensing data from which environmental data was built

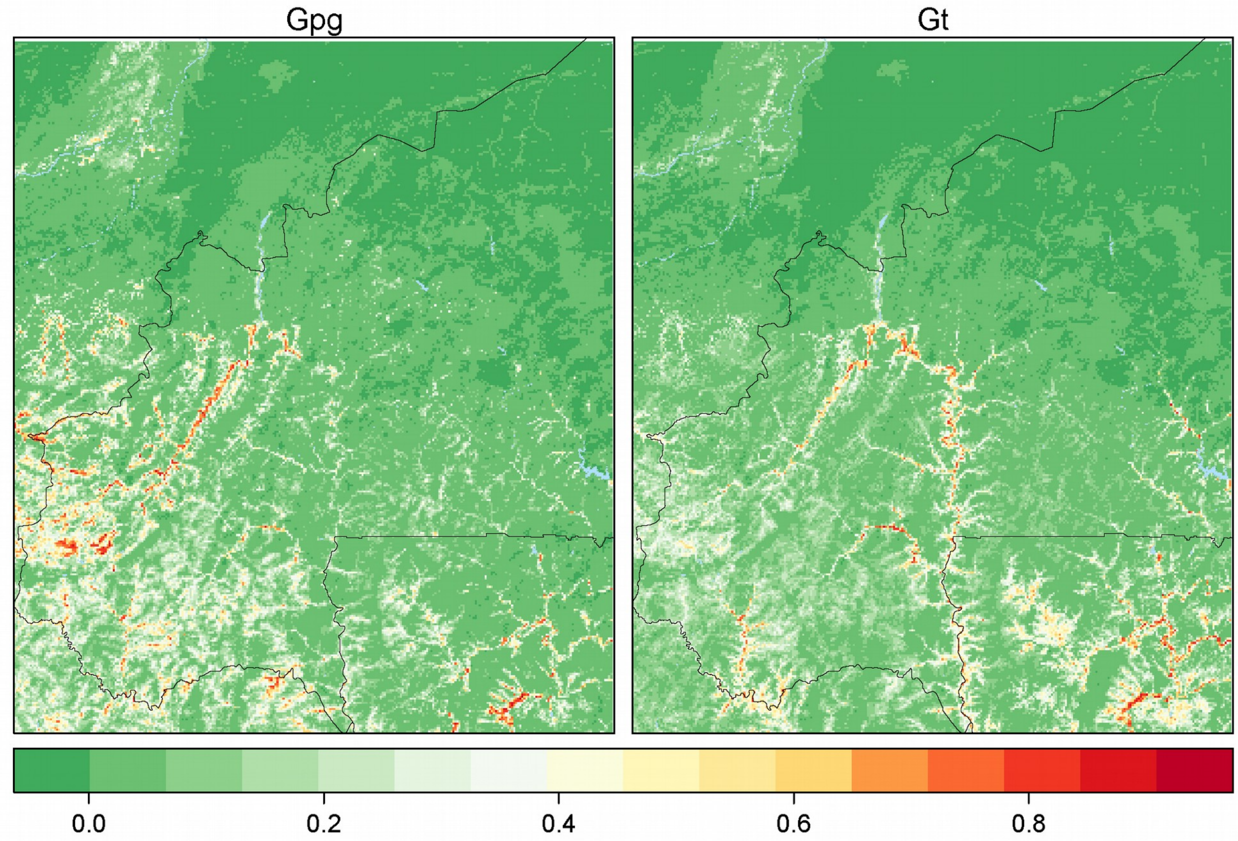

Figure 9: Mean predicted habitat suitability index for both species. The index varies between 0 (less suitable, green scale) and 1 (highly suitable, red scale).

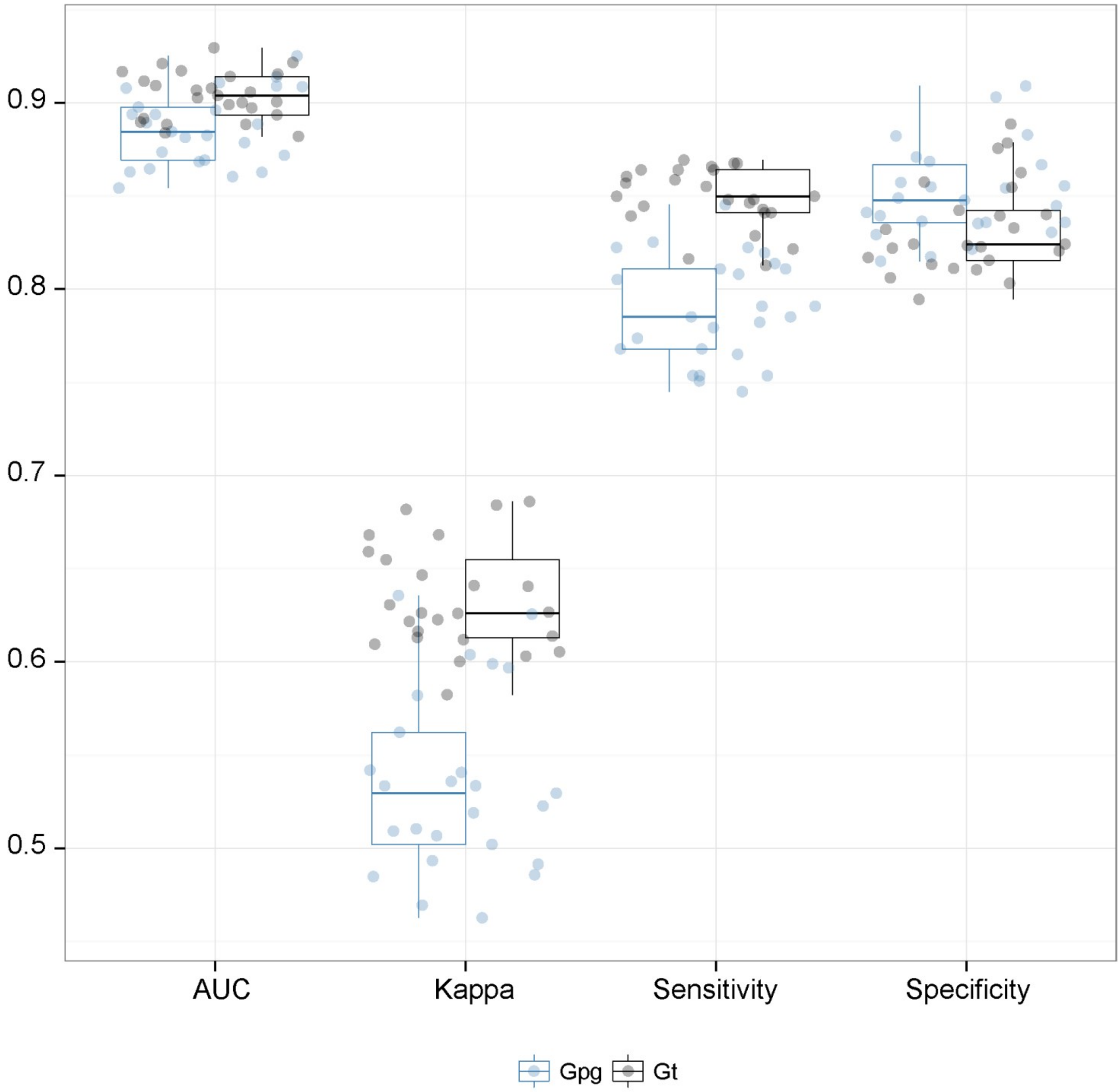

Figure 10: Prediction quality metrics for the habitat suitability model

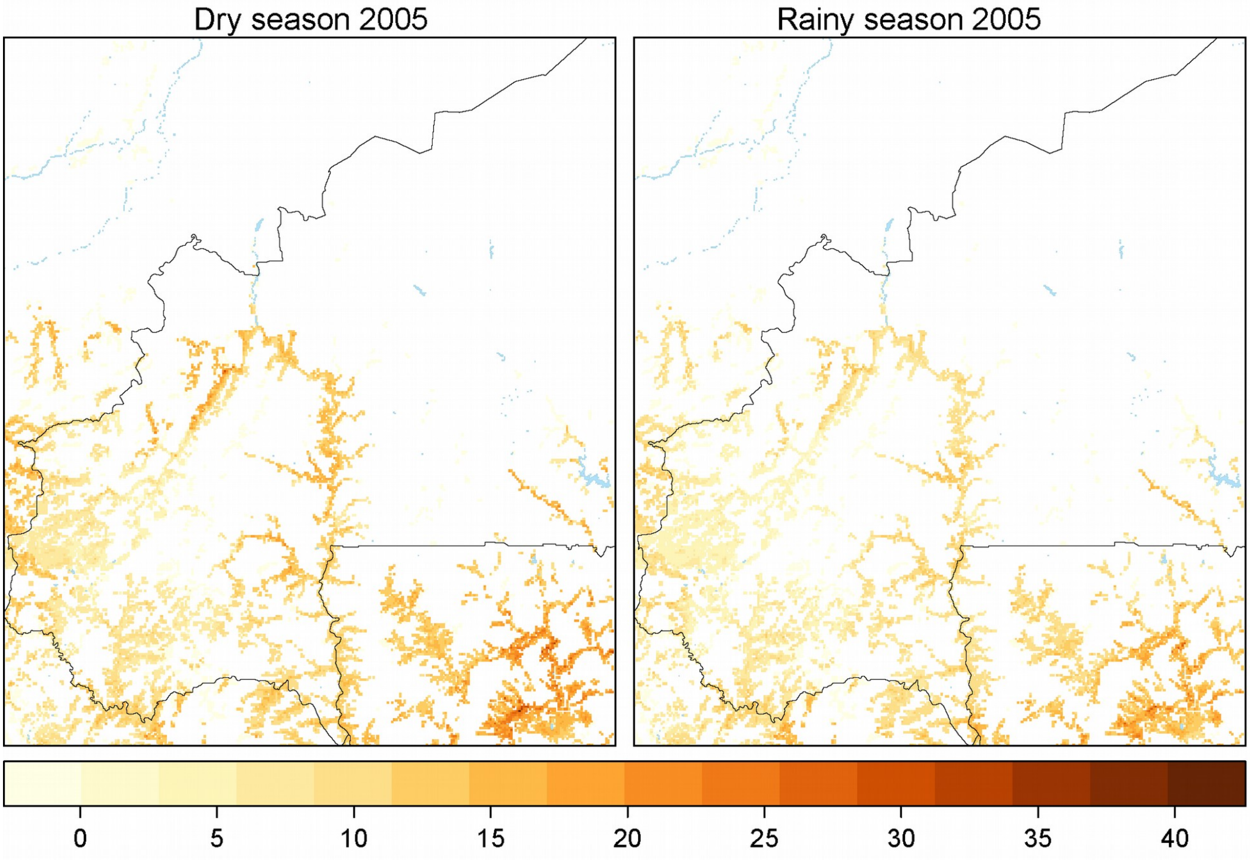

Figure 11: Predicted risk of bovine trypanosomosis for the dry and rainy season 2005

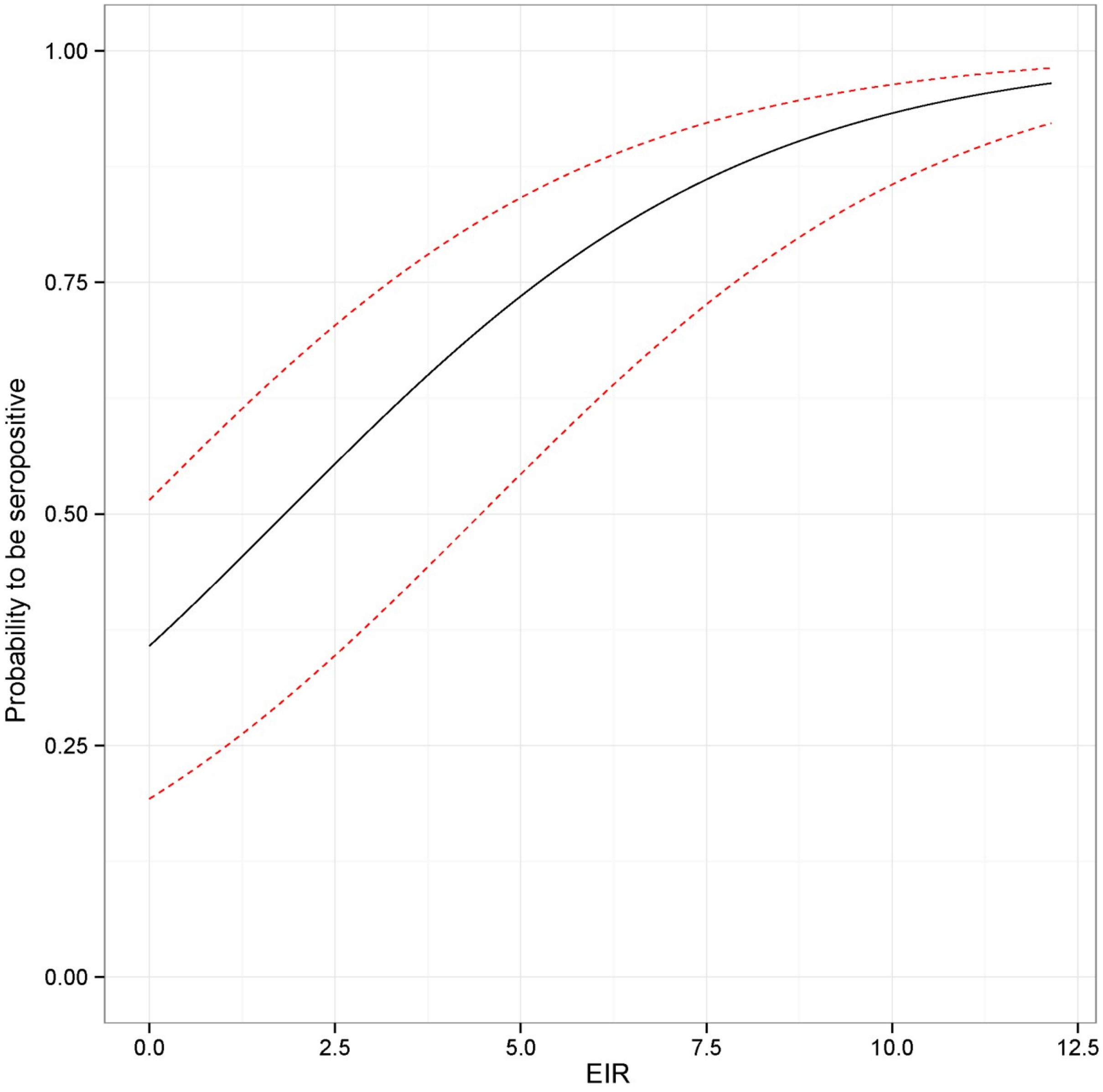

Figure 12: Marginal effect of the Entomological Inoculate Rate on seropositivity probability

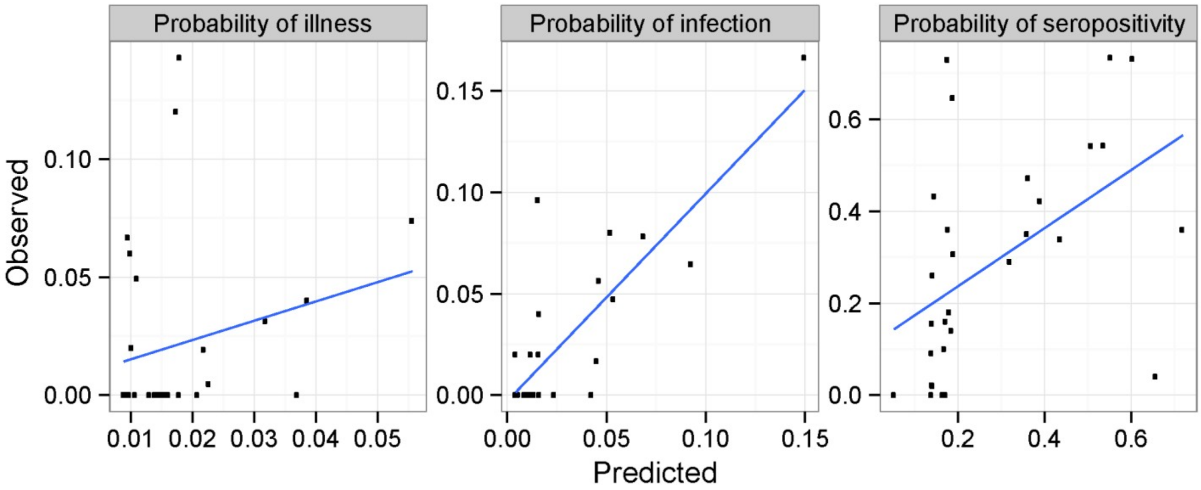

Figure 13: Relationship between observed and predicted disease metrics

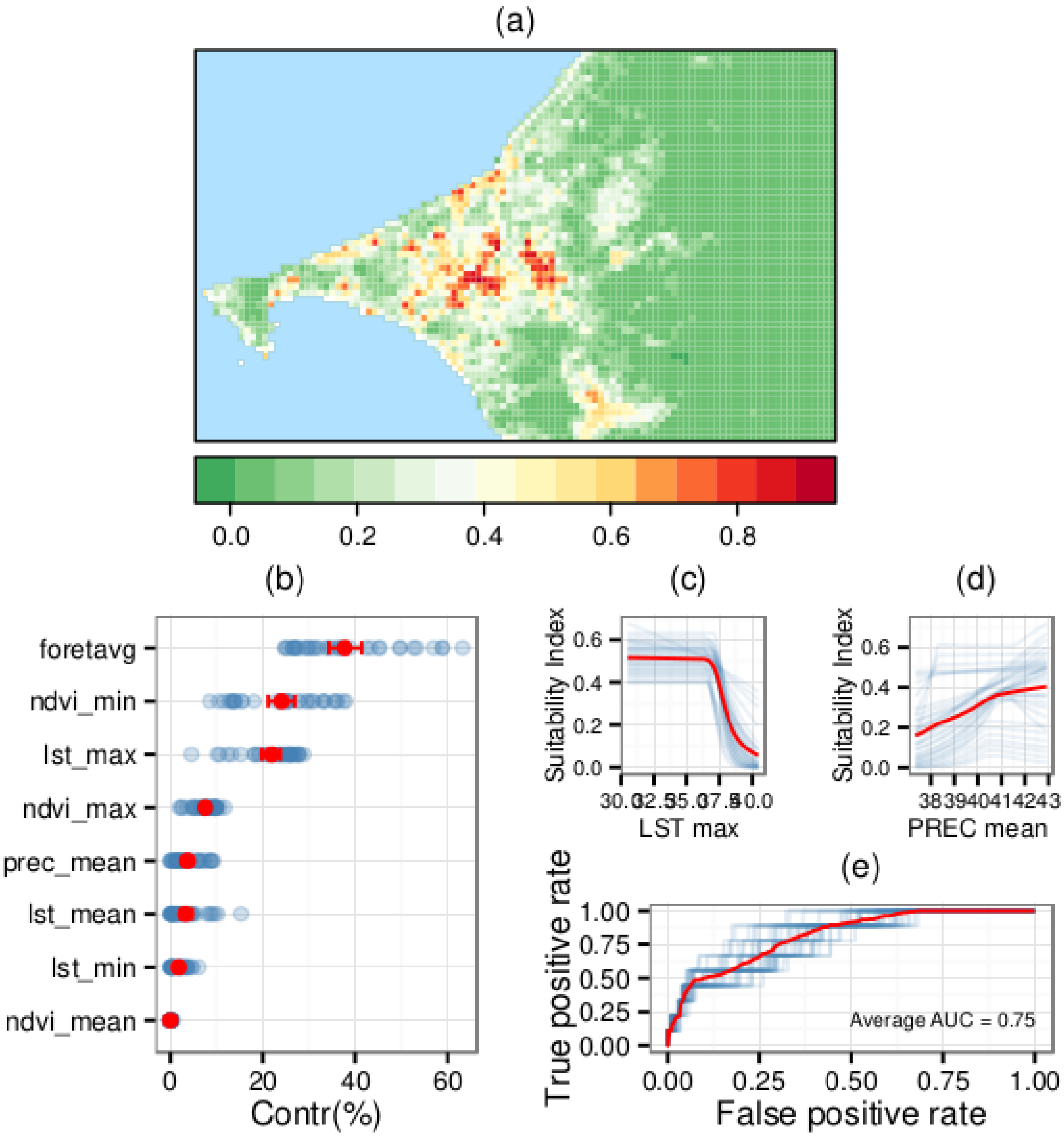

Figure 14: Distribution of Glossina palpalis gambiensis in the Niayes area of Senegal. a. Mean habitat suitability index predicted by a maxent model. The index varies between 0 (less suitable, green scale) and 1 (highly suitable, red scale). b. Contribution of variables to the suitability index by decreasing importance (95% confidence interval in red and individual values in blue).

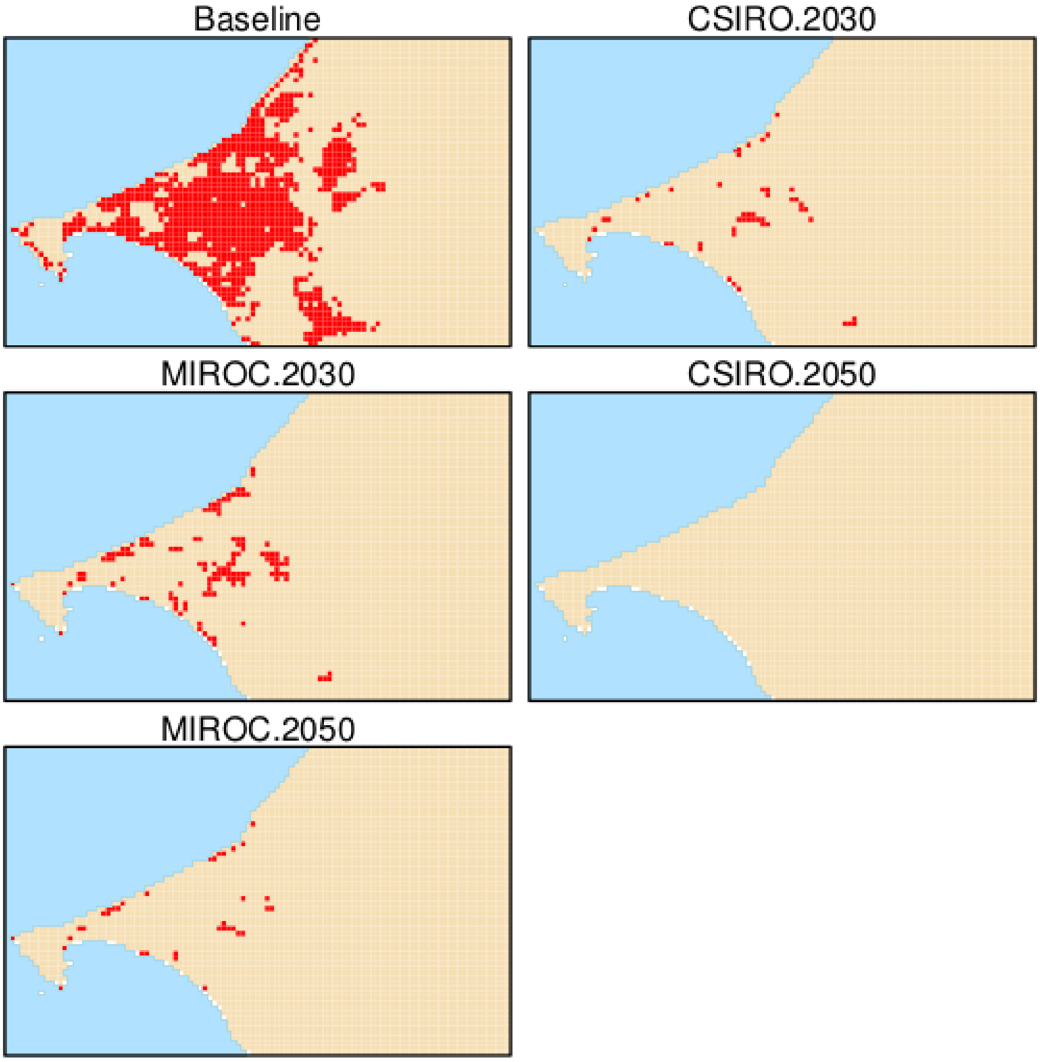

Figure 15: Distribution of G. p. gambiensis under different climate scenarios and horizons

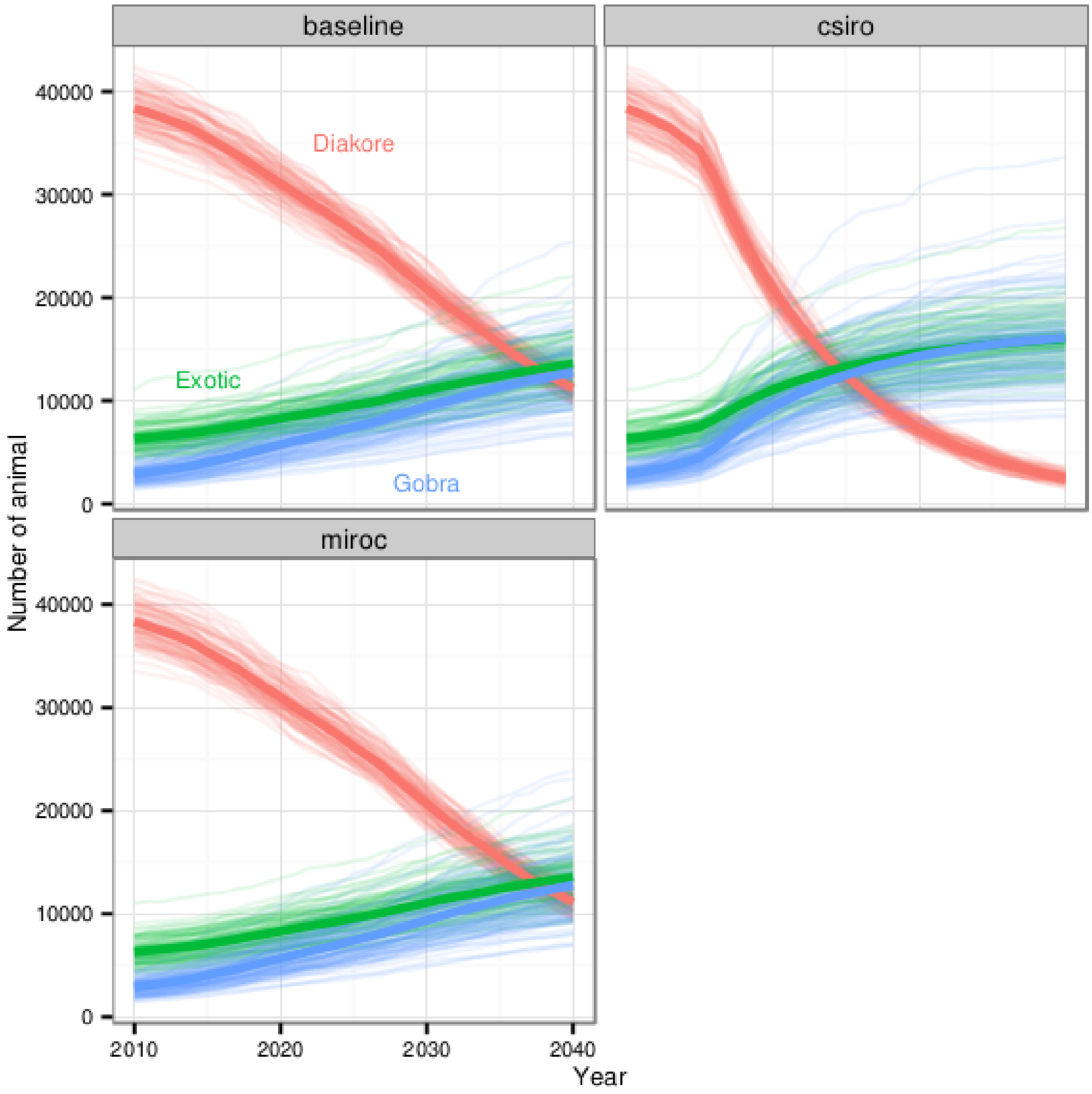

Figure 16: Predicted evolution of the densities of the main cattle breeds in the Niayes area.

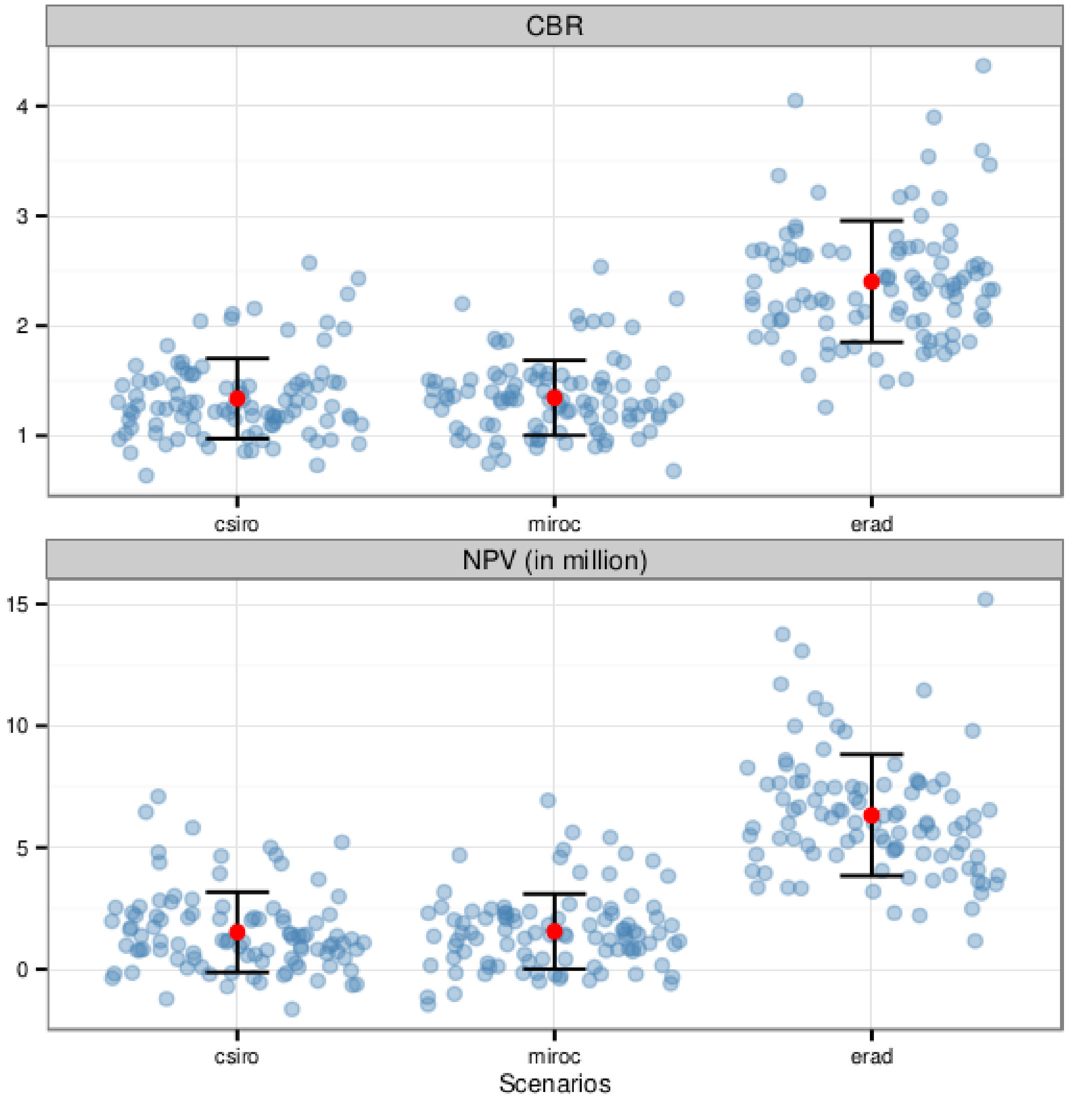

Figure 17: Benefit-cost ratios and net present values for the tsetse elimination campaign depending on the scenario of global climatic change.

Tables

Table 1: Environmental data derived from remote sensing used for the analysis

Variable name (extended)	*Variable name (short)*	*Type*	*Source*
Day Land Surface temperature	*DLST*	*Thermal*	*MODIS*
Night land surface temperature	*NLST*	*Thermal*	*MODIS*
Rainfall Estimate	*RFE2*	*Precipitation*	*FAO*
Normalized Differenced Vegetation Index	*NDVI*	*Vegetation*	*MODIS*
Middle Infra-Red	*MIR*	*Vegetation*	*MODIS*
Digital Elevation model	*DEM*	*Topographic*	*SRTM*
Cattle density	*Cattle_density*	*Other*	*FAO*

Table 2: Mixed effect negative binomial regression with spatiotemporal random effect for apparent densities of both species

Variable	*ADT G. p. gambiensis*	*ADT G. tachinoides*
Intercept	1.95 (0.99)*	0.84 (1.16)
DLST	0.06 (0.02)**	-0.02 (0.02)
NDVI	-1.88 (0.89)*	2.90 (0.95)**
HS	1.01 (0.49)*	1.47 (0.35)***

Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 3: Linear mixed models for trypanosome infection rates in tsetse (both species)

Variables	*IR*
Intercept	*-4.22 (0.83)****
DLST	*0.10 (0.02)****
Cattle_density	*-0.03 (0.01)**
Seasonality	*-0.24 (0.12)**

*Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Table 4: Optimal spatio-temporal lag for the regression model of serological and parasitological prevalences using AICc

	1 month	***2 months***	***3months***
	Serological prevalence		
3km	*12656*	*12669*	*12668*
5km	*12631*	*12653*	*12671*
10km	*12648*	*12729*	*12735*
	Parasitological prevalence		
3km	*4963*	*4966*	*4972*
5km	*4963*	*4965*	*4971*
10km	*4963*	*4965*	*4971*

Table 5: Logistic regression of disease metrics against EIR (Entomological Inoculation Rate) at the cattle level

	Illness	***Parasitological prevalence***	***Serological prevalence***
Intercept	-3.99 (0.37)***	-4.91 (0.51)***	-1.33 (0.00)***
Age	0.03 (0.02)	-0.04 (0.02)**	0.01 (0.01)
EIR	0.14 (0.08).	0.19 (0.09)*	0.42 (0.07)***
Breed: cross	-0.28 (0.33)	0.90 (0.47).	-0.25 (0.16)
Breed: zebu	-0.82 (0.41)*	-0.35 (0.59)	-0.50 (0.22)**

Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 6: Evolution scenarios of the distribution of the farming systems and corresponding herd sizes between 2015 and 2015. The numbers were estimated by farmers of the Niayes area during

Name	Variables	Type	Source
Day Land Surface Temperature	DLST	Climatic	MODIS
Night Land Surface Temperature	NLST	Climatic	MODIS
Precipitation	PREC	Climatic	WorldClim
Normalized Differenced Vegetation Index	NDVI	Vegetation	MODIS
Percentage of forest cover	Forest	Vegetation	Landsat

Table 7: Evolution scenarios of the distribution of the farming systems and corresponding herd sizes between 2015 and 2015. The numbers were estimated by farmers of the Niayes area during a participatory meeting organized in July 2015 in Dakar.

Type	Preferred breeds	Estimated number of herds 2015	Estimated herd size 2015	Predicted number of herds 2025	Predicted herd size 2025
Trypanotolerant	Djakoré	1000	75	400	75
Improved meat	Gobra, Guzerat	250	10	600	15
Improved milk	Exotic dairy breeds	20	15	250	15

Table 8: Data used to calibrate the microsimulation model. These data were estimated from the cost-benefit study conducted in 2010 (Bouyer et al. 2014) after attributing the farms to a trypanosomosis risk level using the MaxEnt model applied to the baseline situation (see text for details).

Breed	Trypanosomosis risk	Weight (kg) at sale	Sample size for the estimation of the parameters	Cattle price / head (in euro)	Milk yearly sales (in euros)	Herd size
Diakore	0	154.35	75.00	316.00	155.01	56.04
Diakore	1	116.91	58.00	201.86	160.32	47.71
Exotic	0	154.17	6.00	251.54	623.92	37.00
Exotic	1	121.50	8.00	217.24	125.95	26.50
Gobra	0	202.00	35.00	444.28	107.16	27.06
Gobra	1	75.00	2.00	152.45	138.21	39.50

Chapter 5: Conclusion and policy recommendations

5.1. Summary of the findings

This thesis has potentially two major contributions: Mapping the risk of African animal trypanosomosis in space and time in order to optimize control and information based control tool, develop a framework to have sound economic evaluation of trypanosomosis control that take into account the variability of the disease system due to climate change.

For the first objective, a statistical approach based on the ecology of the tsetse species present in the Niayes area, Senegal was developed. A habitat suitability index was created using a statistical learning model (MaxEnt). The goal of this modeling exercise was to provide a tool that will help to optimize the control effort ongoing in the elimination project in the Niayes area. In order to generate a binary presence–absence map to delimitate the infested area required to optimize control effort, we chose a threshold providing a high sensitivity (96%). Indeed, in the case of an eradication project, it is necessary to reduce false negatives rate as much as possible, to avoid leaving tsetse-infested pockets not subjected to the control effort. Such areas can act as a source of reinvasion into previously cleared areas. During the entomological baseline data survey, the target area was divided into operational 5 × 5 km grid cells where at least one tsetse had been captured, plus a buffer zone.

Regarding the suppression strategy, the use of the vegetation classification already represented a great improvement in comparison with previous tsetse control programs; 269 targets were set in block 1 from December 2010 to February 2011 using this classification (corresponding to 19.4 targets per km^2 of suitable habitat). They allowed a good suppression of the flies, whereas in the absence of a model of suitable habitat, densities of 60 targets per km^2 were required in Guinea against the same subspecies: Recently, on Fotoba Island, 30 targets per km^2 could only reduce the apparent fly density by 62%. In another block, the model further improved the results, and a significantly higher reduction rate (99.6%) than in the first block was obtained with a lower target density of 16.7 targets per km 2 of suitable habitat (and 2.7 targets per km 2 of the target area only). Considering a target cost of EUR 3 in our project and a deployment cost of 6 per trap, the total reduction of the costs can be estimated at EUR 43,700 for 1,000 km 2. Therefore, this approach allowed the team to optimize the control and the monitoring of tsetse fly in the Niayes area but an important amount of time, resources and money was also saved in the process.

This approach is quite novel and the same approach might be used to optimize any vector or insect pest control program, especially when eradication is the selected strategy.

This analysis was further refined to map the spatio-temporal risk of AAT, in particular when the eradication is not the only option of control. Indeed, such model spatio-temporal was the made to fill a gap in risk analysis of AAT and was the second objective of this thesis. This analysis is a first step in a framework for an efficient risk management approach to control climate-sensitive diseases. The methodology described in this study is generic and can be applied to mitigate the risk of other vector-borne diseases through an evidence-based design of climate service mechanisms. The development and use of climate services in public health has increased recently and continues to grow, especially in the context of a changing climate. More specifically, an optimal transfer of bovine trypanosomosis risk and incentives for disease control by livestock owners can be achieved through the design of index-based animal disease insurance.

Finally, for the last objective, the economic analysis of the tsetse eradication campaign show some interesting results. First, the simulation has shown that climate change are likely to substantially reduce trypanosomosis risk in the Niayes area. These changes in distribution are gradual and can be explained mainly by the increase in temperature, predicted in the area by different global climate models.

Second, the coupled microsimulation models highlight a decrease in cattle number and a shift from traditional herder to modern farming with more productive animals. Therefore, laying out other benefits, since keeping less productive trypanotolerant cattle breeds (Diakore) urge traditional farmers to increase their herd size which in turn increases the competition for land use and end with a negative environmental impact of cattle through overgrazing. In the Niayes area of Senegal for example, it was estimated that eradicating tsetse would result in more than tripling cattle sales whereas the herd size will be reduced by 45%.

Thirdly, the economic evaluation shows that the elimination campaign in the Niayes area is still a sound investment. The figures (BCR, NPV) have indicated that the elimination of the *G. p. gambiensis* population from the Niayes will result in a major overall socio-economic benefits for the farmer community that is composed of several farming systems, more or less exposed to the disease. However, when we take climate change into account, the benefit-cost ratio move from 2.39 on average to 1.34 and 1.33 respectively for CSIRO and MIROC climate models. A similar trend is observed when we analyze the NPV too. We can thus conclude that in this case, the previous economic analysis in the Niayes area overestimated the net benefit from the project.

5.2. Policy implications of the findings

From a policy implementation standpoint, our results can be relevant for tsetse and trypanosomosis control in sub-Saharan Africa. Our research was designed, oriented to answer practical aspects of tsetse and trypanosomosis control. Some results were for some extent applied successfully on the field.

In particular, the analysis developed to help the eradication campaign in the Niayes area and optimize it. It was used after the validation of the results on the ground and is still in use in the Niayes. This analysis was done using existing data, already collected in all standard PATTEC eradication campaign throughout the continent and the other data used are freely available. Consequently, it is possible to scale this analysis at the continental level, and some eradication campaign in Africa are currently testing and integrating similar analyses in order to optimize control operation, save money and time.

The spatiotemporal risk index developed during this thesis can be the basis of a model-based risk management mechanism for AAT in West Africa. Indeed, the use such index as an early warning system can be developed to inform herder on the tsetse challenge in their area. There is also the possibility to design an index-based insurance based on similar index in order to help livestock recovers from AAT related loss and thus increase their resilience to the risk of AAT. Large body such as the Africa Risk Capacity, under the auspices of the Africa Union, can scale up and integrate such analysis in their risk management portfolio.

Finally, the economic evaluation of AAT control in the Niayes area taking into account climate change opened the door to new paradigm in the economics of tsetse control. The most important results from this research, is that all ex-ante economic analysis of tsetse eradication program that rely on an epidemiological risk model should include some climate-change projection in order to not overestimate or underestimate the potential benefit for the society. From this analysis, in the Niayes area, it was demonstrated that taking into account climate change projection, the benefit from the removal of tsetse was overestimated and most importantly that the clearance of the area will allow farmers and livestock keepers to reduce the size of their herd on average. This is an important result for mitigation since cattle farming account for an important part of GHG emission. Thus, providing a link between tsetse control and climate change mitigation can help to integrate new funding scheme for African countries to tackle two problems at the same time.

5.3. Suggestions for future research

At the end of this analysis, several questions were raised and need to be answered in order to better understand how to control AAT under climate change. Furthermore, scaling up some analyses developed in this document represents an interesting methodological challenge.

In terms of future direction, a first research package could be the design of some economic incentives based on the observed and perceived risk of AAT. Designing schemes similar to index-based insurance linked to an early warning system can be a solution to mitigate the risk of AAT where it is difficult to launch an eradication campaign.

In parallel to this research, some new models were developed to find all isolated population of tsetse flies in West Africa. In their analysis, the technical feasibility of the eradication of such population has been investigated, but the analysis of the profitability and the economic evaluation of such project to clear these areas has not been done. Therefore, as a second direction for this research, we advocate for the scaling up such analysis at the continent level and add an economic model in order to have a better tool to help decision maker to prioritize area where we should focus effort to eradicate tsetse fly. Finally, we are also convinced that a global analysis of the impact of climate change on the control of African animal trypanosomosis and its potential economic benefit at the continent level could be an important toward the removal of both African animal trypanosomosis and human sleeping sickness.

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Appendix

List of publications

Dicko, A.H., Lancelot, R., Seck, M.T., Guerrini, L., Sall, B., Lo, M., Vreysen, M.J., Lefrançois, T., Fonta, W.M., Peck, S.L. and Bouyer, J., 2014. Using species distribution models to optimize vector control in the framework of the tsetse eradication campaign in Senegal. *Proceedings of the National Academy of Sciences*, *111*(28), pp.10149-10154.

Bouyer, F., Seck, M.T., **Dicko, A.H**., Sall, B., Lo, M., Vreysen, M.J., Chia, E., Bouyer, J. and Wane, A., 2014. Ex-ante benefit-cost analysis of the elimination of a Glossina palpalis gambiensis population in the Niayes of Senegal. *PLoS Negl Trop Dis*, *8*(8), p.e3112.

Dicko, A.H., Fonta, W.M., Müller, M. and Bouyer, J., 2014, June. Index-based insurance: a new tool to control vector-borne diseases under climate change in West Africa. In *Third International Agricultural Risk, Finance, and Insurance Conference, Zurich, Switzerland*.

Dicko, A.H., Percoma, L., Sow, A., Adam, Y., Mahama, C., Sidibé, I., Dayo, G.K., Thévenon, S., Fonta, W., Sanfo, S. and Djiteye, A., 2015. A spatio-temporal model of African animal trypanosomosis risk. *PLoS Negl Trop Dis*, *9*(7), p.e0003921.

Supplementary figures

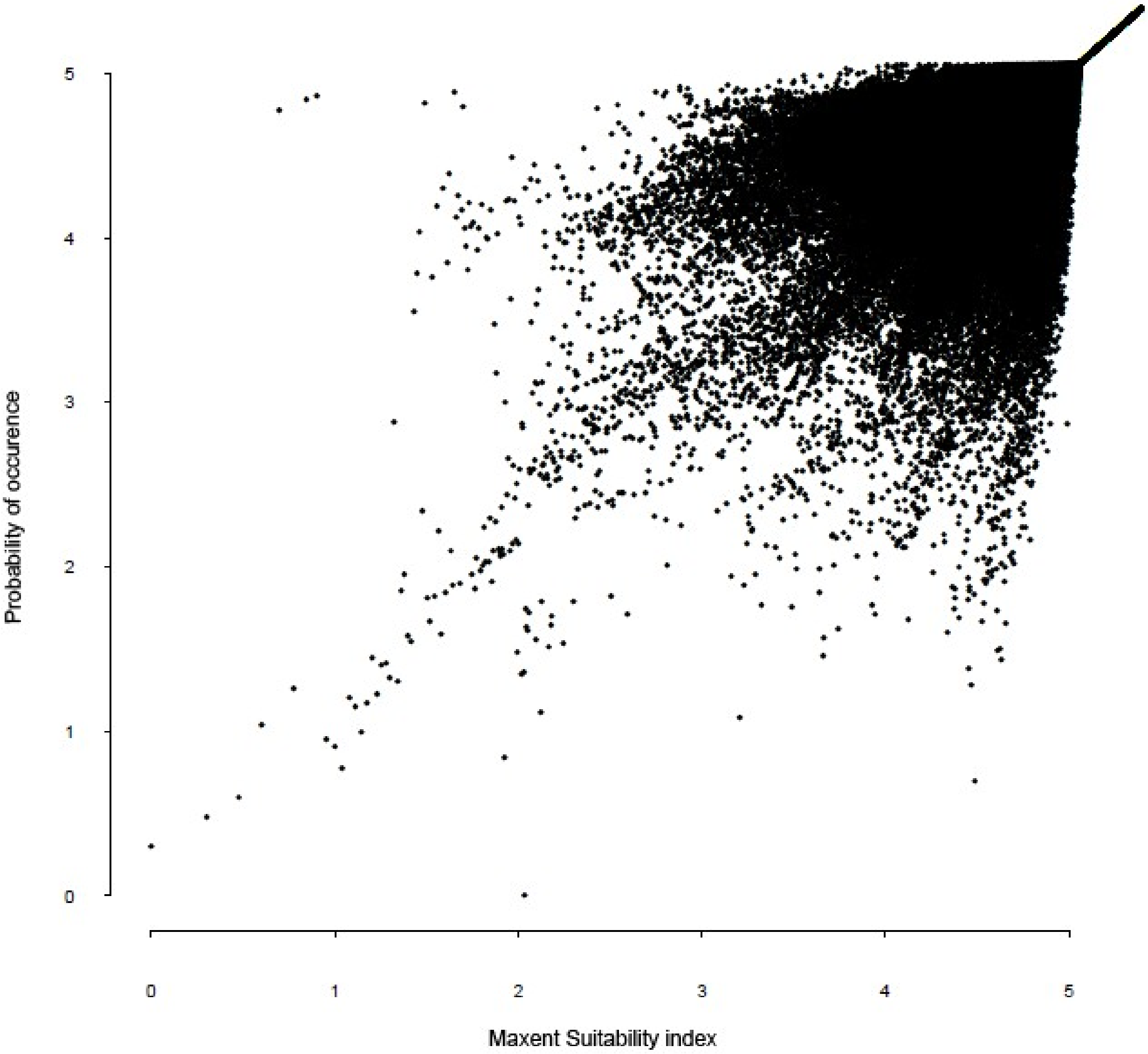

Figure S3- 1: Correlation between the probability of occurrence predicted by the logistic model and the suitability index by MaxEnt

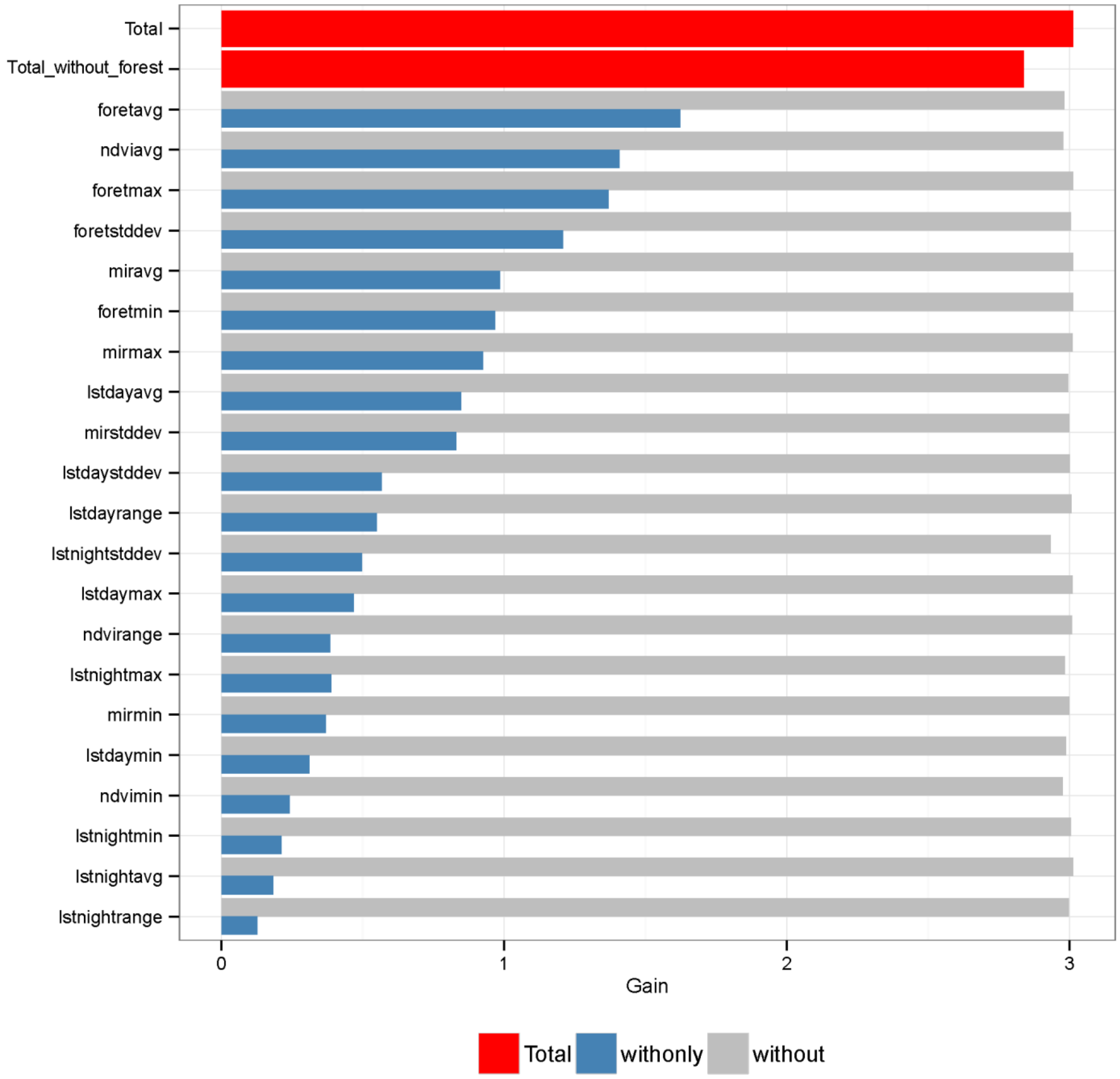

Figure S3- 2: Regularized Training gain of the MaxEnt habitat suitability model of G. p. gambiensis in the Niayes area

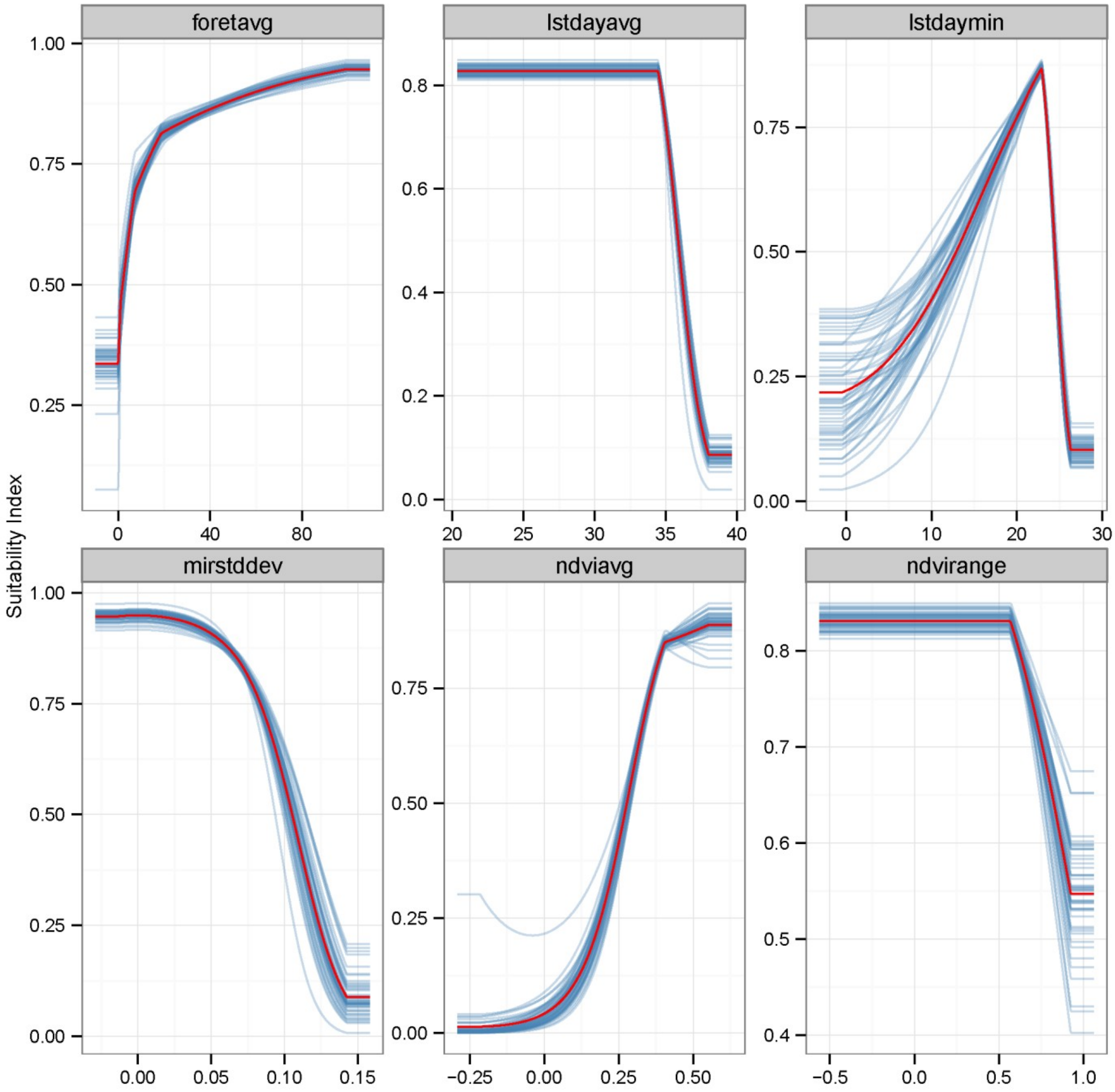

Figure S3- 3: Marginal impact of each variable on the predicted suitability (MaxEnt model)

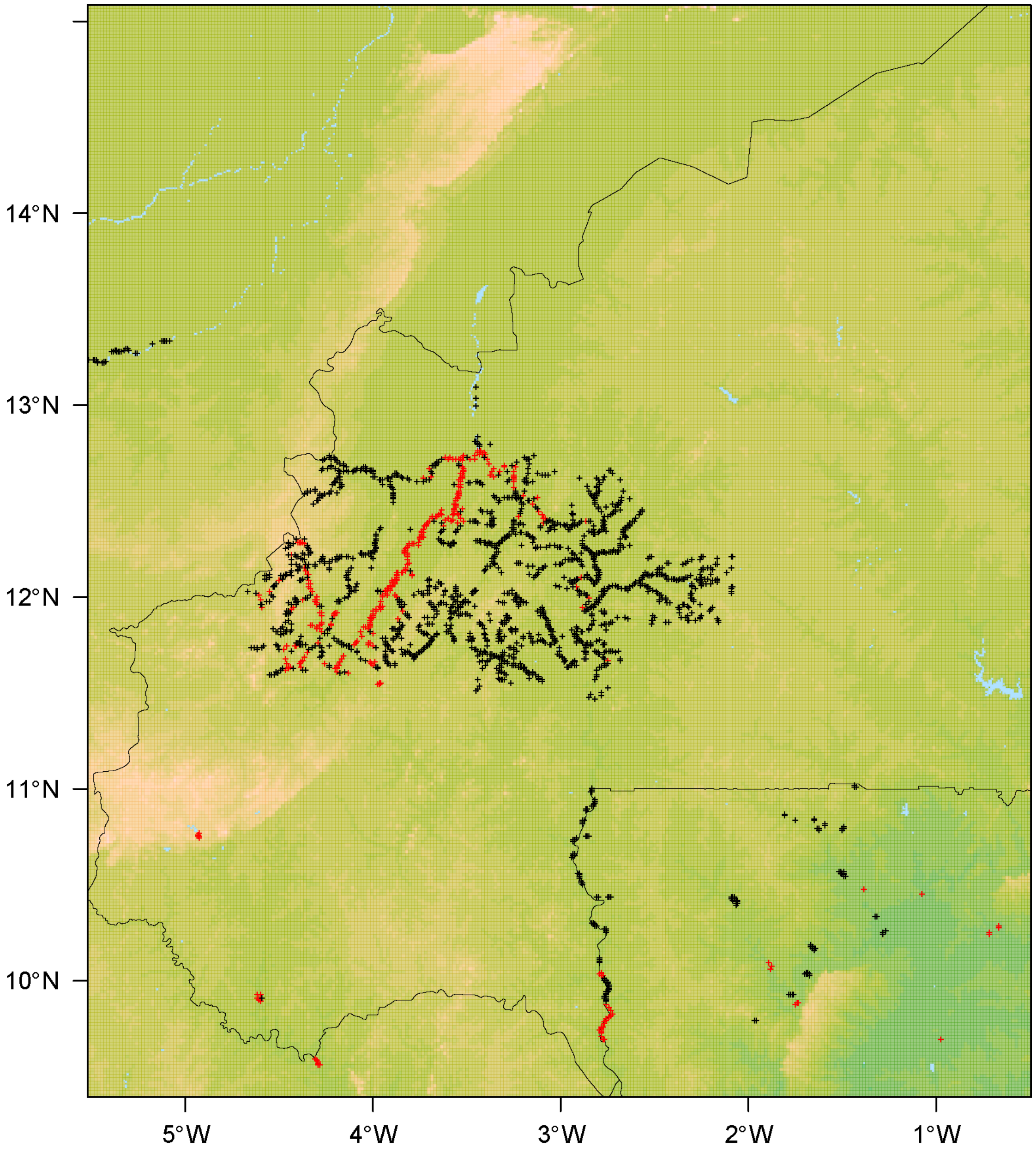

Figure S4 1: Geographical location of entomological data. Presence (black dot) and absence (red dot) data for *G. palpalis gambiensis* in the study area.

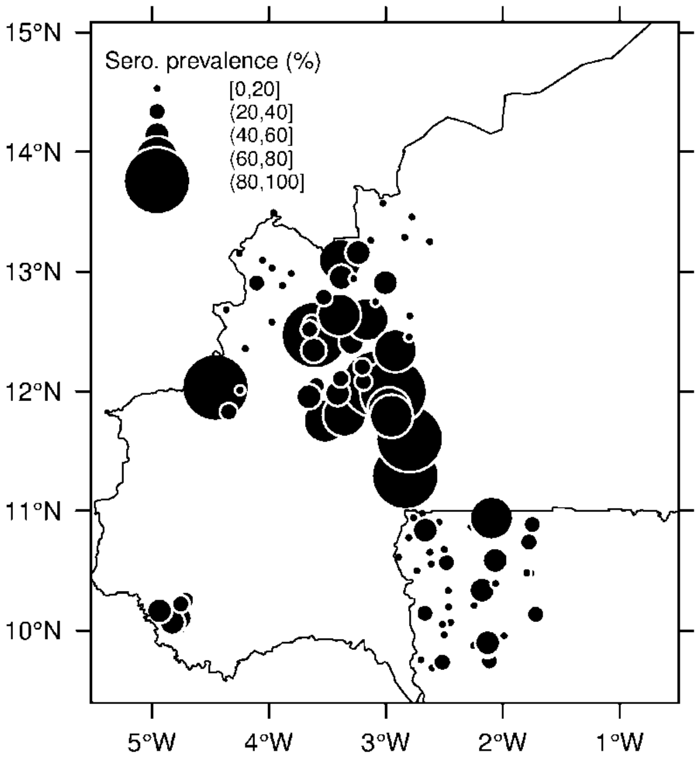

Figure S4- 3: Geographical location of sampled cattle and level of seroprevalence of AAT

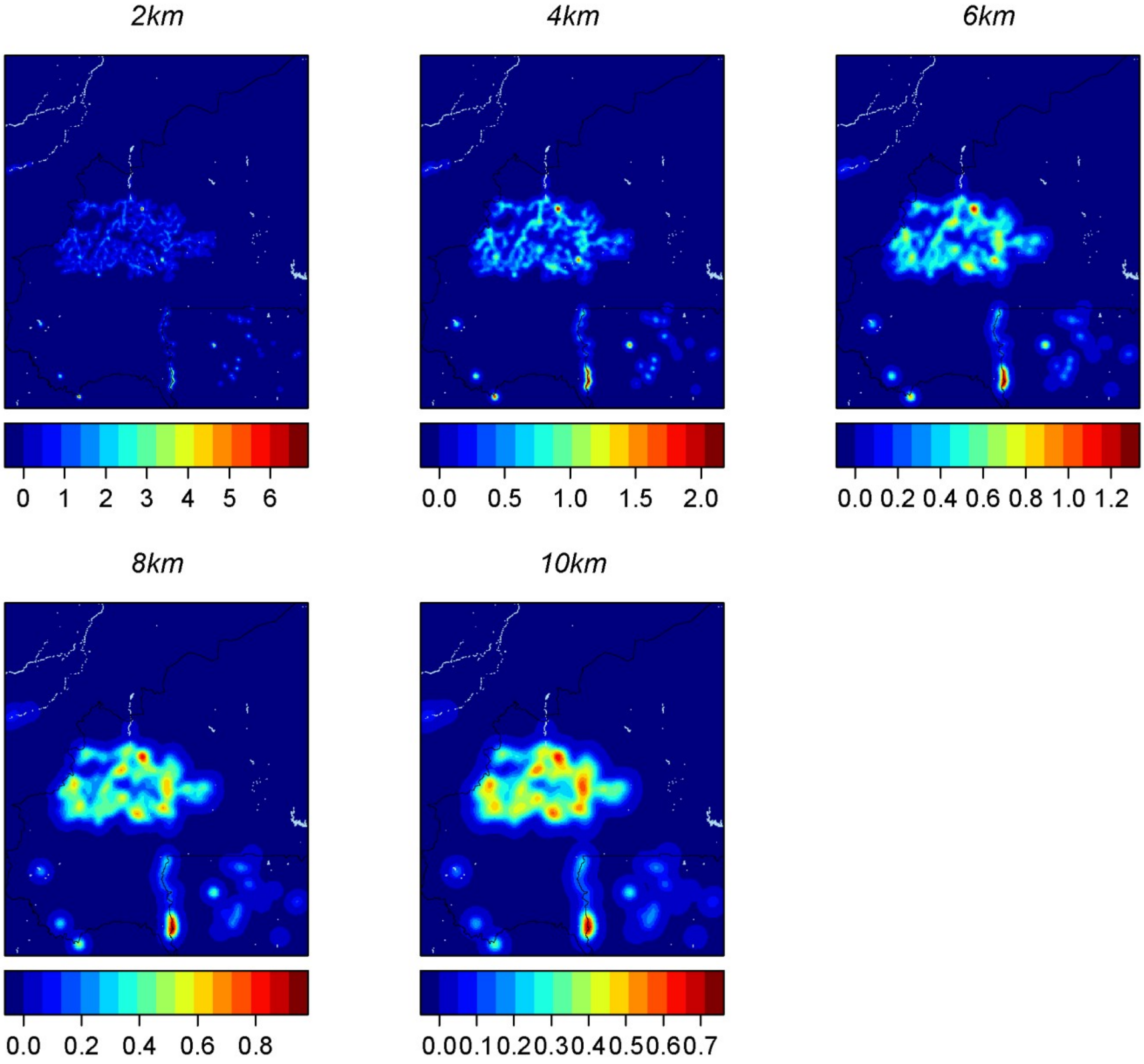
2km 4km 6km 8km 10km

Figure S4- 4: Bias grids for the MaxEnt model

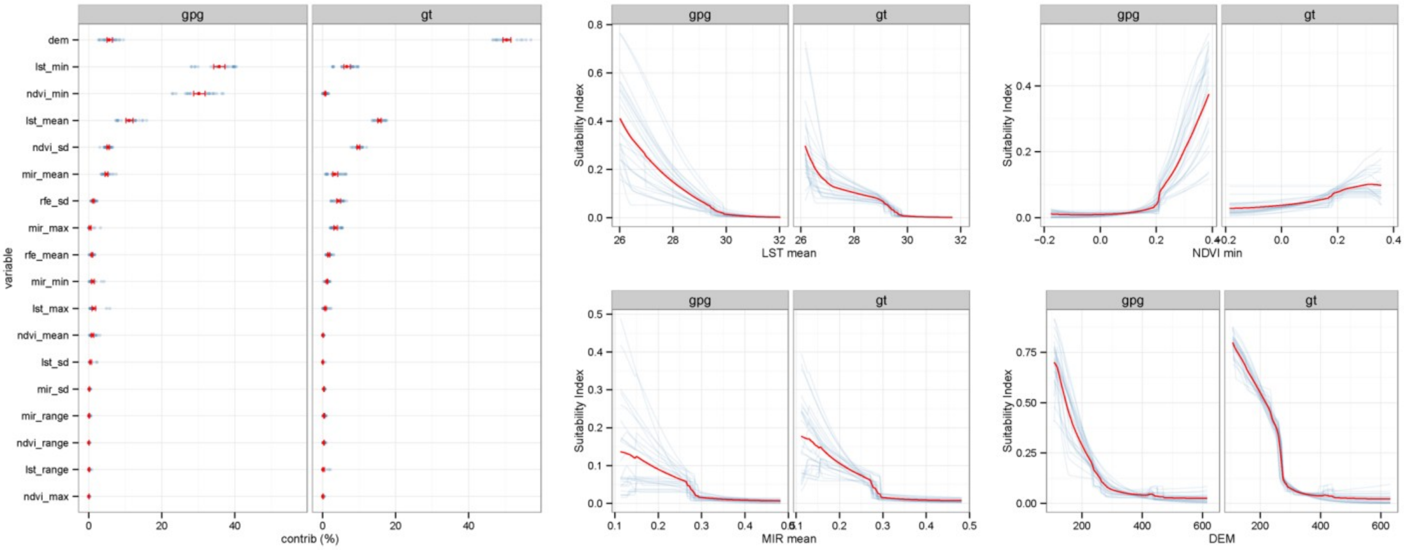

Figure S4- 5: Variables contribution and responses curves of the main variables in the MaxEnt models

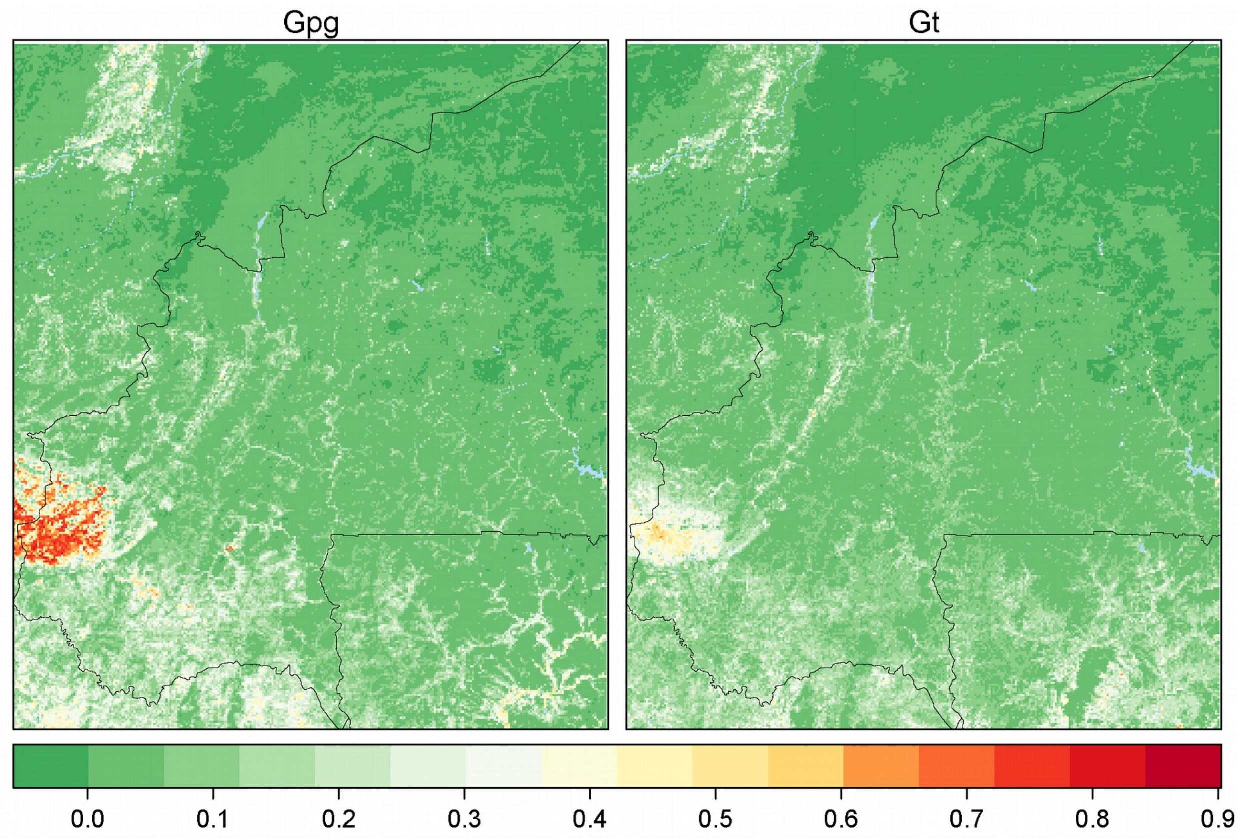

Figure S4- 6: Uncertainty grid for the habitat suitability index model