 Doi: 10.1111/j.1365-2915.2008.00747.x

Land cover and tsetse fly distributions in sub-Saharan Africa

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Abstract. This study aims to provide trypanosomiasis-affected countries with standardized datasets and methodologies for mapping the habitat of the tsetse fly (*Glossina* spp., the disease vector) by customizing and integrating state-of-the-art land cover maps on different spatial scales. Using a combination of inductive and deductive approaches, land cover and fly distribution maps are analysed in a geographic information system (GIS) to estimate the suitability of different land cover units for the three groups (subgenera) of *Glossina.* All land cover datasets used for and produced by the study comply with the Land Cover Classification System (LCCS). At the continental scale, a strong correlation between land cover and tsetse habitat is found for both the *fusca* and *palpalis* groups, whereas a weaker correlation found for the *morsitans* group may be indicative of less restrictive ecological requirements. At the regional and national levels, thematic aggregation of the multi-purpose Africover datasets yielded high-resolution, standardized land cover maps tailored for tsetse habitat for eight East African countries. The national maps provide remarkable spatial resolution, thematic detail and geographical coverage. They may be applied in subsequent phases of tsetse and trypanosomiasis control projects, including the planning of entomological surveys, actual tsetse control operations and planning for land use in reclaimed areas. The methodology and datasets discussed in the paper may have applications beyond the tsetse and trypanosomiasis issue and may be used with reference to other arthropod vectors, vector-borne and parasitic diseases.

Key words. *Glossina*, Africover, GIS, GLC2000, habitat, LCCS, multiple resolution, Programme against African Trypanosomiasis.

Introduction

Trypanosomiases transmitted by tsetse flies (genus *Glossina*) continue to constitute a major factor limiting rural development in vast areas of tropical Africa. A renewed interest in the tsetse and trypanosomiasis problem is reflected in several programmes at national, regional and international level. Novel initiatives comprise the Programme against African Trypanosomiasis (PAAT) and the Pan African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC). The PAAT provides a forum that aims to facilitate the harmonizing and coordination of the activities of its four mandated international organizations (the Food and Agriculture Organization of the United Nations [FAO], the World Health Organization [WHO], the International Atomic Energy Agency [IAEA] and the Inter-African Bureau for Animal Resources of the African Union [AU-IBAR]), in relation to tsetse, human and animal trypanosomiasis and associated sustainable agriculture and rural development. PATTEC is action-focused and AU-led, and stems from the decision by the African Heads of State and Government to collectively embark on a campaign to render Africa tsetse-free through the creation and subsequent expansion of tsetse-free zones.

Strategies to control or eventually eliminate the problem posed by trypanosomiasis must rely on tsetse ecology and

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suitable fly distribution data. In this context, tsetse habitat maps are essential. Unfortunately, our knowledge of the distribution and abundance of flies is still inadequate for the planning of intervention strategies on a large scale. One way to overcome this is to explore how tsetse habitat mapping may be based on readily available land cover datasets.

The importance of land cover was recognized by early tsetse investigators, who used vegetation and other environmental parameters, such as meteorological and altitude data, to estimate the geographic distribution limits of many species of tsetse (Ford & Katondo, 1977a, 1977b; Katondo, 1984). More recently, remote sensing and geographic information system (GIS) techniques have proved promising and powerful in describing tsetse distribution at continental and regional scales (Rogers & Randolph, 1993; Rogers & Williams, 1994; Hay *et al.*, 1996; Rogers *et al.*, 1996; Rogers & Robinson, 2004). There is also a growing amount of literature on the application of satellite imagery for tsetse habitat mapping at a higher spatial resolution (Kitron *et al.*, 1996; de la Rocque *et al.*, 2001; De Deken *et al.*, 2005; Mahama *et al.*, 2005; Bouyer *et al.*, 2006). Despite these advances, the detail and accuracy of most available maps of tsetse distribution are still not adequate for the challenges posed by the planning and implementation of field projects on a large scale (e.g. PATTEC).

Land cover is usually considered in the type of studies described above, but has not previously been analysed *per se* as an indicator of habitats suitable for tsetse. Yet land cover directly or indirectly relates to all the main factors in tsetse ecology, such as global and local climate, vegetation cover and availability of wild or domestic feeding hosts. A new generation of high-resolution, multi-purpose land cover maps, compliant with the Land Cover Classification System (LCCS) (Di Gregorio & Jansen, 2000), is currently available for several African countries. The FAO project Africover produced national maps of 10 countries in East Africa, eight of which are affected by tsetse flies and trypanosomiasis.

The purpose of this study is to examine at different scales the relationship between land cover and tsetse distribution. A further important objective is the definition of a standardized, LCCS-compliant legend for tsetse habitat mapping in order to promote harmony between prospective, large-scale tsetse control projects and to facilitate the use of both available and forthcoming multi-purpose land cover datasets.

Materials and methods

The relationship between tsetse habitat and land cover is analysed at two spatial scales. At continental level, a medium-resolution land cover map is used: the Land Cover of Africa for the year 2000 (Mayaux *et al.*, 2004). At regional and national levels, higher-resolution datasets for eight East African countries are derived from the Africover database. Both types of dataset utilize the LCCS, developed by the FAO and the United Nations Environment Programme (UNEP). The LCCS is based on independent and universally valid diagnostic criteria rather than on a predefined set of land cover classes; it describes land cover according to a hierarchical series of classifiers and attributes and separates vegetated from non-vegetated surfaces, terrestrial from aquatic/flooded areas, and cultivated or managed from natural and semi-natural regions. The system also allows the physiognomy, cover, height, spatial distribution, leaf type and phenology of the vegetation to be described. The LCCS is the only universally applicable classification system for land cover in operational use and is currently in the process of gaining International Organization for Standardization (ISO) approval.

Continental level

The Global Land Cover 2000 (GLC2000) project provided a harmonized land cover database for the whole globe for the year 2000. A regional product for Africa was created under the framework of GLC2000. This has more thematic classes than previously published land cover maps of Africa and presents the most spatially detailed view yet published at continental scale. It is based on daily data collected by the VEGETATION sensor on the SPOT 4 satellite, acquired between 1 November 1999 and 31 December 2000. In addition, data from other sensors were used in an attempt to resolve specific challenges, particularly in regions with persistent cloud cover, especially in equatorial zones (synthetic aperture radar [SAR] on the JERS-1 and ERS satellites), and in the identification of urban areas (Defence Meteorological Satellite Program [DMSP] Operational Linescan System [OLS])). The spatial resolution of GLC2000 is approximately 1 km at the equator and it documents a total of 27 land cover categories. In this paper we refer to the part of Global Land Cover 2000 that pertains to regional Africa simply as GLC2000. Countries and territories in northern Africa (Algeria, Egypt, Libya, Morocco, Tunisia and Western Sahara) and Madagascar are free from tsetse fly and thus are excluded from our analysis.

Based on both their morphological and ecological specifics, the 31 tsetse (*Glossina*) species and subspecies accord to three subgenera or groups, the subgenus *Austenina* (*fusca* group), the subgenus *Nemorhina* (*palpalis* group) and the subgenus *Glossina* s.s. (*morsitans* group) (Newstead *et al.*, 1924; Jordan, 1993). For this study, the spatial distribution of the three groups is derived from the predicted areas of suitability (PAS) for tsetse flies as produced in 1999 by the FAO−PAAT Information System (Gilbert *et al.*, 1999; Wint & Rogers, 2000). These areas were defined by combining historical data on tsetse distribution (Ford & Katondo, 1977a, 1977b) and more recent entomological datasets with environmental predictor variables, including remotely sensed data (e.g. normalized difference vegetation index and land surface temperature), elevation and demographic data on both human and cattle populations. The PAS resolution approximates 5 km at the equator and covers the whole of sub-Saharan Africa. The maps reflect the probability of environmental suitability at both group (subgenus) and species level. For our analysis, the probability threshold of 50% is applied to discriminate suitable from unsuitable areas (see Fig. 1).

For each tsetse group, the land cover units are ranked with an 'index of suitability' ranging from 3 to 0, corresponding to four broad categories of suitability (high, moderate, low, nil). The proportion of suitable areas within each unit is derived by overlaying PAS and GLC2000; thresholds for the definition of the

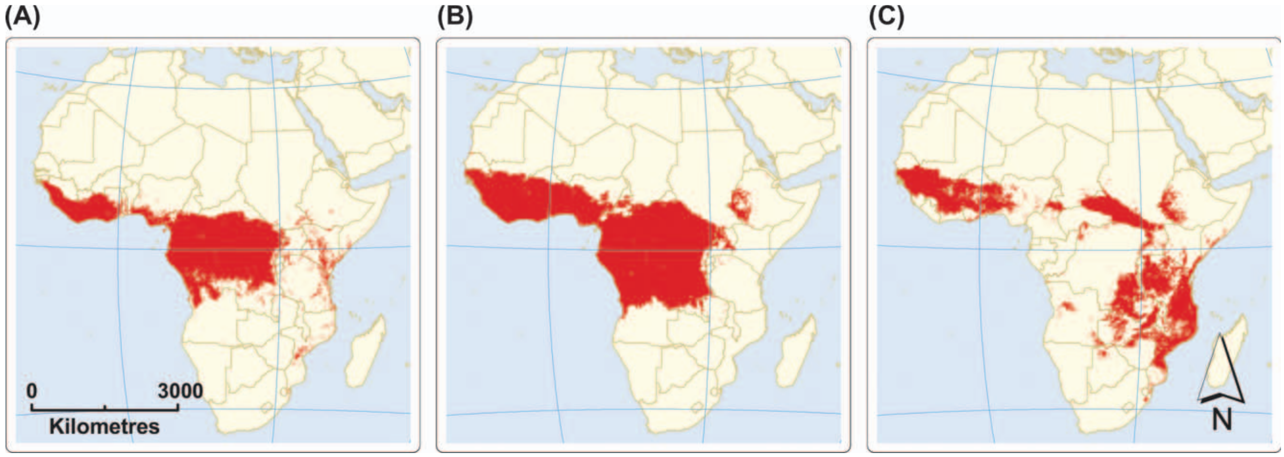

Fig. 1. Predicted areas of suitability, in red, for the three tsetse fly groups (subgenera) in Africa (1999). (A) *Fusca* group, subgenus *Austenina*. (B) *Palpalis* group, subgenus *Nemorhina*. (C) *Morsitans* group, subgenus *Glossina* s.s. Data provided by the Programme against African Trypanosomiasis-Information System (PAAT-IS); the maps reflect the probability of environmental suitability for tsetse flies; for the present study, the threshold of 50% is applied to discriminate suitable from unsuitable areas. The maps are projected in a Lambert Azimuthal equal area projection.

category of suitability are displayed in Table 1. This approach for the definition of a species' environmental requirements relies on the information that is implicit in habitat maps and can be defined as an 'inductive approach' (Corsi *et al.*, 2000).

Regional and national levels

At the regional and national levels, the analysis uses the Africover land cover maps. This dataset is based on visual interpretation of Landsat satellite imagery acquired between 1994 and 2001 by the thematic mapper (TM) sensor, as well as ground data and expert knowledge. Data on 10 countries are presently available in the Africover repository, eight of which are affected by trypanosomiasis (years in brackets refer to the period of acquisition of satellite images): Burundi (1999); Democratic Republic of the Congo (2000–01); Kenya (1995); Rwanda (1999); Somalia (1995–98); Sudan (1994–99); Tanzania (1997), and Uganda (2000–01). These datasets are all included in the East Africa module, the first Africover Project operational component. The resulting maps are in vector format, with scales varying from 1 : 250 000 to 1 : 100 000 (the latter is used for small countries or specific areas). They apply the LCCS and their legend includes more than 500 classes, plus mutual combinations of up to three classes that bring the total number of pure and mixed codes beyond 2000.

Table 1. Categories of suitability of land cover classes for tsetse fly.

Predicted area of presence within the class (%)	Category of suitability for tsetse	Index of suitability
> 50	High	3
> 25 and ≤ 50	Moderate	2
> 5 and ≤ 25	Low	1
≤ 5	Nil	0

The purpose of the analysis at regional and national levels is twofold: firstly, the Africover legend needs to be simplified through thematic aggregation of classes in order to define a customized LCCS-compliant legend for tsetse habitat mapping and, secondly, the potential of these newly generated maps to describe and depict tsetse habitat is evaluated.

A legend with 26 units aggregates the original classes of the Africover maps and represents the land cover units relevant to tsetse ecology. Although it was derived from land cover maps of East Africa, the legend is applicable to future LCCS-compliant, multi-purpose datasets. The main guiding principle in the definition of the legend is to fully exploit the detailed description of the natural vegetation, a critical factor in tsetse ecology and habitat demarcation; 17 of the 26 classes describe natural, primarily vegetated areas, either terrestrial or aquatic. In the LCCS, land cover categories are defined by a combination of independent diagnostic criteria, the so-called classifiers, which are hierarchically ordered. In our study, two major classifiers are used to discriminate the classes: 'life form' and 'cover'. These respectively describe the structure and density of the vegetation, both key factors for tsetse habitat. The 'life form' of a plant or a group of plants is defined by its physiognomic aspect: herbaceous life forms are distinguished from woody life forms, which are, in turn, subdivided into 'trees' (higher than 5 m) and 'shrubs' (lower than 5 m). A special class, called 'woody', includes plants in the 2–7 m height range when no further definition into trees or shrubs is specified. The 'cover' classifier refers to the percentage of surface covered by a layer of plants (Eiten, 1968); a distinction is made between 'closed' (> 60–70%), 'open' (between 60–70% and 10–20%) and 'sparse' (< 10–20% but > 1%) cover. More details on these and other aspects of the classification system used can be found in the LCCS manuals (Di Gregorio & Jansen, 2000; Di Gregorio, 2005).

The 26 land cover classes are ranked to determine their suitability to support each of the three tsetse fly groups. The scores are derived from the literature and opinions of experts (deductive approach). The suitability of a land cover class as a predictor of tsetse fly habitat is based on its intrinsic features, with no a priori assumption on how such land cover classes shape the landscape overall pattern.

Comparison between the two approaches

The results of the analyses at the continental (GLC2000) and regional levels (Africover) are matched to determine how closely the results of the two approaches correspond. Although GLC2000 and Africover are both LCCS-compliant, it is not possible to directly link the 27 (original) land cover classes of GLC2000 to the 26 (customized) Africover classes. However, the relationship between the two classifications can still be defined statistically through correspondence analysis across the eight countries included in the regional study. This allows the suitability for tsetse of the Africover classes to be estimated as an area-weighted average of the suitability established for the corresponding GLC2000 classes.

Results

Continental level

Results are given in Table 2. The tsetse habitat within each land cover unit is expressed in thousands of square km; the table also shows the class contribution to the total suitable area as well as the proportion of suitable habitat within each unit. An index of tsetse suitability is derived from the area suitable for tsetse inside the class, using the thresholds indicated in Table 1. In the first section of Table 2, relevant to the *fusca* group, the category 'others' forms an aggregation of four GLC2000 classes that describe non-vegetated areas that are very unsuitable as tsetse fly habitat: 'bare rock'; 'stony desert'; 'sandy desert and dunes', and 'salt hardpans'.

The relative amount of the land cover units within the habitat of each of the three subgenera of *Glossina* is presented in Fig. 2. The sequence of the classes here follows the proportion of tree cover in the GLC2000 classes as measured on the vegetation continuous fields product (Hansen *et al.*, 2003; Mayaux *et al.*, 2004), derived from the moderate-resolution imaging spectroradiometer (MODIS).

The results for the *fusca* group show closed forest as the common habitat for these flies. Trees are key to the first five classes in Table 2, accounting for over 80% of the total area suitable for *fusca* group flies. Interestingly, the analysis highlights the high suitability of some forested land cover units occupying only a small proportion of the *fusca* habitat (e.g. 'swamp forest', 'submontane forest' and 'degraded evergreen lowland forest'). The 16% of 'cities' classified as potentially suitable for the *fusca* group gives an indication of the error that can affect the less abundant GLC2000 classes.

For the *palpalis* and *morsitans* groups, Table 2 displays only land cover categories that account for a minimum of 1% of total tsetse distribution.

Broadly speaking, members of the *palpalis* group are strongly associated with areas of high humidity and deep shade. The analysis shows that all land cover units classified as highly suitable for this group are forests or mixed classes with a forest component. It is interesting to note that the GLC2000 class 'mosaic forest/savannah' mainly describes tree formations, called 'gallery forests', that have developed along river banks in the middle of shrub or grass vegetation; this class covers large portions of the transition zone to the north of the Congo basin and falls almost entirely (93%) within the predicted distribution of the *palpalis* group. Tsetse species belonging to the subgenus *Nemorhina* are commonly referred to as 'riverine' species and this characteristic is confirmed by the current results. However, the riparian vegetation often covers only a narrow band a few metres wide along river banks and the resolution of GLC2000 (around 1 km) is mostly insufficient to depict these types of formation correctly. The habitat of riverine tsetse flies is better described by the Africover maps used for the analysis at regional and national levels. Notwithstanding its preference for forests, the *palpalis* group's chosen habitat comprises a significant proportion of less densely vegetated areas such as 'deciduous woodland' and 'deciduous shrubland with sparse trees', commonly referred to in the tsetse literature as 'woodland savannah', 'tree savannah' and 'shrub savannah'. These classes, although classified as 'moderately suitable', represent around 30% of the total habitat of the group. In this regard, it is worth mentioning that a single species, *Glossina tachinoides* Westwood, although it belongs to the group of riverine flies, extends its habitat into more arid environments and contributes to the conspicuous presence of savannahs in the overall land cover profile of the group.

For the *morsitans* group, the important role of savannah habitats is clearly apparent: 'deciduous woodland' and 'deciduous shrubland with sparse trees' account for over 50% of total distribution. One major difference between the *morsitans* group and the *fusca* and *palpalis* groups is that six land cover units are identified as highly suitable (i.e. with an index of suitability = 3) for the latter two groups, whereas only one single class ('deciduous shrubland with sparse trees') is classified as such for the *morsitans* group. The *morsitans* group shows a weaker statistical correlation between habitat suitability and land cover typology, as shown by the chi-square statistics for the three separate tsetse fly groups (Table 3). As indicated in Table 3, the *fusca* group shows a strong correlation (56%) with land cover units, the *palpalis* group shows a slightly weaker relationship (47%) and the *morsitans* group a much lower correlation (19%).

Regional and national levels

The Africover-derived legend in 26 land cover classes and the assigned suitability score for each of the three tsetse groups (depicted in Table 4 as 'estimated suitability') provide an accurate and consistent delineation of all major fly habitats. As already indicated, the underlying criteria are based on a review of the most comprehensive literature (Challier, 1982; Pollock, 1982; Jordan, 1986; Leak, 1998). For both the *fusca* and *palpalis* groups, a high suitability is attributed to just two classes, both characterized by a closed cover of trees (i.e. 'forest' and 'closed swamp'). For the *morsitans* group, 'woodland savannah' is considered the most

Table 2. Land cover of tsetse habitat in sub-Saharan Africa. Tsetse habitat is derived from the predicted areas of suitability for tsetse (1999), provided by the Information System of the Programme against African Trypanosomiasis (see Fig. 1); the source of land cover is the Land Cover of Africa for the year 2000 (Mayaux *et al.*, 2004), by the Joint Research Centre of the European Commission. The index of suitability in the last column is derived from the percentage of surface affected by tsetse inside the land cover class, using the thresholds indicated in Table 1. For the *palpalis* and *morsitans* groups, only land cover categories accounting for a minimum of 1% of the habitat are reported.

Land cover class	Surface affected by tsetse (km^2 × 10^3)	Percentage of the class in the total tsetse distribution area	Percentage of surface affected by tsetse inside the class	Index of suitability for tsetse (0–3)
Fusca group				
Closed evergreen lowland forest	1639	39.7	95.5	3
Mosaic forest/croplands	628	15.2	82.9	3
Deciduous woodland	458	11.1	15.9	1
Mosaic forest/savannah (gallery forests)	422	10.2	61.5	3
Closed deciduous forest (*miombo*)	175	4.2	14.8	1
Open deciduous shrubland	168	4.1	16.4	1
Swamp forest	134	3.2	100.0	3
Submontane forest (900–1500 m)	107	2.6	80.4	3
Deciduous shrubland with sparse trees	107	2.6	6.4	1
Closed grassland	95	2.3	11.1	1
Croplands (> 50%)	51	1.2	2.3	0
Open grassland with sparse shrubs	39	0.9	2.4	0
Degraded evergreen lowland forest	33	0.8	94.9	3
Open grassland	19	0.5	1.7	0
Montane forest (> 1500 m)	15	0.4	21.8	1
Mangrove	13	0.3	46.4	2
Sparse grassland	10	0.3	0.7	0
Swamp bushland and grassland	8	0.2	7.5	1
Croplands with open woody vegetation	5	0.1	0.5	0
Cities	3	0.1	16.4	1
Irrigated croplands	1	0.0	4.1	0
Others	2	0.0	–	–
Total (*fusca* group)	4132	100.0		
Palpalis group				
Closed evergreen lowland forest	1675	26.1	97.5	3
Deciduous woodland	1283	20.0	44.6	2
Mosaic forest/croplands	708	11.0	93.4	3
Deciduous shrubland with sparse trees	702	10.9	41.9	2
Mosaic forest/savannah (gallery forests)	644	10.0	93.8	3
Closed deciduous forest (*miombo*)	320	5.0	26.9	2
Croplands with open woody vegetation	266	4.1	28.0	2
Open deciduous shrubland	219	3.4	21.3	1
Croplands (> 50%)	158	2.5	7.2	1
Swamp forest	134	2.1	100.0	3
Submontane forest (900–1500 m)	113	1.8	84.6	3
Closed grassland	96	1.5	11.2	1
Others	98	1.6	–	–
Total (*palpalis* group)	6415	100.0		
Morsitans group				
Deciduous woodland	1297	32.0	45.1	2
Deciduous shrubland with sparse trees	923	22.8	55.1	3
Closed deciduous forest (*miombo*)	407	10.0	34.3	2
Croplands (> 50%)	371	9.2	16.8	1
Mosaic forest/savannah (gallery forests)	205	5.1	29.8	2
Mosaic forest/croplands	203	5.0	26.7	2
Croplands with open woody vegetation	192	4.7	20.1	1
Open deciduous shrubland	124	3.1	12.1	1
Closed grassland	102	2.5	11.9	1
Closed evergreen lowland forest	65	1.6	3.8	0
Open grassland with sparse shrubs	64	1.6	4.0	0
Others	100	2.0	–	–
Total (*morsitans* group)	4052	100.0		

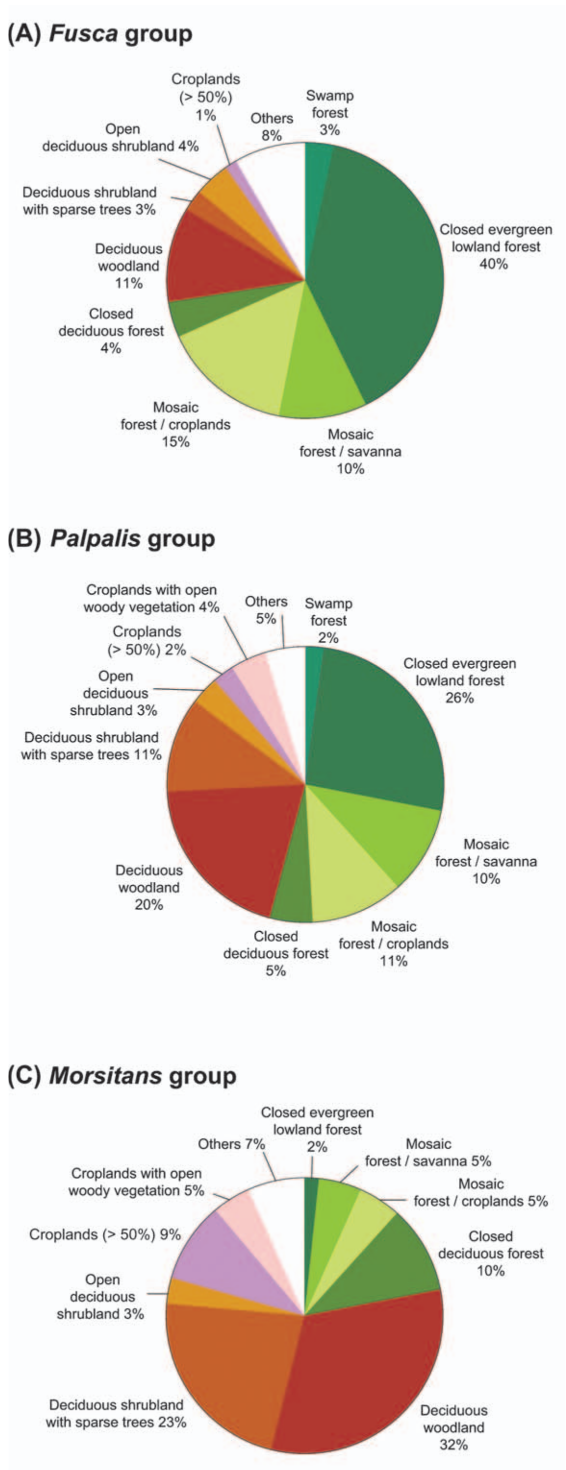

Fig. 2. Land cover of the habitat of the three subgenera of *Glossina*. (A) *Fusca* group, subgenus *Austenina*. (B) *Palpalis* group, subgenus *Nemorhina*. (C) *Morsitans* group, subgenus *Glossina* s.s. (see Table 2). The source of land cover is the Land Cover of Africa for the year 2000 (Mayaux *et al.*, 2004); tsetse habitat is derived from the predicted areas of suitability for tsetse provided by the Information System of the Programme against African Trypanosomiasis (PAAT-IS).

suitable habitat. It should be noted here that the lack of standardization in the description of tsetse-related vegetation types in the available literature often complicates the assignment of suitability scores: for some vegetation units, correspondence with standardized land cover classes is reasonably simple to establish, but for other units, that are much less explicitly described, estimates require support from expert opinions. With reference to the estimates presented in Table 4, it should be noted that some classes (e.g. 'thicket' and 'shrubs on flooded land', both characterized by shrubs as the main layer) may include secondary layers of sparse vegetation (e.g. trees for the two examples above), which strongly influence their suitability as habitat. This means, for instance, that the class 'thicket with sparse trees', as defined by the LCCS, is in this legend incorporated within the class 'thicket'; the suitability for tsetse of the latter class is evaluated accordingly.

Comparison between the two approaches

Matching the Africover maps with GLC2000 permitted verification of the estimated suitability of the standardized land cover classes (Table 4). Given the assumptions that underlie the estimates and the resolution of the PAS and GLC2000 on which the calculations rely, the fit between estimated suitability and 'calculated suitability' is remarkable, with a match of 73% of classes for the *fusca* group and 77% for the *palpalis* group. For the *morsitans* group, the interpretation of the results is more complex: for most of the classes, calculated suitability differs from estimated suitability. The *morsitans* group stands out again because its highest value of calculated suitability is 30.4%, compared with 82.0% and 86.0% for the *fusca* and *palpalis* groups, respectively. This may be associated with less stringent ecological requirements on the part of the *morsitans* group and with the discontinuous pattern of its distribution, resulting in a weaker and fuzzier correlation between land cover and habitat. It may be reasonably assumed that understanding of the ecology of the *morsitans* group would greatly benefit from the availability of finer-resolution tsetse maps to assist the validation of estimates.

Figure 3 provides an example of a possible way to represent the results, with two maps of land cover suitability for tsetse species of the *palpalis* group in the area around Kampala (Uganda). The first map is derived from the GLC2000 for Africa and the second is based on the Africover database (Africover multipurpose land cover database for Uganda, 2000–01). The suitability of GLC2000 classes is extracted from the index of suitability in Table 2, and that for Africover from the literature-based values in Table 4 (estimated suitability). The concordance between the two maps illustrates the convergence of the deductive and inductive approaches and the potential of multi-resolution analysis.

Discussion

The current study benefits from the most recent and detailed land cover and tsetse habitat datasets available. More accurate

Table 3. Shared variance (r^2) between the habitat of the three tsetse fly groups and land cover classes of the Land Cover of Africa for the year 2000 (chi-square test).

Tsetse group	r^2
Fusca	0.56
Palpalis	0.47
Morsitans	0.19

information still should become available in the future. At the continental level, the Globcover project is currently targeting the production of a 300-m resolution land cover map of the world for the year 2005, using satellite imagery acquired by the Medium Resolution Imaging Spectrometer (MERIS) sensor on the Envisat environmental satellite (European Space Agency). This will substantially improve the spatial detail of GLC2000. However, from the perspective of the present study, which aims to delineate the land cover preferences of the tsetse fly, the main limitation remains the resolution and accuracy of the tsetse habitat maps available, which have never undergone extensive field validation and for which updating and upgrading at the continental level would require longterm studies and investments. Ongoing large-scale projects, such as the PATTEC initiative, might provide additional information and data, which in turn might contribute towards refining the findings of this study.

The results of the analysis at continental level demonstrate the central role of land cover in shaping the habitat of tsetse flies in Africa. They also demonstrate that GLC2000 units are capable of accurately translating the different ecological requirements of the three fly groups. Furthermore, the analysis highlights the limitations inherent in the low spatial resolution of the available global datasets.

The Africover maps offer a unique opportunity to access high-resolution, standardized land cover maps of an increasing number of trypanosomiasis-affected countries. The high number of classes used in Africover still hinder direct application, but the inherent flexibility and modularity of the LCCS allow for the derivation of a simplified legend customized for tsetse fly habitat demarcation and, indirectly, for building strategies for tsetse and trypanosomiasis interventions. Several ecological variables known to affect environmental suitability for tsetse flies are not explicitly considered in the estimates (e.g. host availability, climatic conditions, vicinity of water bodies, etc.). Nonetheless, these factors may be assumed to be strongly correlated with land cover.

Although the comparison between estimated and calculated suitability gave a positive outcome, the mismatches between

Table 4. Estimated and calculated suitability of standardized land cover classes for the three tsetse fly groups. Estimates are based on the available literature (deductive approach); the calculated suitability relies on the correspondence between GLC2000 and Africover datasets in East Africa and on the results of the analysis at continental level (inductive approach) (see Table 2).

	Fusca group		*Palpalis* group		*Morsitans* group	
Class name	Estimated suitability (0–3)	Calculated suitability (%)	Estimated suitability (0–3)	Calculated suitability (%)	Estimated suitability (0–3)	Calculated suitability (%)
Forest plantations and tree plantations	1	13.0	2	30.9	1	19.0
Shrub crops	1	40.2	1	48.6	1	15.8
Herbaceous crops	0	11.0	1	20.2	0	16.1
Vegetated urban areas	1	9.5	2	16.0	1	16.6
Forest	3	82.0	3	86.0	2	7.4
Woodland savannah	1	16.1	2	34.6	3	23.4
Closed woody vegetation	1	8.6	2	27.7	2	20.8
Open woody vegetation	1	6.2	1	18.8	2	20.8
Thicket	1	5.4	1	10.7	2	8.2
Shrubland	0	8.6	1	19.9	2	16.4
Grassland	0	2.1	0	4.7	0	5.6
Shrub savannah	0	2.6	1	5.7	1	6.6
Tree savannah	0	5.7	1	17.6	2	18.3
Sparse trees	0	1.4	0	6.3	1	7.4
Sparse shrubs	0	0.5	0	0.8	0	1.2
Sparse herbaceous vegetation	0	0.3	0	0.2	0	0.3
Rice fields	0	5.0	0	12.3	0	15.2
Closed swamp	3	67.5	3	72.2	1	6.5
Open swamp	2	16.8	2	30.4	2	18.5
Woody vegetation on flooded land	1	6.5	2	19.1	1	30.4
Shrubs on flooded land	1	15.1	2	33.0	1	28.0
Herbaceous vegetation on flooded land	0	9.4	1	21.7	0	23.3
Artificial surfaces	0	12.1	0	20.2	0	13.2
Bare soil	0	0.1	0	0.2	0	0.2
Water bodies	0	3.4	0	4.2	0	1.7
Snow	0	0.8	0	0.1	0	0.5

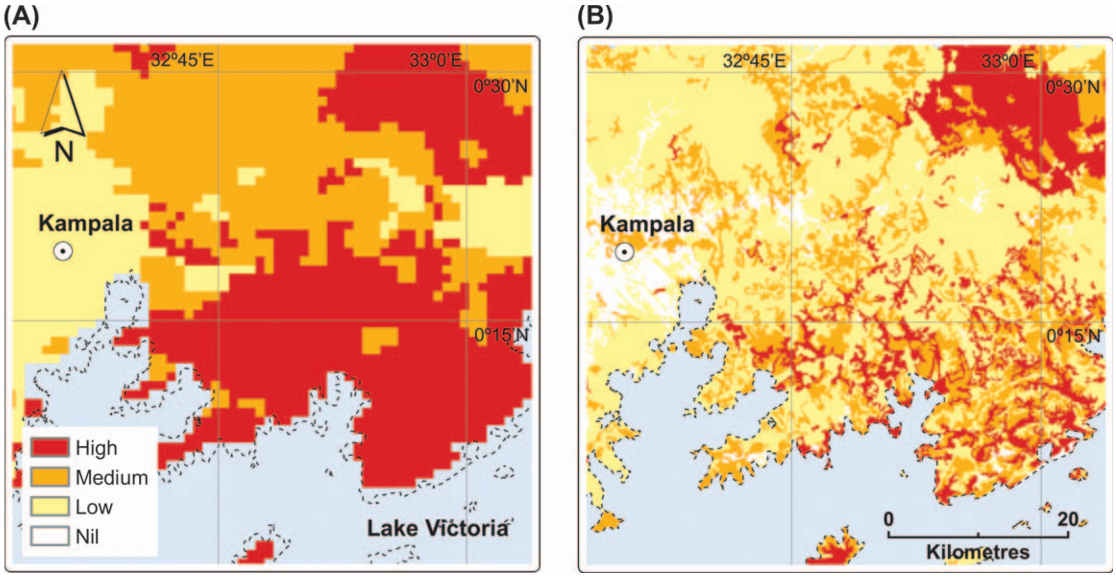

Fig. 3. Land cover suitability for tsetse fly species of the *palpalis* group in the area around Kampala (Uganda). (A) Excerpt from the map derived from the Land Cover of Africa for the year 2000 (Mayaux *et al.*, 2004) (approximate scale 1 : 10 000 000); classes of suitability result from the analysis of tsetse habitat and land cover at continental level (inductive approach). (B) Map derived from the Africover multi-purpose land cover database for Uganda 2000–01 (approximate scale 1 : 100 000); classes of suitability are based on a review of the literature (deductive approach).

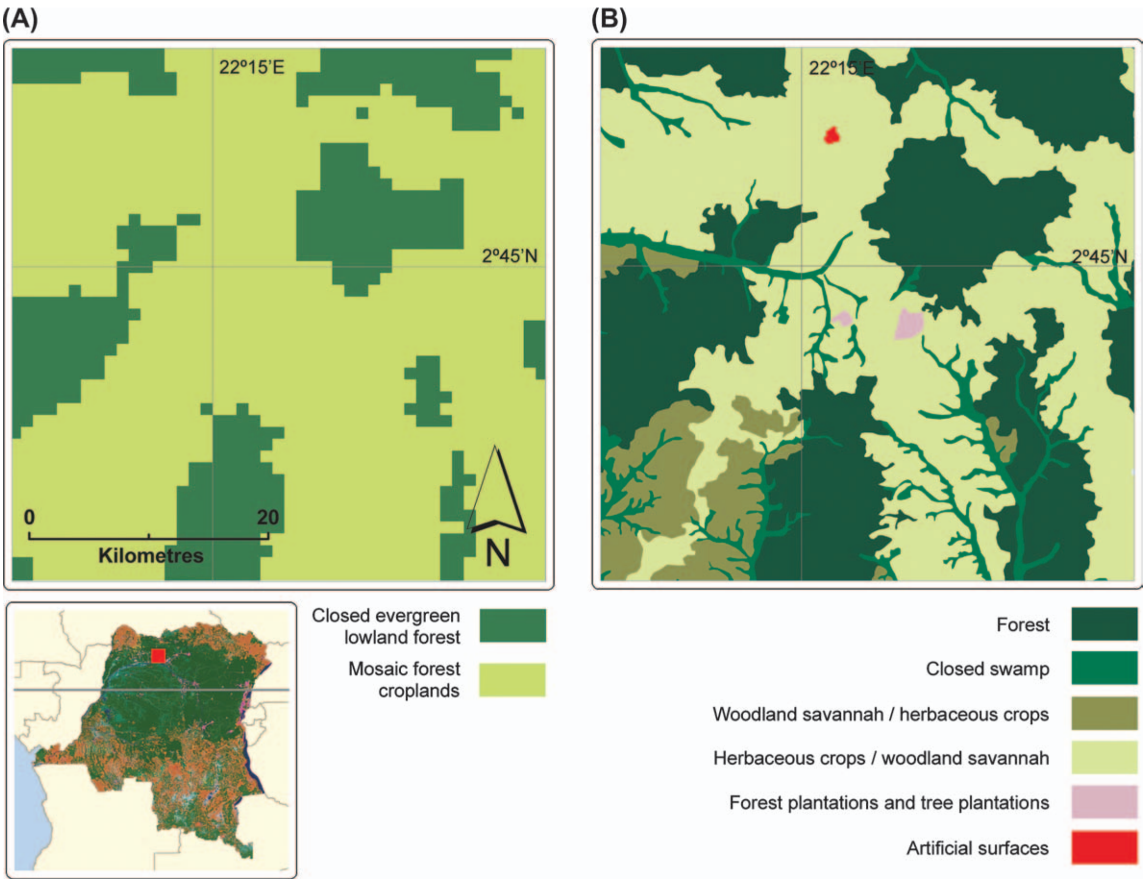

Fig. 4. The encroachment of agriculture on native vegetation in an area in the Congo River basin, depicted by existing land cover datasets. (A) Global Land Cover of Africa for the year 2000 (Mayaux *et al.*, 2004). (B) Africover land cover of the Democratic Republic of the Congo (2000–01). For this study, the classes of Africover are tailored for tsetse habitat mapping.

GLC2000 and Africover (Torbick *et al.*, 2005), as well as the intrinsic limitations of applying the low-resolution datasets (GLC2000 and PAS), do not permit this approach to be used for the validation of literature-based estimates. This holds especially true for the *morsitans* group. However, a more rigorous validation is hampered by a range of practical and conceptual difficulties. Foremost among the practical problems is the lack of consistent field-based information on the present distribution of tsetse flies in Africa. Further complications are related to intra-group differences in habitat requirements among the 31 species and subspecies of tsetse flies. Although the broad definitions of 'forest', 'riverine' and 'savannah' flies are commonly accepted for the *fusca*, *palpalis* and *morsitans* groups, respectively, the ecology and spatial distribution of some of the species within each group vary considerably (e.g. both *Glossina longipennis* Corti, of the *fusca* group, and *Glossina tachinoides*, of the *palpalis* group, require a more arid environment than do other species in the same groups). The problem is further compounded by the ability of flies to disperse from their resting and breeding sites in search of feeding sources (at least twice per week). There are also seasonal variations associated with temperature and humidity fluctuations in the overall tsetse belt distribution limits. These considerations help explain why only broad, qualitative suitability classes are applied in this study.

Conclusions

The role of vegetation, along with those of climate and availability of hosts, as a key element in the suitability of habitat for tsetse, has long been recognized. More recently, the development of remote sensing and GIS techniques have provided novel tools to predict the distribution of flies at continental and regional levels, using low-resolution satellite imagery. Other research has demonstrated the potential of high-resolution images for mapping the habitat of *Glossina* on a local scale, as well as in increasingly larger areas. However, the costs involved in the purchase and processing of high-resolution datasets are often beyond the scope of large-scale, area-wide tsetse and trypanosomiasis control projects. The present study demonstrates the potential of standardized, multi-purpose land cover maps, released in the public domain, for deriving novel, detailed maps of habitat suitable for tsetse at a much improved scale, which subsequently offers unprecedented opportunities to assist tsetse habitat mapping across and within countries. As an illustration, some of the outputs of the current study have been provided to the tsetse and trypanosomiasis control units of countries involved in the PATTEC initiative, namely, Uganda and Kenya, both of which are carrying out baseline entomological surveys. The maps may help to streamline and rationalize field data collection exercises, which, in turn, may provide an opportunity to further validate the results obtained by the present study. The standardization of the legend for tsetse habitat will also permit the customization of forthcoming datasets produced in compliance with the LCCS (e.g. the land cover maps of Burkina Faso, Gambia and Senegal, in production under the framework of the Global Land Cover Network [GLCN], and the updated land cover map of Uganda for 2005, by the Ugandan National Forestry Authority). Land cover maps should also be used to study interactions between tsetse control and changes in land use, to monitor ecological properties at landscape scale (Reid *et al.*, 2000) and, possibly, to define mitigation measures that may redress any negative environmental impacts (Reid *et al.*, 1997; Wilson *et al.*, 1997).

The outcomes of the present study may also find direct application in ongoing research projects, such as the Wellcome Trust-supported 'Fragfly', which is studying changes in the distribution and density of tsetse resulting from human encroachment, and, subsequently, repercussions on the epidemiology and control of trypanosomiasis. Figure 4 illustrates how the expansion of agriculture, as depicted by both GLC2000 and Africover, erodes the native forest habitat, thus altering land cover suitability for tsetse flies. The adoption of a standard classification system for land cover by tsetse ecology research groups would permit results to be more easily extrapolated to areas outwith that of their studies. It is believed that the methodology and datasets described in this paper may also help to develop a deeper understanding of the spatial epidemiology of other vector-borne, human, animal and zoonotic diseases, including malaria (Omumbo *et al.*, 2005), bluetongue (de la Rocque *et al.*, 2004) and Rift Valley fever.

Acknowledgements

The authors would like to acknowledge the financial support of the Programme against African Trypanosomiasis (PAAT) and the International Fund for Agricultural Development (IFAD). The Africover datasets were provided by the Food and Agriculture Organization of the United Nations (FAO) Environment and Natural Resources Service, which also verified the compliance of products with the rules of the Land Cover Classification System.

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Accepted 7 June 2008
First published online 9 September 2008