Seasonal variations and other changes in the geographical distributions of different cytospecies of the *Simulium damnosum* complex (Diptera: Simuliidae) in Togo and Benin

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ABSTRACT

Simulium damnosum s.l., the most important vector of onchocerciasis in Africa, is a complex of sibling species described on the basis of differences in their larval polytene chromosomes. These (cyto) species differ in their geographical distributions, ecologies and epidemiological roles. In Togo and Benin, distributional changes have been recorded as a consequence of vector control and environmental changes (e.g. creation of dams, deforestation), with potential epidemiological consequences. We review the distribution of cytospecies in Togo and Benin and report changes observed from 1975 to 2018. The elimination of the Djodji form of *S. sanctipauli* in south-western Togo in 1988 seems to have had no long-term effects on the distribution of the other cytospecies, despite an initial surge by *S. yahense*. Although we report a general tendency for long-term stability in most cytospecies' distributions, we also assess how the cytospecies' geographical distributions have fluctuated and how they vary with the seasons. In addition to seasonal expansions of geographical ranges by all species except *S. yahense*, there are seasonal variations in the relative abundances of cytospecies within a year. In the lower Mono river, the Beffa form of *S. soubrense* predominates in the dry season but is replaced as the dominant taxon in the rainy season by *S. damnosum* s.str. Deforestation was previously implicated in an increase of savanna cytospecies in southern Togo (1975–1997), but our data had little power to support (or refute) suggestions of a continuing increase, partly because of a lack of recent sampling. In contrast, the construction of dams and other environmental changes including climate change seem to be leading to decreases in the populations of *S. damnosum* s.l. in Togo and Benin. If so, combined with the disappearance of the Djodji form of *S. sanctipauli*, a potent vector, plus historic vector control actions and community directed treatments with ivermectin, onchocerciasis transmission in Togo and Benin is much reduced compared with the situation in 1975.

1. Introduction

For nearly a century it has been known that the blackfly *Simulium damnosum* Theobald *sensu lato* (s.l.) (Diptera: Simuliidae) is the main vector in Africa of *Onchocerca volvulus* Leuckart, the causal agent of human onchocerciasis (river blindness) (Blacklock, 1926). Hence, the geographical distribution of the disease is determined by the geographical distribution of its vector. However, Vajime and Dunbar (1975) showed, based on their analyses of the polytene chromosomes found in the blackfly salivary glands, that *S. damnosum* was not a single species, but a complex of species, which are commonly called sibling species (because they are morphologically more or less identical) or cytological species (cytospecies, because they have been defined on the basis of chromosomal differences). Vajime and Dunbar (1975) found that the different members of this complex, often occurred in different habitats. Thus, cytospecies found in savanna areas were linked to transmission of a savanna 'blinding' strain of onchocerciasis and forest blackflies with a less virulent forest strain of the disease, in a so-called *Onchocerca-Simulium* complex (Duke et al., 1966). Although the evidence for such strains of *O. volvulus* is now equivocal (Cheke et al.,

2021), there is no doubt that the vectors differ in habitat requirements (Vajime and Dunbar, 1975; Quillévéré, 1979), types of rivers that they breed in (Cheke et al., 2017), migratory abilities (Garms et al., 1979; Walsh et al., 1981; Cheke and Garms, 1983; Baker et al., 1990) and vectorial efficiencies (Cheke and Garms, 2013). During the insecticidal activities of the WHO Onchocerciasis Control Programme (OCP) in West Africa the cytospecies also differed in their abilities to become resistant to the organophosphate larvicide temephos (Abate) (Kurtak et al., 1987). Thus, differences in the cytospecies present in an area have practical effects on onchocerciasis epidemiology and its control.

The first record of a cytospecies of the *S. damnosum* complex in Togo and Benin was in the original descriptions. Vajime and Dunbar (1975) recorded *S. soubrense* from the lower course of the Mono river. Later, Vajime and Quillévéré (1978) recorded breeding by *S. damnosum* s.str., *S. sirbanum, S. squamosum* and *S. yahense*, in addition to *S. soubrense*, within the areas being treated with insecticide by the OCP. The first coverage of most rivers of both Togo and Benin was documented by Garms et al. (1982) who showed that S. *damnosum* s.str. was widespread whilst *S. squamosum*, a predominantly highland species, became rarer from west to east. They also mapped the geographical distributions of the other species and provided evidence of migrations by *S. damnosum* s. str., *S. sirbanum* and *S. squamosum,* a phenomenon confirmed by Cheke and Garms (1983). Later, it was noted that *S. soubrense* in both Togo and Benin was represented by a unique new cytoform termed the Beffa form of *S. soubrense* (Meredith et al., 1983), subsequently found to be widespread and even reaching eastern Ghana (Cheke et al., 1987a) and Nigeria (Post et al., 2011). Other subsequent discoveries include (1) the classification of *S. squamosum* into different forms, with the C form recorded from Togo and Benin (Boakye, 1993; Post et al., 2011); (2) the discovery (Surtees, 1986; Surtees et al., 1988) and subsequent elimination (Cheke et al., 2008) of the Djodji form of *S. sanctipauli*; (3) the finding of two forms of *S. damnosum* s.str., the Nile form and the Volta form, present at least in Benin (Post et al., 2011) and (4) that *S. sirbanum* s.str. and *S. sirbanum* Sudanense Type IV form are present in Togo and Benin, with the latter restricted to the far north of both countries (Cheke et al., 1987b; Fiasorgbor and Cheke, 1992). Boakye et al. (1998) summarised in map form the geographical distributions of the various cytospecies and cytoforms found within the OCP area until 1993.

In this paper we present a collation of all available data on the geographical distributions of the different cytospecies and cytoforms found within Togo and Benin and analyse them in relation to long-term changes that have occurred since 1975 and in relation to seasonal differences that are apparent between dry and rainy seasons. Thus, this is a companion paper to a similar one for Ghana (Post et al., 2013). In order to facilitate comparisons between the situations in Ghana and in Togo and Benin, we have reproduced here a map of the geographical distributions of the different cytoforms recorded in Ghana, based on the data in Post et al. (2013) (Fig. 1).

2. Methods

2.1. Study area

West Africa is characterized by a general south to north pattern of decreasing rainfall. Monsoon winds blowing from the southwest bring humid air from the Atlantic Ocean which results in rainfall, whereas Harmattan winds blowing from the northeast bring dry air from the Sahara Desert. The monsoon winds predominate in the second and third quarters of the year pushing back the Harmattan and bringing rain from the south to the north, whereas the Harmattan pushes south during the last and first quarter of the year (Ojo, 1977). This climatological pattern, with longer rainy seasons in the south and progressively shorter rainy seasons in areas further north, has had a major influence on the ecology of West Africa, particularly on the vegetation (Hopkins, 1974). In the south there is usually rain forest, which to the north gives way to an area of forest-savanna mosaic, which in turn gives way to savanna, Sahel and
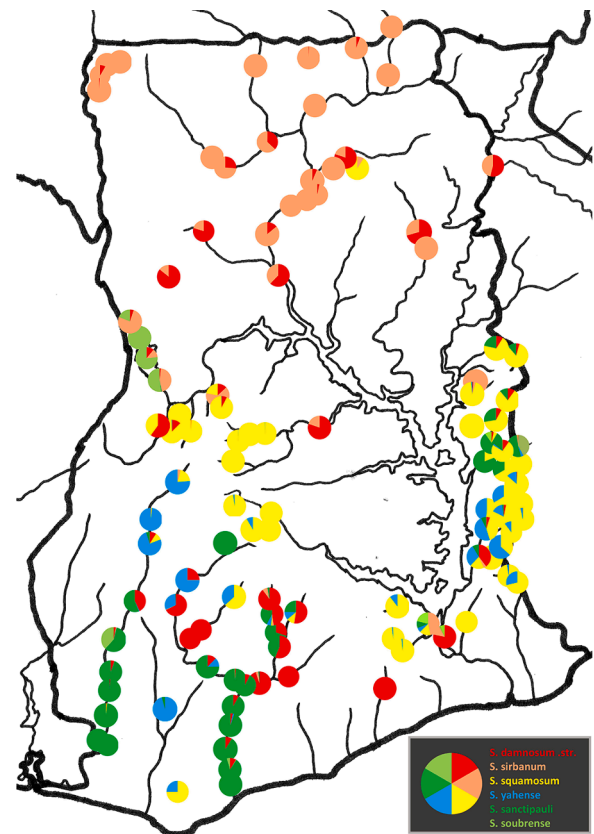

Fig. 1. Map of Ghana with geographical distributions of breeding sites of different members of the *Simulium damnosum* complex taken from data presented and analysed by Post et al. (2013). The river names and other geographical features are presented in the base-map also published by Post et al. (2013).

finally to the Sahara Desert.

Togo and Benin are situated in, and comprise most of, the area known to biologists and climatologists as the Dahomey Gap, sometimes referred to as the Togo-Benin gap to reflect Togo's substantial portion of it and to eschew the now disused name (Dahomey) for the Republic of Benin (Garms et al., 1982; Turner and Cheke, 1983). On either side (Nigeria to the east and Ghana to the west) lowland tropical rainforest lies just north of the coast, and savanna vegetation lies north of the rain forest. This east-west belt of lowland rainforest is more or less continuous with, and very similar to, the large expanse of rain forest which occupies most of the Congo basin, except that there is a break between Nigeria and Ghana where the savanna reaches the coast – the Togo-Benin (Dahomey) Gap. There is less rainfall within the Togo-Benin gap (for reasons which are not fully understood but are probably related to the shape of the coastline), and this is presumably responsible (or partly responsible) for the absence of rain forest, although anthropogenic deforestation may also have played a role. It is probable that rain forest would have been absent from the coastal areas of Togo and Benin 18,000 years ago during the last of the Pleistocene glaciations (as part of the world-wide retreat of the tropical rain forests), but by the Holocene 'climatic optimum' (8000 years ago, which was warm and damp) it may have become forested, only to become deforested again after the aridification event that marked the beginning of the Meghalayan Age (approx. 4200 years BP) when the climate took a sharp turn towards being cold and dry (Hardy et al., 2013). The coastal areas of Togo and Benin currently consist of forest-savanna mosaic, and it remains unclear the extent (if any) to which ancient or recent anthropogenic deforestation may also have been involved. Whatever the historical origin, the current-day vegetation pattern is shown in Fig. 2 according to White
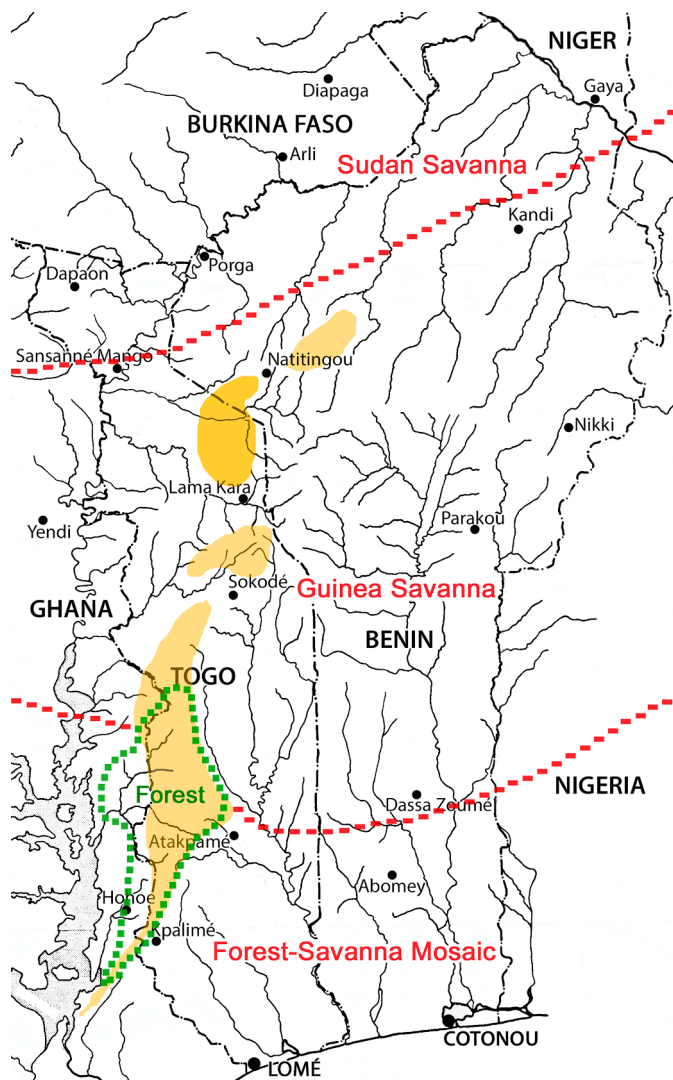
Fig. 2. Map of Togo and Benin map showing different habitats. Yellow shading indicates upland areas. North is at the top of the map. The distance between Lomé and Cotonou is 134 km. Green dotted lines indicate areas of forest, and red dashed lines indicate the boundaries between the different bioclimatic zones (sudan savanna, guinea savanna and forest-savanna mosaic).

Fig. 3. Map of Togo and Benin showing the main rivers.

(1983), but using the less-complicated and well-known nomenclature proposed by Keay (1953), with the distribution of rain forest updated according to Sayer et al. (1992). Fig. 2 also shows the distribution of uplands, which occur as a chain of mountains extending northwards from Kpalimé along the Togo-Ghana border and then north-northeast across Togo into the Natitingou district of Benin. These uplands, known as the Atacora chain, create locally increased rainfall and support 'lowland' rain forest, although this has been significantly degraded by recent commercial logging (Dowsett-Lemaire and Dowsett, 2019). Further north and northeast, these uplands do not currently support rain forest. Fig. 3 shows the hydrological network of rivers in Togo and Benin and names the main rivers. The main towns and surrounding countries are also named to assist orientation.

2.2. Sources of information and database construction

Published and unpublished records of cytospecies identifications were compiled and are presented in Supplementary Material Tables S1 and S2 (for Togo and Benin, respectively), in which the data are arranged alphabetically according to river name. The date notation we use in Tables S1 and S2 follows the day-month-year format, with the month
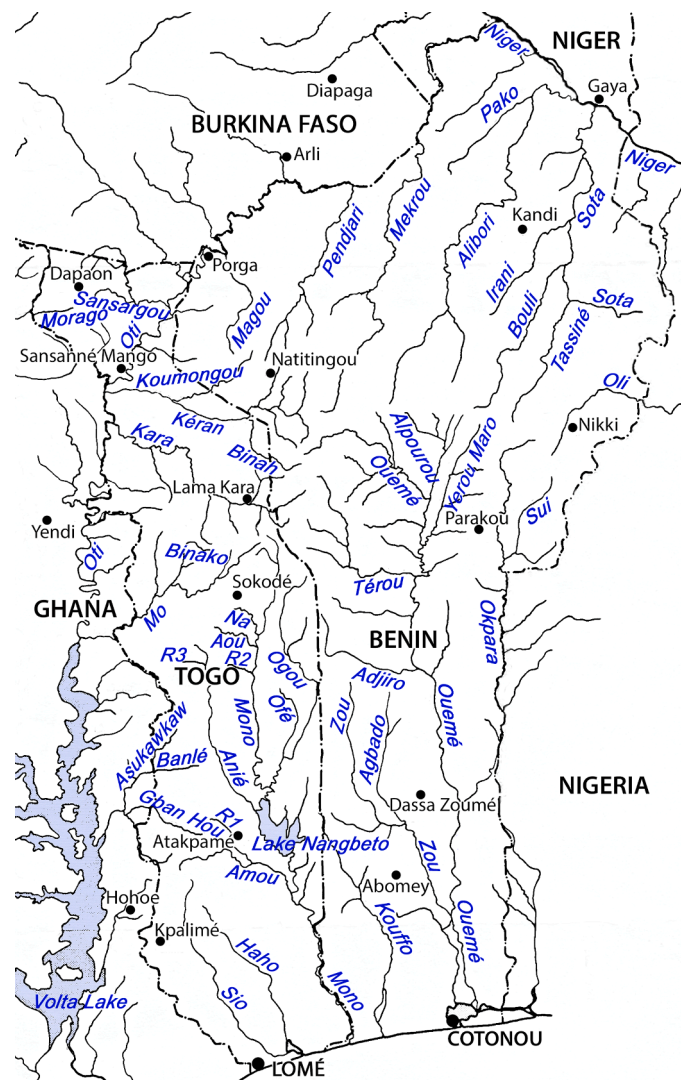
in roman numerals. Many records were the result of research carried out or sponsored by the OCP which ran from 1974 to 2002. Much of the data were obtained from OCP reports, but additional data were compiled from various documents held by the authors. In addition, a smaller number of identifications were made by various authors during research sponsored by other organizations such as the British Medical Research Council. Whenever possible, the source documents for the identifications are indicated in Tables S1 and S2 along with the name of the person (s) who collected the specimens and the name of the cytotaxonomist responsible for the identifications. The methods used for collection of larval specimens of *S. damnosum* s.l. from rivers and the subsequent dissection of the salivary glands for examination of the polytene chromosomes were fairly well standardized (Dunbar,1972; Quillévéré, 1975; Boakye, 1988; 1993) with only minor variations between entomologists. The earliest cytotaxonomic identifications in Tables S1 and S2 are from a sample collected in 1968, and the criteria for the identifications were based upon the seminal publications of Vajime and Dunbar (1975) and Quillévéré (1975). The most recent identifications are from 2018. In all cases, it has been possible to ensure that cytospecies identifications within Tables S1 and S2 correspond with modern usage. That is to say, the identifications of *S. damnosum* s.str. *S. sirbanum, S. squamosum, S. yahense, S. soubrense* and *S. sanctipauli,* are correct according to Boakye (1993) and Boakye et al. (1998) and therefore we have used these six cytospecies as the mapping units. However, this taxonomic certainty has

not always been extended to the cytoforms currently recognized within the named cytospecies listed above. Consequently, cytoforms have not been mapped, but in cases where they are known, they are listed in Tables S1 and S2 under the column headed 'Cyto. notes'.

2.3. Mapping

The information available concerning the precise locality from which larval specimens were collected for cytotaxonomic identifications was sometimes incomplete and sometimes obviously incorrect. Collections, especially in the early years, were often made without the benefit of Global Positioning Systems, and sometimes without the availability of large-scale maps. As a result, latitude-longitude co-ordinates were often estimated from maps without a clear idea of exactly where collectors were. This was especially problematic when collections were made using helicopters to prospect for breeding sites. This has been further compounded by variation in local names for rivers and a lack of accepted spelling for rivers and villages. However, in spite of these difficulties, the localities were in most cases clear enough and we corrected them when the original data were obviously wrong. In those few cases which could not be resolved, we have kept the identification records listed in Table S1 or S2, but have not included them on the maps, and have indicated the nature of the problem in the Table.

There are too many larval collection sites to plot all of them individually onto the maps at a scale which would reveal country-wide patterns. To solve this problem, localities which are close to each other on the same river (but never on separate rivers or tributaries) have been pooled. This was done subjectively with the general aim of only pooling samples sparingly and usually from within 10′ latitude or longitude of each other. The pools are indicated on Tables S1 and S2 by the groupings of rows separated by empty rows. Three distribution maps have been produced. The first map (Fig. 4) showing all data and the other two representing dry season (Fig. 5) and rainy season (Fig. 6) identifications, respectively. However, the seasons are not simultaneous throughout the country, and to take this into account (as far as possible) we divided the country subjectively into three more or less equal zones. The southern zone extends from the coast northwards to latitude 8°30′N, the central zone extends from 8°30′N to 10°00′N, and the northern zone includes the remainder of each country north of latitude 10°00′N. For the purposes of this study, in the southern zone the rainy season is considered to be from April to October (and dry season November to March). In the central zone, the rainy season is considered to be from May to October (and dry season November to April). In the northern zone, the rainy season is considered to be from June to September (and dry season October to May).

3. Results and discussion

Collection data and identifications are shown in Supplementary Tables S1 and S2 for Togo and Benin, respectively. The distribution data for cytospecies are mapped in Fig. 4 for all data without regard to seasonality and in Figs. 5 and 6 for dry and rainy seasons, respectively, and their typical habitats summarized in Table 2. We report on 1005 larval collections made in Togo and 229 in Benin. The discrepancy is partly because Benin is much less densely populated and with a less extensive infrastructure making accessibility to rivers more difficult there, but also because the Togo data include some from collections along the Togo/Ghana border at well-studied sites such as Djodji, where teams from both countries collected on either side of the river. The same applies to the lower Mono river, the data for which have been included within Togo and not Benin. In addition, the OCP maintained a regional headquarters at Kara, in Togo, which meant that research teams, studying insecticide resistance, reinvasion and taxonomy for instance, were attracted there rather than to Benin because of the facilities available in Kara.

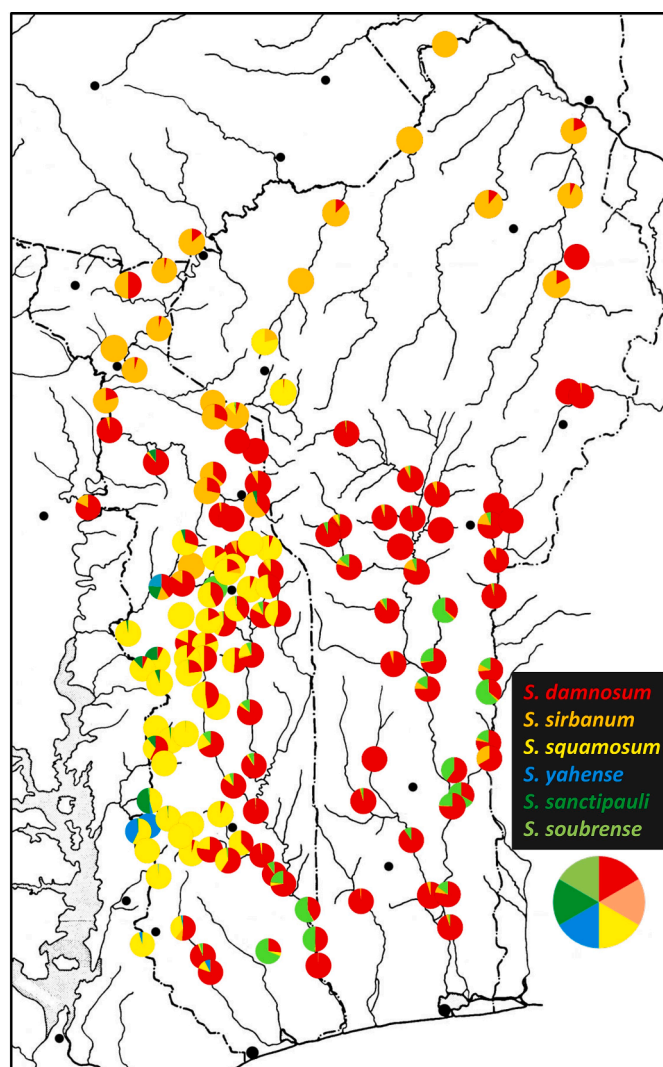Regarding the mainly forest-dwelling cytospecies, it is clear from

Fig. 4. Map of Togo and Benin with geographical distributions of breeding sites of different members of the *Simulium damnosum* complex. Black spots represent major towns as indicated in Fig. 3.

Fig. 4 that, as mentioned in the introduction, *S. squamosum* is predominantly found only in central Togo, being rare in Benin where it is recorded only from the Natitingou area. In the dry season (Fig. 5) the species is concentrated in the southwestern highlands of Togo, whence it spreads during migrations to the northeast (Fig. 6; Cheke and Garms, 1983). However, Vajime and Quillévéré (1978) recorded it as far north as the Pandjari river in Benin, whence it has never been found since. *Simulium sanctipauli* is unknown in Benin and its only representative in Togo was the Djodji form that was extinguished by OCP larviciding (Cheke et al., 2008). *Simulium sanctipauli* was even more restricted geographically within the Togolese highlands and neighbouring Ghana (Figs. 3 and 4) than *S. squamosum* but it also migrated northeast as the rainy season progressed (Garms et al., 1989), but it did not do so as extensively as *S. squamosum. Simulium yahense* is similarly restricted to forest zones (Fig. 4) but is generally found further south than was the Djodji form of *S. sanctipauli* yet, after the extinction of the Djodji form, *S. yahense* spread out from its usual habitat to occupy sites vacated by the Djodji form (Fiasorgbor et al., 1992) and even into the Amou and Sio rivers where the Djodji form had never been found. However, this expansion was apparently only temporary since *S. yahense*, absent from collections at Djodji from 1978 until April 1986, was first recorded in September 1986 and again in December 1986, September 1987 and May 1989 in collections that lacked any *S. sanctipauli*, but was not found
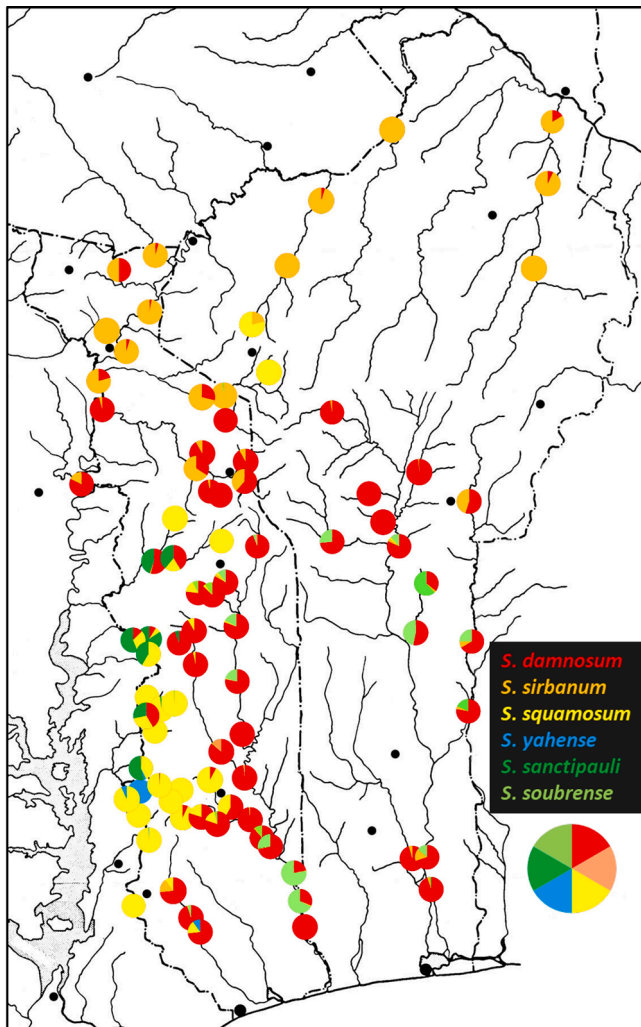
Fig. 5. Map of Togo and Benin with geographical distributions of breeding sites of different members of the *Simulium damnosum* complex during the dry season. For definitions of the seasons in different areas, see Methods section. Black spots represent major towns as indicated in Fig. 3.

Fig. 6. Map of Togo and Benin with geographical distributions of breeding sites of different members of the *Simulium damnosum* species complex during the rainy season. For definitions of the seasons in different areas, see Methods section. Black spots represent major towns as indicated in Fig. 3.

thereafter despite the collection of numerous samples from 1990 to 2011. Similarly, at Menusu in the Menu river, Ghana, *S. yahense* was absent between 1981 and 1986, then appeared from April to June 1989 but was absent in May 2009 and March 2010 (supplementary material in Post et al., 2013).

The Beffa form of *S. soubrense* has a much wider geographical distribution than *S. yahense* and is essentially a denizen of the forest-savanna mosaic (Fig. 4). In the dry season the form contracts its geographical range to the lower reaches of the Mono river and some scattered localities in the Ouémé river basin (Fig. 5) before expanding much further along these rivers and many of their tributaries (Fig. 6).

The species most often associated with the savanna, *S. damnosum* s. str. and *S. sirbanum*, are actually found in most habitats except forested areas, with *S. sirbanum* being the rarer of the two, but becoming more common in the far north of both Togo and Benin where it predominates. Both species retreat to perennial rivers in the dry season (Fig. 5). As these species are the most migratory members of the *S. damnosum* complex and adapted to survive in most habitats, it is likely that the migratory habit evolved so that they can expand their populations each rainy season by travelling northeastwards with the prevailing winds associated with the northward movement of the Inter-tropical Convergence Zone and returning as the rainy season subsides on the harmattan winds.
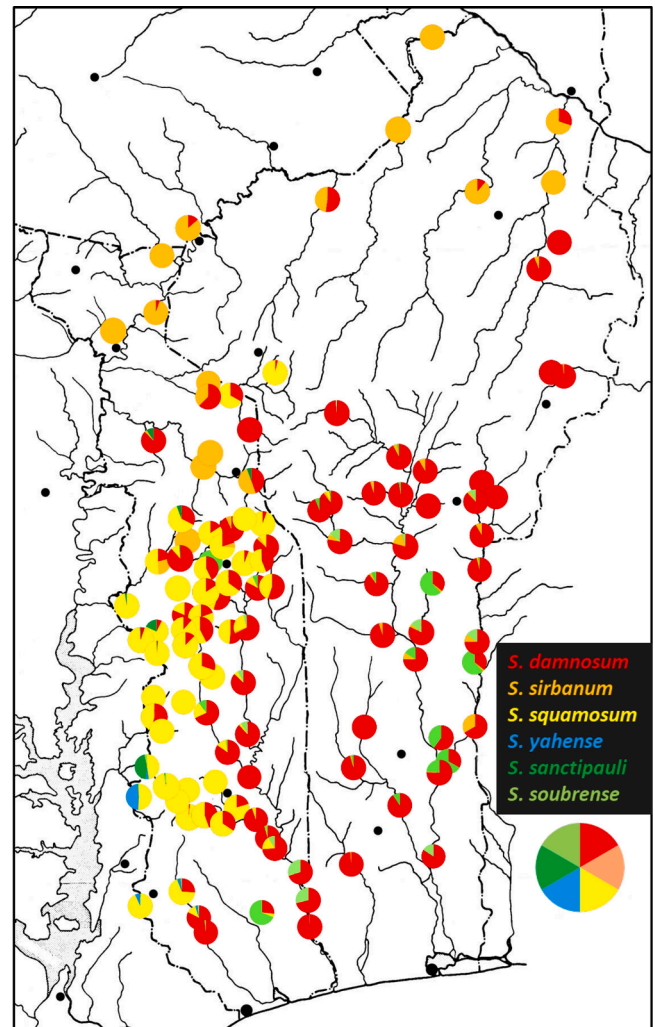
In addition to seasonal changes in geographic distributions, there are also changes in the relative abundances of the various cytospecies. For instance, in the lower Mono river the Beffa form of *S. soubrense* predominates but as the rainy season progresses *S. damnosum* s.str. becomes relatively more common to the extent that it then predominates from April until August (Table 1). Both of these taxa are important vectors of onchocerciasis (Cheke and Garms 2013), so human populations in the lower Mono basin will have been subject to continuous high intensity transmission throughout the year in contrast to northern zones where high intensity transmission will be restricted to the rainy season when *S. damnosum* s.l. and *S. sirbanum* re-establish themselves each summer. The demise of the Djodji form of *S. sanctipauli* will have had some epidemiological effects since it was a very potent vector (Cheke and Denke, 1988; Cheke and Garms, 2013) and most of its previous haunts are now occupied solely by *S. squamosum*, which is a less efficient vector.

Ghana's greater extent of forest is reflected in its being host to more sites harbouring *S. yahense* and *S. sanctipauli*, particularly in the south-western forest zones (Fig. 1) than are found in Togo and these species are absent from Benin. Although present in the east, close to the Togo border, the Beffa form of *S. soubrense* is rare in Ghana. The savanna species, *S. damnosum* s.str. and *S. sirbanum*, are found in similar habitats in Ghana as found in Togo and Benin and have been subject to similar environmental changes (Wilson et al., 2002). Other comparisons

Table 1

Numbers of larvae of different members of the *S. damnosum* complex identified cytotaxonomically in collections from the lower Mono river according to month of collection and the ratio of *S. damnosum* to *S. soubrense* (Beffa form).

MONTH	*S. damnosum* s.str.	*S. sirbanum*	*S. squamosum*	*S. soubrense* (Beffa form)	Ratio *S. damnosum: S. soubrense*
January	401	0	0	799	0.50
February	17	0	14	228	0.07
March	11	7	0	121	0.09
April	6	0	0	0	Undefined
May	202	0	0	97	2.08
June	285	3	0	79	3.61
July	338	2	1	107	3.16
August	339	2	0	72	4.71
September	NO DATA				–
October	25	0	0	172	0.14
November	71	0	2	274	0.26
December	30	0	0	131	0.23
TOTAL	1725	14	17	2080	0.83

Note: The dates of collections are available in Tables S1 and S2.

between situations in Ghana and Togo and Benin are less easy to make since different forms of *S. sanctipauli* occur in Ghana and west of the Volta Lake in Ghana the cytoform of *S. squamosum* is different from the form that occurs in Togo and Benin.

The activities of humans have led to some changes in species' geographical distributions and abundance during the study period. The intense larviciding carried out by the OCP led, as already explained, to the demise of the Djodji form of *S. sanctipauli* and probably selected for different genotypes amongst all taxa as they became resistant to some of the various larvicides applied. Hydrological changes have also had effects. The completion of the Nangbeto dam on the Mono river in Togo in 1987 and the subsequent upstream flooding for 75 km of the Mono river and parts of the lower Anié river to create Lake Nangbeto (Fig. 3) eliminated sites that had previously been very productive of *S. damnosum* s.str. and the Beffa form of *S. soubrense*. The consequent alterations to river discharges have also led to lower population densities of these blackflies at perennial sites such as Tetetou and Kpoba on the lower Mono river (P. Boko-Collins, pers. comm.). Similarly, a dam on the Oualé river has altered the flow of the Oti river. These hydrological changes and the potential effects of plans for an additional dam on the Mono at Adjarala and others on the Ouémé river can be expected to have negative effects on blackfly populations. Furthermore, deforestation has meant that *S. damnosum* s.str. and *S. sirbanum* have prospered at the expense of forest-dwelling species in southern Togo (Wilson et al., 2002) and, in addition, urban expansion, increasing human populations, land degradation and illegal gold-mining activities have led to more water-courses becoming polluted to the detriment of blackflies (Lamberton et al., 2014; Garms et al., 2015). The main changes to the species' distributions are summarized in Table 2.

Climate change is also influential as the timing of the start of rainy seasons is becoming increasingly unpredictable, usually starting later than expected according to anecdotal farmers' reports (Van de Giesen et al., 2010) as well as meteorological studies showing changing sea-sonality and other rainfall indices in West Africa from 1930 to 1990 (Atiah et al., 2021; Feng et al., 2013) and predictions of later onsets and shorter durations of rainy seasons in simulations of future changes in relation to simulations of historical data from 1980 to 1999 (Dunning et al., 2018). Furthermore, for West Africa, the sixth assessment report of the Intergovernmental Panel on Climate Change confirms an observed increase in drying and agricultural and ecological droughts and an observed increase in monsoon precipitation during the 20th century due to warming from greenhouse gas emissions masked by the decrease due to cooling from human-caused aerosol emissions (https://www.ipcc.ch/report/ar6/wg1/resources/factsheets/). Late onsets of rainy seasons delay blackfly population growth as the latter is associated with increasing rainfall at the beginnings of rainy seasons. Rising temperatures are likely to be detrimental to *S. yahense* that is adapted to cooler temperatures than the other cytospecies (see Table 1 of Cheke et al.,

Table 2

Typical habitats of the cytospecies present in Togo and Benin and comments on changes in their geographical distributions.

Cytospecies	Usual Habitat	Comments on seasonal changes and other changes recorded during the study period	References
S. sirbanum	Savanna	Increased as proportion of cytospecies present in degraded forest in southwestern Togo, attributable to deforestation.	Wilson et al. (2002)
S. damnosum s.str.	Savanna Forest/ savanna mosaic	Increased as proportion of cytospecies present in degraded forest in southwestern Togo, attributable to deforestation. Increases relative to *S. soubrense* as rainy season progresses in lower Mono river.	Wilson et al. (2002) This study (Table 1)
S. squamosum	Upland forest and adjoining savanna	Moves northeastwards as rainy season progresses, but no longer as far as the Pendjari river, Benin, where found in 1970s.	Cheke and Garms (1983). This study
S. soubrense	Forest/ savanna mosaic	Dominates over *S. damnosum* s. str. at starts of rainy seasons in lower Mono but declines proportionately as the season progresses.	This study (Table 1)
S. sanctipauli	Forest	Its sonly representative, the Djodji form, used to expand northeastwards into savanna areas during rainy seasons but was rendered extinct in 1988 by control operations.	Garms et al. (1989) Cheke et al. (2008).
S. yahense	Forest	In late 1980s expanded its range into zones vacated by the extirpated Djodji form of *S. sanctipauli*, but has since retreated to its original forest zones.	This study

2015) that may benefit as a consequence. Higher temperatures will also reduce development times of both the blackflies and any larvae of *Onchocerca volvulus* within them, thereby exacerbating the transmission of onchocerciasis before elimination of the disease is achieved (Cheke et al., 2015). However, any temperature-related changes will only lead to increases up to a certain temperature threshold, beyond which further temperature increases will have negative effects on blackfly populations. Negative effects may also be induced if climate change leads to lower rainfall and hence lower river discharges.

4. Conclusions

Most cytospecies' distributions have tended to be stable from 1975 to 2018, although the Djodji form of *S. sanctipauli* has been made extinct and there have been some other notable changes in the species' distributions. There are no obvious causes for the temporary appearance and subsequent disappearance of cytospecies in a particular location, but a major influence has been vector control and seasonal blackfly migrations into previously dry areas each rainy season. Deforestation was previously implicated in an increase of savanna cytospecies in southern Togo (1975–1997), but our data had little power to support (or refute) suggestions of a continuing increase, partly because of a lack of recent sampling. In contrast, the construction of dams and other environmental changes including climate change seem to be leading to decreases in the populations of *S. damnosum* s.l. in Togo and Benin. If so, combined with the disappearance of the Djodji form of *S. sanctipauli*, a potent vector, plus historic vector control actions and community directed treatments with ivermectin, onchocerciasis transmission in Togo and Benin is much reduced compared with the situation in 1975.

Authorship statement

RAC and RJP conceived and designed the project. Historical data were gathered by RAC. Cytotaxonomic interpretation was carried out by RJP, DAB and RAC, and distributional interpretation was carried out by RAC, RJP and DAB. The manuscript was first written by RAC and RJP with subsequent contributions from all authors. RJP created the maps. All authors read and approved the final version of the manuscript.

Additional file 1: Cytotaxonomic identifications of the *Simulium damnosum* complex from Togo 1968–2018.

Additional file 2: Cytotaxonomic identifications of the *Simulium damnosum* complex from Benin 1976–2018.

Declaration of Competing Interest

"We wish to confirm that the manuscript has not been published before and is not being considered for publication elsewhere. We confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. We confirm that all authors have contributed to the creation of this manuscript and had approved the submitted manuscript. We further confirm that the order of authors listed in the manuscript has been approved by all of us. We understand that the Corresponding Author is the sole contact for the Editorial process. "

Data availability

The data are included in 2 supplementary material files.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.actatropica.2023.106970.

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