Biodiversity Pattern of Mosquitoes in Southeastern Senegal, Epidemiological Implication in Arbovirus and Malaria Transmission

Diawo Diallo,^{1,7,*} Cheikh T. Diagne,¹ Michaela Buenemann,² Yamar Ba,¹
 Ibrahima Dia,¹ Oumar Faye,³ Amadou A. Sall,³ Ousmane Faye,³ Douglas M. Watts,⁴
 Scott C. Weaver,⁵ Kathryn A. Hanley,⁶ and Mawlouth Diallo¹

¹Unité d'entomologie médicale, Institut Pasteur de Dakar, Dakar, Sénégal, ²Department of Geography, New Mexico State University, Las Cruces, NM, ³Pole virologie, Institut Pasteur de Dakar, Sénégal, ⁴Office of Research and Sponsored Projects, University of Texas at El Paso, El Paso, 79968 TX, ⁵Institute for Human Infections and Department of Microbiology and Immunology, University of Texas Medical Branch, Galveston, 77555 TX, ⁶Department of Biology, New Mexico State University, Las Cruces, NM and ⁷Corresponding author, e-mail: diawo.diallo@pasteur.sn

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Abstract

The composition, density, diversity, and temporal distribution of mosquito species and the influence of temperature, relative humidity, and rainfall on these data were investigated in 50 sites across five land cover classes (forest, savannah, barren, village, and agriculture) in southeastern Senegal. Mosquitoes were collected monthly in each site between June 2009 and March 2011, with three people collecting mosquitoes landing on their legs for one to four consecutive days. In total, 81,219 specimens, belonging to 60 species and 7 genera, were collected. The most abundant species were *Aedes furcifer* (Edwards) (Diptera: Culicidae) (20.7%), *Ae. vittatus* (Bigot) (19.5%), *Ae. dalzieli* (Theobald) (14.7%), and *Ae. luteocephalus* (Newstead) (13.7%). *Ae. dalzieli*, *Ae. furcifer*, *Ae. vittatus*, *Ae. luteocephalus*, *Ae. taylori* Edwards, *Ae. africanus* (Theobald), *Ae. minutus* (Theobald), *Anopheles coustani* Laveran, *Culex quinquefasciatus* Say, and *Mansonia uniformis* (Theobald) comprised $\geq 10\%$ of the total collection, in at least one land cover. The lowest species richness and Brillouin diversity index ($HB = 1.55$) were observed in the forest-canopy. The urban-indoor fauna showed the highest dissimilarity with other land covers and was most similar to the urban-outdoor fauna following Jaccard and Morisita index. Mosquito abundance peaked in June and October 2009 and July and October 2010. The highest species density was recorded in October. The maximum temperature was correlated positively with mean temperature and negatively with rainfall and relative humidity. Rainfall showed a positive correlation with mosquito abundance and species density. These data will be useful for understanding the transmission of arboviruses and human malaria in the region.

Key words: biodiversity, land cover class, mosquitoes, arbovirus, malaria

Mosquitoes are among the animals with the highest medical and veterinary impact because they transmit many arboviruses, protozoa, helminths, and bacteria that cause significant human and animal morbidity and mortality (Peters 1992, Service 1993, Gubler 2009). In Senegal, particularly in the southeast, mosquitoes are vectors of many arboviruses of medical and veterinary importance (dengue, yellow fever, chikungunya, Zika, West Nile, and Rift Valley fever) and of human malaria (Monlun et al. 1993; Fontenille et al. 1998; Diallo et al. 1999, 2003; Dia et al. 2003, 2008; Faye et al. 2007). In addition to the known pathogenic arboviruses, many other viruses for which the potential to harm human and animal health is not

yet known (Ngari, Kédougou, etc.) have been isolated from mosquitoes in the area (Monlun et al. 1993, Zeller et al. 1996). Moreover, this region is experiencing substantial environmental changes driven by uncontrolled industrial gold mining. Indeed, this activity has led to an exponential increase of the human population and consequently an increase in the destruction and fragmentation of natural environments (forest galleries and savannah) within these environments. In the long term, this transformation of natural habitats due to human activities is likely to decrease mosquito species diversity (Thongsripong et al. 2013, Young et al. 2017, Mangudo et al. 2018) and leads to a loss of sylvatic mosquito species that will not be able

to adapt to artificial breeding habitats. At the outset, however, this accelerating transformation will probably increase the number of sylvatic mosquito populations frequenting human environments at the edge of the forest-galleries and may change sylvatic arbovirus transmission patterns (Patz and Reisen 2001, Patz et al. 2004, Richman et al. 2018). Deforestation, agriculture, urban development, and human encroachment into previously undisturbed areas have been suggested to be catalysts for changes in vector community composition and the introduction of new pathogens (Hayes et al. 1996, Conn et al. 2002, Cox et al. 2007).

Since 1972, several entomoepidemiological studies have been conducted in Kédougou, the southeastern region of Senegal with the main objective being to conduct surveillance on arboviruses and malaria and, to a lesser extent, to conduct bioecological studies of their vectors (Monlun et al. 1993; Traore-Lamizana et al. 1994; Traoré-Lamizana et al. 1996; Fontenille et al. 1998; Diallo et al. 1999, 2003, 2012a,b, 2014a,b; Faye et al. 2007; Dia et al. 2008). Data from these studies were leveraged to model the distribution and transmission of *Aedes*-borne viruses and their main vectors (Althouse et al. 2012, 2015, 2018; Richman et al. 2018). However, little is known about mosquito biodiversity per se in the region or about the impact of environmental factors on such biodiversity in this focus of sylvatic arbovirus transmission. A better understanding of these parameters is essential for predicting the distribution and dynamics of vector-borne diseases, understanding their epidemiology, and developing and implementing effective vector control measures.

Our primary goal in this project was to characterize the spatial and temporal biodiversity of mosquitoes in Kédougou and to determine the impact of environmental factors on biodiversity. This paper is an extension of our previous studies in the area, using pooled mosquito data collected and presented partially in Diallo et al. (2012b, 2014b) and analyzed, here, using biodiversity indices and tools.

Materials and Methods

Study Area

The study was conducted in the Kédougou region of southeastern Senegal (central coordinates: 12°33' N, 12°11' W) at the borders of Mali and Guinea (Fig. 1, slightly modified from Diallo et al. 2012b). This area was described in detail previously (Diallo et al. 2012b). Briefly, the area has mainly six land cover classes. Villages, representing <5% of the area, are sites composed mostly of a mixture of dwellings (most of them with mud walls and thatched roofs) and roads. Agricultural land encompasses mostly croplands (e.g., maize, peanuts, rice, fonio, millet, and sorghum fields) and pastures. Forests are densely wooded areas with *Combretum glutinosum*, *Bombax costatum*, *Cordia pinnata*, *Pterocarpus erinaceus*, *Terminalia macroptera*, *Oxythanasia abyssinica* being among the most common tree species, and other species like *Saba senegalensis* being much more localized. Savannas are sparsely wooded grasslands. Barren lands are areas in which less than one-third of the landscape has vegetation or other cover and are typically characterized by exposed soil or rocks.

Fig. 1. Study area in Kédougou, Senegal. This figure is modified from Diallo et al. (2012b).

Finally, water in the study area is limited to the Gambia River, which runs through much of the eastern portion of the study area.

The Kédougou region is hilly, with mean annual temperatures varying between 33 and 40°C and about 1,200 mm of annual rainfall. The area has one rainy season, generally from June to October. The natural environment of the area is being transformed by agricultural, gold mining, and other human activities. Despite the recent increase of the population due to the gold mining activities, the region is still rural with a low density of inhabitants of 9/km². Some human activities in the area such as farming and hunting bring people in contact with the forest. Mining camps have been created near gold veins, which are often located close to or even within the forests.

Mosquito Sampling

The mosquito data used in this paper are those collected and presented partially in Diallo et al. (2012b, 2014b). Mosquito sampling site selection, description, and sampling schemes were thoroughly described in earlier papers (Diallo et al. 2012b, 2014b; Richman et al. 2018). Briefly, mosquitoes were collected in an area of 1,650 km² (30 km in N-S direction; 55 km in E-W direction) from June 2009 to March 2011 (except April 2010) in 50 sites belonging to 5 land cover classes (forest, barren, savannah, agriculture, and urban) identified by remote sensing and geospatial analyses. Mosquitoes were collected monthly in each site from 6–9 PM using human landing catches. In savannah, agriculture, and barren lands, teams of three collectors were positioned at ground level. In forests, two teams of three collectors each were positioned at ground level and on platforms in the canopy. In urban areas (villages), two teams of three collectors each were installed indoors and outdoors. All landing collectors participated in informed oral consent. They were provided malaria prophylaxis, monitored for signs of febrile illness, and provided any medical treatment needed. Mosquitoes were identified using external morphology via didactic keys (Ferrara et al. 1984, Diagne et al. 1994, Jupp 1997, Edwards 1941).

Weather Data

Daily maximum, minimum, and mean temperature, rainfall, and relative humidity data, representative of the study area, were obtained from the Kédougou Aerodrome weather station (12°34'0" N, 12°13'0" W). This station is located 5 km north-west of Kédougou city. These data were used to calculate mean monthly maximum, minimum, and mean temperature, rainfall, and relative humidity values. We obtained weather data from May 2009 (1 mo prior to the beginning of the study) to consider possible lagged responses of mosquito populations to these weather elements.

Data Analysis

Mosquito biodiversity was measured using the species density (Sd; number of collected species in each habitat), species richness (Sr; estimated number of species in each habitat given equal sample sizes), and the Brillouin diversity indices (HB). The species density is the number of observed species. Individual-based rarefaction curves were used to estimate and compare spatial and temporal species richness (Sr) (Gotelli and Colwell 2001). Rarefaction-based estimates and 95% CIs were computed with the software Analytical Rarefaction 1.3 (Holland 2003). The Brillouin diversity index is a measure of the proportion of individuals of each species in each community and incorporates relative abundance of collected specimens to estimate

species diversity. This index is preferred when the randomness of a sample (data from human landing catches here, with species representation based on differential attraction to men) cannot be guaranteed (Magurran 2004).

The similarity between environments was evaluated using the Morisita index (IM) for quantitative data and the Jaccard index (IJ) for qualitative data (Magurran 2004). These indices and 95% CIs were obtained using the program PAST, version 2.14 (Hammer et al. 2001). Dominance was calculated according to the formula: $D(\%) = (i/t) \times 100$, where i denotes total of individuals of the species and t denotes total of individuals collected and clustered following the categories established by Friebe (1983): eudominant $D \geq 10\%$, dominant $10\% > D \geq 5\%$, subdominant $5\% > D \geq 2\%$, eventual $2\% > D \geq 1\%$, and rare $D < 1\%$. Proportions of rare species and singletons between land cover classes were compared by the χ^2 test. To test influences of selected weather variables on the abundance of mosquitoes, the Spearman's rank correlation test was employed using data from the meteorological station of the Kédougou Aerodrome. Influences of weather variables on mosquito abundance were tested using weather measurements taken concurrent with collection and with measurements taken 1 mo previous to the collection. The Spearman's rank correlation test was used because the mean temperature and rainfall data were not normally distributed and were not rendered normal via data transformation. All statistical analyses were conducted using R (R Core Team 2017).

Results

In total, 81,219 mosquitoes belonging to the subfamilies Culicinae (91.6% of the total) and Anophelinae (8.4% of the total) was collected over the course of the two study seasons (Table 1). *Aedes*, *Anopheles*, and *Mansonia* genera accounted for 84.7, 8.4, and 5.3% of the specimens captured, respectively. The remaining genera (*Culex*, *Uranotaenia*, *Toxorhynchites*, and *Eretmapodites*) comprised <3.0% of the specimens. The most abundant species, presented in Table 2, were *Aedes furcifer* (Edwards) (20.7% of the total collection), *Aedes vittatus* (Bigot) (19.5%), *Aedes dalzieli* (Theobald) (14.7%), and *Aedes luteocephalus* (Newstead) (13.7%). It was possible to identify 60 species belonging to the genera *Aedes* (25), *Anopheles* (16), *Culex* (14), *Mansonia* (02), *Eretmapodites* (01), *Uranotaenia* (01), and *Toxorhynchites* (01). Only six species occurred in relative abundance above 5%, totaling >4,000 individuals collected; 7 had abundances between 1 and 4%. The remaining 47 species occurred in relative abundance <1%, from which five were represented by only two individuals (doubletons) and four by only one specimen (singletons).

Total mosquito abundance was highest in agriculture (16,178 individuals/19.9% of all catches), followed by forest-canopy (14,801/18.2%), forest-ground (13,985/17.2%) and savannah (13,919/17.1%), which were extremely similar, barren (13,202/16.3%), urban-outdoor (7,218/8.9%), and urban-indoor land covers (1,916/2.4%).

Those species occurring at $\geq 10\%$ (hereafter termed eudominant) were *Ae. dalzieli* (23.7% of the total collection), *Ae. furcifer* (21.8%), *Ae. vittatus* (12.4%) and *Ma. uniformis* (Theobald) (11.6%) in agriculture; *Ae. vittatus* (34.9%), *Ae. furcifer* (18.4%) and *Ae. dalzieli* (17.4%) in barren; *Ae. luteocephalus* (41.9%), *Ae. furcifer* (27.6%), *Ae. taylori* Edwards (14.4%) and *Ae. africanus* (Theobald) (10.0%) in forest-canopy; *Ae. luteocephalus* (26.8%), *Ae. furcifer* (15.5%), *Ae. vittatus* (14.1%) and *Ae. dalzieli* (13.0%) in forest-ground; *Ae. vittatus* (25.6%), *Ae. dalzieli* (21.6%), *Ae. furcifer* (18.1%) and *Anopheles coustani* Laveran (11.4%) in savannah; *Ae.*

Table 1. Mosquito abundance by genus and subfamily in specified land cover classes, Kédougou; data from June 2009 through Mar. 2010 and May 2010 through Mar. 2011 combined

General/ Subfamily	Agriculture		Barren		Savannah		Forest-canopy		Forest-ground		Urban-outdoor		Urban-indoor		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
<i>Aedes</i>	11,681	72.20	11,039	83.62	10,954	78.70	14,497	97.95	12,619	90.23	6,571	91.04	1,441	75.21	68,802	84.71
<i>Anopheles</i>	1,728	10.68	1,322	10.01	2,364	16.98	106	0.72	806	5.76	315	4.36	165	8.61	6,806	8.38
<i>Culex</i>	167	1.03	154	1.17	107	0.77	137	0.93	120	0.86	307	4.25	286	14.93	1,278	1.57
<i>Eretmapodites</i>	7	0.04	1	0.01	4	0.03	1	0.01	7	0.05	0	0.00	1	0.05	21	0.03
<i>Mansonia</i>	2,594	16.03	685	5.19	490	3.52	60	0.41	433	3.10	25	0.35	22	1.15	4,309	5.31
<i>Toxorhynchites</i>	1	0.01		0.00		0.00		0.00		0.00		0.00		0.00	1	0.00
<i>Uranotaenia</i>		0.00	1	0.01		0.00		0.00		0.00		0.00	1	0.05	2	0.00
Culicinae	14,450	89.32	11,880	89.99	11,555	83.02	14,695	99.28	13,179	94.24	6,903	95.64	1,751	91.39	74,413	91.62
Anophelinae	1,728	10.68	1,322	10.01	2,364	16.98	106	0.72	806	5.76	315	4.36	165	8.61	6,806	8.38
Total	16,178	100	13,202	100	13,919	100	14,801	100	13,985	100	7,218	100	1,916	100	81,219	100

No., number of mosquitoes collected.

furcifer (28.4%), *Ae. vittatus* (20.9%), *Culex quinquefasciatus* Say (14.4%), and *Aedes minutus* (Theobald) (10.8%) in urban-indoor; and *Ae. furcifer* (42.1%) and *Ae. vittatus* (20.8%) in urban-outdoor. Together, these highly dominant species represented 69.6, 70.8, 94.0, 69.3, 76.8, 74.5, and 63.0% of the total abundance of agriculture, barren, forest-canopy, forest-ground, savannah, urban-indoor, and urban-outdoor respectively. Twenty-five of the sixty species (41.7%) were shared among all land cover classes. The proportions of rare species, representing <1% of the mosquito fauna (Table 3) were statistically comparable among land cover classes ($\chi^2 = 7.2$; $df = 6$; $P = 0.3$), whereas the proportions of singletons were significantly different ($\chi^2 = 17.3$; $df = 6$; $P = 0.008$). The highest proportion of species represented by a singleton was observed in the urban-indoor followed by the forest-canopy, urban-outdoor, savannah, forest-ground, agriculture and barren.

The highest species density was observed in the savannah ($Sd = 50$), followed by agriculture ($Sd = 48$), forest-ground ($Sd = 46$), barren ($Sd = 45$), forest-canopy ($Sd = 44$), urban-outdoor ($Sd = 42$), and urban-indoor ($Sd = 34$) land covers (Table 4). Individual-based rarefaction curves (Fig. 2) suggested that, for equal sample sizes, the lowest species richness (S_r) was observed in the forest-canopy. The lowest Brillouin diversity index was observed in the forest-canopy ($HB = 1.55$) and urban-outdoor ($HB = 1.87$) indicated higher skew in relative abundance of different species in these land covers (Table 4). The savannah, agriculture, and barren land covers were the most similar according to the Jaccard index (Fig. 3), whereas the urban-indoor showed the highest dissimilarity among land covers. The Morisita index showed three clusters of similarity composed of the savannah, barren, and agricultural land covers (1); the urban-indoor and urban-outdoor (2); and forest-canopy and forest-ground (3).

Summing across all land covers, peak mosquito abundances were observed in June and October 2009 and July and October 2010. The highest species densities were recorded in October 2009 and 2010 with 42 and 49 species, respectively (Fig. 4). December had the highest Brillouin diversity index in 2009, whereas September and October had the highest Brillouin index in 2010.

Figure 4 presents weather data (temperature, relative humidity, and rainfall) obtained from the Kédougou Aerodrome station. August and September were the wettest months in 2009, whereas July and September were wettest in 2019. Temperatures peaked in March in 2010 and 2011 and reached their nadir in January 2009, 2010, and 2011 and December 2009 and 2010. The maximum temperature was positively and significantly correlated with mean temperature ($\rho = 0.8$; $P < 0.0001$) and negatively and significantly correlated with rainfall ($\rho = -0.8$; $P < 0.0001$) and relative humidity ($\rho = -0.8$; $P < 0.0001$). Rainfall and relative humidity showed a strong positive and significant correlation ($\rho = 0.9$; $P < 0.0001$). Rainfall showed a positive and significant correlation with mosquito abundance ($\rho = 0.8$; $P < 0.0001$) and species density ($\rho = 0.6$; $P = 0.007$). Moreover, correlations between rainfall and abundance of mosquitoes were higher after a lag time of a month ($\rho = 0.9$; $P < 0.0001$).

Discussion

Largely due to the fact that the geographical scope of this study was broader and that a higher number of human collectors were used, we collected more mosquito species than all previously reported studies using human landing collection in the Kédougou region (Cornet et al. 1978, Traoré-Lamizana et al. 1996, Diallo et al. 2003, Dia et al. 2005). However, the 60 mosquito species detected in the current study are fewer than the 102 species previously reported from

Table 2. Mosquito abundance and dominance category by species and land cover class in Kédougou; data from June 2009 through Mar. 2010 and May 2010 through Mar. 2011 combined

Species	Agriculture			Barren			Savannah			Forest-canopy			Forest-ground			Urban-outdoor			Urban-indoor			Total		
	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC
<i>Aedes aegypti</i>	97	0.6	Ra	43	0.3	Ra	97	0.7	Ra	29	0.2	Ra	247	1.8	Ev	305	4.2	Sd	55	2.9	Sd	873	1.1	Ev
<i>Aedes africanus</i>	2	0	Ra				2	0	Ra	1,485	10	Ed	773	5.5	do	1	0	Ra				2,263	2.8	Sd
<i>Aedes argenteopunctatus</i>	381	2.4	Sd	455	3.4	Sd	298	2.1	Sd	11	0.1	Ra	44	0.3	Ra	90	1.2	Ev	4	0.2	Ra	1,283	1.6	Ev
<i>Aedes bromeliae</i>																								
<i>Aedes centropunctatus</i>	89	0.6	Ra	65	0.5	Ra	43	0.3	Ra	2	0	Ra	40	0.3	Ra	7	0.1	Ra				2	0	Ra
<i>Aedes cozi</i>	1	0	Ra	3	0	Ra	3	0	Ra				1	0	Ra							246	0.3	Ra
<i>Aedes cumminsi</i>	106	0.7	Ra	24	0.2	Ra	26	0.2	Ra				65	0.5	Ra	3	0	Ra				224	0.3	Ra
<i>Aedes dalzielii</i>	3,842	23.7	Ed	2,304	17.5	Ed	3,001	21.6	Ed	130	0.9	Ra	1,813	13	Ed	672	9.3	do	169	8.8	do	11,931	14.7	Ed
<i>Aedes fowleri</i>	42	0.3	Ra	41	0.3	Ra	26	0.2	Ra	1	0	Ra	16	0.1	Ra	23	0.3	Ra	7	0.4	Ra	156	0.2	Ra
<i>Aedes furcifer</i>	2,008	12.4	Ed	2,432	18.4	Ed	2,523	18.1	Ed	4,089	27.6	Ed	2,169	15.5	Ed	3,068	42.5	Ed	545	28.4	Ed	16,834	20.7	Ed
<i>Aedes hirsutus</i>	50	0.3	Ra	31	0.2	Ra	26	0.2	Ra	3	0	Ra	11	0.1	Ra	27	0.4	Ra	5	0.3	Ra	153	0.2	Ra
<i>Aedes longipalpis</i>										1	0	Ra									1	0	Ra	
<i>Aedes luteocephalus</i>	205	1.3	Ev	235	1.8	Ev	547	3.9	Sd	6,208	41.9	Ed	3,750	26.8	Ed	125	1.7	Ev	40	2.1	Sd	11,110	13.7	Ed
<i>Aedes mcintoshi</i>	117	0.7	Ra	78	0.6	Ra	28	0.2	Ra	1	0	Ra	6	0	Ra	11	0.2	Ra	1	0.1	Ra	242	0.3	Ra
<i>Aedes metallicus</i>	93	0.6	Ra	80	0.6	Ra	76	0.5	Ra	27	0.2	Ra	71	0.5	Ra	22	0.3	Ra	2	0.1	Ra	371	0.5	Ra
<i>Aedes minutus</i>	1,021	6.3	do	454	3.4	Sd	463	3.3	Sd	51	0.3	Ra	1,236	8.8	do	666	9.2	do	207	10.8	Ed	4,098	5	do
<i>Aedes mixtus</i>	5	0	Ra				8	0.1	Ra	3	0	Ra	8	0.1	Ra							24	0	Ra
<i>Aedes neoafricanus</i>				1	0	Ra	6	0	Ra	81	0.5	Ra	34	0.2	Ra	1	0	Ra				123	0.2	Ra
<i>Aedes ochraceus</i>	14	0.1	Ra	43	0.3	Ra	11	0.1	Ra				4	0	Ra	3	0	Ra				75	0.1	Ra
<i>Aedes opok</i>										4	0	Ra									4	0	Ra	
<i>Aedes soudanensis</i>							2	0	Ra													2	0	Ra
<i>Aedes taylori</i>	53	0.3	Ra	92	0.7	Ra	151	1.1	Ev	2,133	14.4	Ra	340	2.4	Sd	20	0.3	Ra	4	0.2	Ra	2,793	3.4	Sd
<i>Aedes unilineatus</i>	21	0.1	Ra	43	0.3	Ra	49	0.4	Ra	8	0.1	Ra	23	0.2	Ra	3	0	Ra	2	0.1	Ra	149	0.2	Ra
<i>Aedes vexans</i>	3	0	Ra	5	0	Ra							1	0	Ra	6	0.1	Ra				15	0	Ra
<i>Aedes vittatus</i>	3,531	21.8	Ed	4,610	34.9	Ed	3,568	25.6	Ed	230	1.6	Ev	1,967	14.1	Ed	1,516	21	Ed	400	20.9	Ed	15,822	19.5	Ed
<i>Anopheles brohierii</i>	3	0	Ra	3	0	Ra	3	0	Ra				2	0	Ra	2	0	Ra				13	0	Ra
<i>Anopheles brunnipes</i>	1	0	Ra																		1	0	Ra	
<i>Anopheles coustani</i>	1,241	7.7	do	882	6.7	do	1,593	11.4	Ed	29	0.2	Ra	325	2.3	Sd	85	1.2	Ev	29	1.5	Ev	4,184	5.2	do
<i>Anopheles domicola</i>	10	0.1	Ra	18	0.1	Ra	22	0.2	Ra	1	0	Ra	7	0.1	Ra	9	0.1	Ra	1	0.1	Ra	68	0.1	Ra
<i>Anopheles flavicosta</i>	18	0.1	Ra	39	0.3	Ra	60	0.4	Ra	2	0	Ra	12	0.1	Ra	5	0.1	Ra				136	0.2	Ra
<i>Anopheles freetownensis</i>							2	0	Ra												2	0	Ra	
<i>Anopheles funestus</i> s.l.	191	1.2	Ev	193	1.5	Ev	358	2.6	Sd	10	0.1	Ra	147	1.1	Ev	65	0.9	Ra	35	1.8	Ev	999	1.2	Ev
<i>Anopheles gambiae</i> s.l.	84	0.5	Ra	34	0.3	Ra	34	0.2	Ra	7	0	Ra	32	0.2	Ra	63	0.9	Ra	64	3.3	Sd	318	0.4	Ra
<i>Anopheles hancocki</i>	22	0.1	Ra	29	0.2	Ra	70	0.5	Ra	2	0	Ra	12	0.1	Ra	6	0.1	Ra				141	0.2	Ra
<i>Anopheles nili</i> s.l.	96	0.6	Ra	65	0.5	Ra	134	1	Ra	50	0.3	Ra	237	1.7	Ev	56	0.8	Ra	26	1.4	Ev	664	0.8	Ra
<i>Anopheles pharoensis</i>	11	0.1	Ra	8	0.1	Ra	6	0	Ra	2	0	Ra	2	0	Ra	3	0	Ra	2	0.1	Ra	34	0	Ra
<i>Anopheles pretoriensis</i>							1	0	Ra							2	0	Ra				3	0	Ra
<i>Anopheles rufipes</i>	23	0.1	Ra	17	0.1	Ra	31	0.2	Ra	2	0	Ra	5	0	Ra	8	0.1	Ra	5	0.3	Ra	91	0.1	Ra

Table 2. Continued

Species	Agriculture			Barren			Savannah			Forest-canopy			Forest-ground			Urban-outdoor			Urban-indoor			Total		
	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC	No.	%	DC
<i>Anopheles squamosus</i>	2	0	Ra	3	0	Ra	1	0	Ra							6	0.1	Ra	1	0.1	Ra	13	0	Ra
<i>Anopheles wellcomei</i>	14	0.1	Ra	28	0.2	Ra	48	0.3	Ra	1	0	Ra	21	0.2	Ra	5	0.1	Ra	1	0.1	Ra	118	0.1	Ra
<i>Anopheles ziemanni</i>	12	0.1	Ra	3	0	Ra	1	0	Ra				4	0	Ra				1	0.1	Ra	21	0	Ra
<i>Culex annulioris</i>	13	0.1	Ra	6	0	Ra	22	0.2	Ra	1	0	Ra	11	0.1	Ra				1	0.1	Ra	54	0.1	Ra
<i>Culex antennatus</i>	19	0.1	Ra	4	0	Ra	1	0	Ra	4	0	Ra	4	0	Ra	5	0.1	Ra				37	0	Ra
<i>Culex</i>	12	0.1	Ra	7	0.1	Ra	48	0.3	Ra	3	0	Ra	17	0.1	Ra							87	0.1	Ra
<i>bitaeniorhynchus</i>																								
<i>Culex cinerellus</i>							1	0	Ra													1	0	Ra
<i>Culex cinerus</i>							1	0	Ra										3	0.2	Ra	3	0	Ra
<i>Culex decens</i>	2	0	Ra				5	0	Ra	1	0	Ra							1	0.1	Ra	5	0	Ra
<i>Culex ethiopicus</i>										3	0	Ra	1	0	Ra	1	0	Ra				10	0	Ra
<i>Culex macfie</i>	1	0	Ra							1	0	Ra										2	0	Ra
<i>Culex neavei</i>	12	0.1	Ra	5	0	Ra	6	0	Ra	4	0	Ra	2	0	Ra	1	0	Ra				30	0	Ra
<i>Culex nebulosus</i>				90	0.7	Ra				3	0	Ra	2	0	Ra							96	0.1	Ra
<i>Culex perfuscus</i>	8	0	Ra	4	0	Ra	13	0.1	Ra	55	0.4	Ra	58	0.4	Ra	1	0	Ra	1	0.1	Ra	140	0.2	Ra
<i>Culex poicilipes</i>	90	0.6	Ra	26	0.2	Ra	5	0	Ra	59	0.4	Ra	20	0.1	Ra	1	0	Ra				201	0.2	Ra
<i>Culex</i>	6	0	Ra	10	0.1	Ra	2	0	Ra	2	0	Ra	1	0	Ra	297	4.1	Sd	276	14.4	Ed	594	0.7	Ra
<i>quinquefasciatus</i>																								
<i>Culex</i>	4	0	Ra	2	0	Ra	4	0	Ra				4	0	Ra	1	0	Ra	3	0.2	Ra	18	0	Ra
<i>tritaeniorhynchus</i>																								
<i>Eretmapodites</i>	7	0	Ra	1	0	Ra	4	0	Ra	1	0	Ra	7	0.1	Ra				1	0.1	Ra	21	0	Ra
<i>quinquevittatus</i>																								
<i>Mansonia africana</i>	717	4.4	Sd	116	0.9	Ra	171	1.2	Ev	23	0.2	Ra	131	0.9	Ra	25	0.3	Ra	10	0.5	Ra	1,193	1.5	Ev
<i>Mansonia uniformis</i>	1,877	11.6	Ed	569	4.3	Sd	319	2.3	Sd	37	0.2	Ra	302	2.2	Sd				12	0.6	Ra	3,116	3.8	Sd
<i>Toxorhynchites brevipalpis</i>	1	0	Ra																			1	0	Ra
<i>Uranotaenia mayeri</i>				1	0	Ra													1	0.1	Ra	2	0	Ra
Total	16,178	100		13,202	100		13,919	100		14,801	100		13,985	100		7,218	100		1916	100		81,219	100	

No., number of mosquitoes collected; DC, dominance categories; Ed, eudominant; Do, dominant; Sd, subdominant; Ev, eventual; Ra, rare

Table 3. Mosquito diversity in different land cover classes, Kédougou data from June 2009 through Mar. 2010 and May 2010 through Mar. 2011 combined

	Agriculture	Barren	Savannah	Forest-canopy	Forest-ground	Urban-outdoor	Urban-indoor
HB	2.29 ^a	2.11 ^c	2.21 ^b	1.55 ^e	2.28 ^a	1.87 ^d	2.1 ^c
(CI)	(2.27–2.30)	(2.08–2.13)	(2.19–2.23)	(1.53–1.56)	(2.26–2.30)	(1.84–1.90)	(2.04–2.14)
Species density	48	45	50	44	46	42	34

HB with different letters are significantly different.

HB, Brillouin diversity indices; CI, confidence intervals of the Brillouin diversity indices.

Table 4. Diversity categories of mosquito species collected by human landing catch in different land cover classes in Kédougou, June 2009 through Mar. 2010 and May 2010 through Mar. 2011

Diversity categories	Land cover classes													
	Agriculture		Barren		Forest-canopy		Forest-ground		Savannah		Urban-indoor		Urban-outdoor	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%
Eudominant	4	8.3	3	6.7	3	6.8	4	8.7	4	8.0	4	11.8	2	4.8
Dominant	2	4.2	1	2.2		0.0	2	4.3		0.0	1	2.9	2	4.8
Subdominant	2	4.2	3	6.7		0.0	3	6.5	5	10.0	3	8.8	2	4.8
Eventual	2	4.2	2	4.4	1	2.3	3	6.5	2	4.0	3	8.8	3	7.1
Rare	38	79.2	36	80.0	40	90.9	34	73.9	38	76.0	23	67.6	32	76.2
Singleton	4	8.3	3	6.7	10	22.7	4	8.7	5	10.0	11	32.3	7	16.7
Total species	48	100	45	100	44	100	46	100	50	100	34	100	42	100

Fig. 2. Individual-based rarefaction curves for mosquitoes collected in different land cover classes, Kédougou, Senegal during June 2009 through March 2010 and May 2010 through March 2011.

this area by four sampling methods (human landing catch, Centers for Disease Control and Prevention (CDC)-light traps supplemented with dry ice, CDC-light traps located in sheepfolds, and animal + light-baited traps) over a longer period (Fontenille et al. 1998). Our study showed the presence and dominance of the *Aedes* spp. that are vectors of sylvatic DENV, CHIKV, ZIKV, and YFV in forest galleries and villages in southeastern Senegal. This predominance of *Aedes* was reported previously by several others for the Kédougou region using human landing catch alone (Cornet et al. 1978, Traoré-Lamizana et al. 1994, Diallo et al. 2003) or associated with other sampling methods (Fontenille et al. 1998). We also observed for the first time the dominance of these vector species in three major land

covers in the study area (savannah, barren, and agriculture), thus supporting the widespread risk for transmission of viruses carried by these mosquitoes.

Our findings also revealed important differences in mosquito species diversity among land cover classes, as shown by other investigations in Africa (Muturi et al. 2006), Asia (Thongsriping et al. 2013, Young et al. 2017, Mangudo et al. 2018), and the Americas (Yanoviak et al. 2006, Johnson et al. 2008). *Aedes furcifer*, a known vector of DENV, CHIKV, ZIKV, and YFV in the region (Traoré-Lamizana et al. 1994, Traoré-Lamizana et al. 1996, Diallo et al. 1999, Boyer et al. 2018), was the only species eudominant in all land cover classes investigated, thus corroborating its role in the

Fig. 3. Cluster analysis using the Morisita and Jaccard indexes between land cover classes in Kédougou, June 2009 through March 2010 and May 2010 through March 2011.

epidemiology of these viruses. This species has been responsible for the most important outbreaks of enzootic yellow fever in Africa and also has been reported as the only abundant and YFV-infected species in villages, and is, thus, considered a likely bridge vector of this arbovirus to humans (Salaun et al. 1981, Baudon et al. 1984, Cordellier 1991, Diallo et al. 2014b).

The results of our study also indicated that the eudominant mosquito species varied according to the land cover class, a pattern that may be driven by larval development, adult feeding, and/or resting habitats of each species, or both. *Culex quinquefasciatus*, for example, was eudominant only indoors in urban settings and *Ma. uniformis* only in agriculture. The eudominance of *Cx. quinquefasciatus* in the urban-indoors is not surprising, as it exhibits highly anthropophilic and endophilic behavior in West Africa and oviposits in anthropogenic polluted water rich in organic matter (Subra 1981). *Mansonia uniformis* is eudominant in areas of agriculture surrounded by temporary marshes, which serve as the larval habitats for this species when they are covered by hygrophites at the end of the rainy season (Wharton 1962, Apiwathnasorn et al. 2006). All of the eudominant species in agriculture and urban-indoor environments have been associated with several arboviruses of medical and/or veterinary importance, including Rift valley fever, West Nile, and Zika viruses (Fontenille et al. 1998; Diallo et al. 2005, 2014a; Boyer et al. 2018).

The forest-canopy contained the lowest mosquito diversity, whereas the forest-ground and agriculture contained the highest diversity. The low diversity in the canopy compared with the ground level was similar to the results of an equivalent study in Latin America (Juliao et al. 2010). The higher diversity of forest-ground mosquito community compared with the more urbanized environments was also observed by others in Thailand, Malaysian Borneo, and Argentina (Thongsripong et al. 2013, Young et al. 2017, Mangudo et al. 2018). Spatial and seasonal variation in mosquito biodiversity is known to result from the variation of several abiotic and biotic parameters, including temperature, relative humidity, rainfall, larval and resting habitat, and bloodmeal sources (Bates 1949, Yanoviak 1999). The lower mosquito diversity in the forest-canopy

as compared with the forest-ground is discordant with the higher amount and diversity of vertebrate hosts living in the canopy (Erwin 2001, de Thoisy et al. 2003, Haugaasen and Peres 2007). It is likely that this pattern is driven by the low diversity of larval and resting habitats in the forest-canopy as compared with the other landscapes. Indeed, only tree-holes are available as larval habitats for mosquitoes in the canopy; thus, mainly tree-hole mosquitoes (*Ae. furcifer*, *Ae. africanus*, and *Ae. luteocephalus*) may be found host-seeking in the canopy. Larval habitat availability and diversity may also explain why the mosquito diversity was higher between August and December when all the larval habitat types generally contain water in Kédougou (Raymond et al. 1976, Diallo et al. 2012a).

Among the anophelines, we collected specimens belonging to the *Anopheles gambiae* complex and *Anopheles funestus* and *Anopheles nili* groups in the forest and savannah land covers. This was surprising because the only known members of these complex or groups of species in the Kédougou area are highly anthropophilic species (*An. gambiae* s.s., *Anopheles arabiensis*, *An. funestus*, and *An. nili*), usually found in domestic environments, and incriminated in the transmission of malaria in Southeastern Senegal (Dia et al. 2003, 2005). Confirmation of the identity of these sylvatic populations of *An. gambiae* s.l., *An. funestus* s.l., and *An. nili* s.l. must be confirmed with genetic analyses, because they are known to belong to species groups with different epidemiological importance. Indeed, *An. gambiae* s.l. is a complex of at least eight species (*An. gambiae*, *Anopheles coluzzi*, *Anopheles arabiensis*, *Anopheles melas*, *Anopheles merus*, *Anopheles bwambae*, *Anopheles quadriannulatus* A and B), *An. funestus* s.l. is a group of 11 species (*An. funestus* s.s., *An. funestus*-like, *Anopheles rivulorum*, *Anopheles vaneedeni*, *Anopheles leesoni*, *Anopheles confusus*, *Anopheles fusciventris*, *Anopheles brucei*, *Anopheles parensis*, *Anopheles aruni*, and *An. rivulorum*-like), and *An. nili* s.l. is a group of four species (*An. nili* s.s., *Anopheles somalicus*, *Anopheles carnevalei*, and *Anopheles ovengensis*). Of these, only *An. gambiae* s.s., *An. arabiensis*, *An. funestus*, and *An. nili* are considered important malaria vectors in Africa (Fontenille and Simard 2004). If the sylvatic populations are the same species and are found infected, this

Fig. 4. Monthly distribution of mosquito diversity indices, mean temperature (°C), relative humidity (%), and rainfall (mm) in Kédougou, June 2009 through March 2010 and May 2010 through March 2011. Error bars in the Brillouin diversity indices indicate 95% confidence intervals. Abundance is measured as mean number of mosquitoes collected per person per evening.

finding would complicate malaria elimination and eradication strategies, because when these mosquitoes could move between sylvatic and domestic environments. This pattern was reported in South America, where forest dwelling *An. cruzii* and *An. fluminensis* are believed to transmit malaria to people by migrating from the forest to human dwellings for blood-feeding and then returning to the forest (Forattini et al. 2000).

The high number of rare species ($N = 47$) found in this study was probably due to the low effectiveness of human landing collections for some species as well as diurnal variation in activity among species. Indeed, some of these species are collected more efficiently by larval sampling, CDC-light traps, or sheep-baited traps in the study area (Raymond et al. 1976, Fontenille et al. 1998, Diallo et al.

2012a). Moreover, our sampling was limited to the evening, the period when the *Anopheles* species are not very active. These species are known to seek blood-meals later during the night. Additionally, some rare species may have very low population abundance due to highly specific and unstable larval habitats.

In conclusion, this study describes for the first time the biodiversity of mosquitoes in a focus of sylvatic arbovirus activity. Diversity of mosquito species varied substantially according to the land cover classes, the period of the collection, and weather variables. Species known to be vectors of arboviruses were eudominant in all the landscapes investigated, suggesting a high risk of arboviral diseases emergence as human populations continue to grow and to intrude upon sylvatic environments in the Kédougou region.

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